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**Taxonomic revision and biogeography of the *Tamarix*-feeding
Diorhabda elongata (Brullé, 1832) species group
(Coleoptera: Chrysomelidae: Galerucinae: Galerucini)
and analysis of their potential in biological control of Tamarisk**

JAMES L. TRACY & THOMAS O. ROBBINS



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Dedication

This work is dedicated to Culver Jack DeLoach, Jr., our long time friend and mentor in weed biological control research who has inspired us with his dedication and energy for bringing the natural marvel of insect biological control of invasive plants into the process of native ecosystem restoration, especially in his last two decades of research and implementation in the use of *Diorhabda* as tamarisk biological control agents in North America.

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Abstract

The primarily Palearctic *Diorhabda elongata* species group is established for five *Tamarix*-feeding sibling species (tamarisk beetles): *D. elongata* (Brullé, 1832), *D. carinata* (Faldermann, 1837), *D. sublineata* (Lucas, 1849) REVISED STATUS, *D. carinulata* (Desbrochers, 1870), and *D. meridionalis* Berti & Rapilly, 1973 NEW STATUS. *Diorhabda koltzei* ab. *basicornis* Laboissière, 1935 and *D. e. deserticola* Chen, 1961 are synonymized under *D. carinulata* NEW SYNONYMY. Illustrated keys utilize genitalia, including male endophallic sclerites and female vaginal palpi and internal sternite VIII. Distribution, comparative biogeography, biology, and potential in biological control of *Tamarix* in North America are reviewed. *Diorhabda elongata* is circummediterranean, favoring Mediterranean and temperate forests of Italy to western Turkey. *Diorhabda carinata* resides in warm temperate grasslands, deserts, and forests of southern Ukraine south to Iraq and east to western China. *Diorhabda sublineata* occupies Mediterranean woodlands from France to North Africa and subtropical deserts east to Iraq. *Diorhabda carinulata* primarily inhabits cold temperate deserts of Mongolia and China west to Russia and south to montane grasslands and warm deserts in southern Iran. *Diorhabda meridionalis* primarily occupies maritime subtropical deserts of southern Pakistan and Iran to Syria. Northern climatypes of *D. carinulata* are effective in *Tamarix* biological control, especially in the Great Basin desert. *Diorhabda elongata* is probably best suited to Mediterranean woodlands of northern California. Northern climatypes of *D. carinata* may be best suited for central U.S. grasslands. *Diorhabda sublineata*, *D. meridionalis*, and southern climatypes of *D. carinata* and *D. carinulata* may each be uniquely suited to areas of the southwestern U.S.

Key words: *Diorhabda elongata* species group; Chrysomelidae; Taxonomy; Comparative Biogeography; Biology; Host Range; *Tamarix*; Tamarisk; Saltcedar; Weed Biological Control; Sibling Species; Hybrid Morphology; Morphometry; Genitalic Phenogram; Biomic Dendrogram; Habitat Suitability Index Models

Резюме

Видовая группа *Diorhabda elongata* основана для пяти палеарктических, питающихся на *Tamarix*, видов-двойников (тамарисковые жуки): *D. elongata* (Brulle, 1832), *D. carinata* (Faldermann, 1837), *D. sublineata* (Lucas, 1849) REVISED STATUS, *D. carinulata* (Desbrochers, 1836) и *D. meridionalis* Berti & Rapilly, 1973 NEW STATUS. *Diorhabda koltzei* ab. *basicornis* Laboissiere, 1935 и *D. e. deserticola* Chen, 1961 синонимизированы с *D. carinulata* NEW SYNONYMY. Иллюстрированный определитель использует гениталии, включая мужской эндофаллус, женские вагинальные пальпы и внутренний стернит VIII. Рассмотрено распространение, сравнительная биogeография, биология и возможности использования для биологического контроля *Tamarix* в Северной Америке. *Diorhabda elongata* является циркум-средиземноморским видом, предпочитающим средиземноморские и умеренные леса Италии до западной Турции. *Diorhabda carinata* обитает в теплых умеренных остепненных биотопах, пустынях и лесах южной Украины и далее на юг до Ирана и восток до Западного Китая. *Diorhabda sublineata* обитает в лесах Средиземноморья от Франции до Северной Африки и субтропических пустынях на восток до Ирака. *Diorhabda carinulata* в основном населяет холодные и умеренные пустыни Монголии и Китая и далее на запад до России и на юг до горных степей и теплых пустынь южного Ирана. *Diorhabda meridionalis* населяет приморские субтропические пустыни южного Пакистана и Ирана до Сирии. Северный климатип *D. carinulata* является эффективным агентом биологического контроля *Tamarix*, особенно в пустынях Большого Бассейна. *Diorhabda elongata*, вероятно, наиболее подходит для контроля *Tamarix* в средиземноморских лесах Северной Калифорнии. Северный климатип *D. carinata* может быть наиболее подходящим для травянистых биоценозов центральной части США. *Diorhabda sublineata*, *D. meridionalis*, южный климатип *D. carinata* и *D. carinulata* могут быть подходящими для различных мест юго-запада США.

Introduction

Tamarix-feeding leaf beetles in the genus *Diorhabda* Weise (1883), or tamarisk beetles, are probably the most damaging specialized defoliators of Old World tamarisks (Kulinich 1962; Sinadsky 1968; Tomov 1979; Samedov and Mirzoeva 1985; Tian *et al.* 1988; Bao 1989; Sha and Yibulayin 1993; Myartseva 1999; Mityaev and Jashenko 1999, 2007; DeLoach *et al.* 2003b). Consequently, tamarisk beetles are valued as current and

potential biological control agents for invasive deciduous tamarisks in North America (DeLoach *et al.* 2003b, 2004; Lewis *et al.* 2003b, Milbrath and DeLoach 2006a; Carruthers *et al.* 2006, 2008). Accurate taxonomic recognition of the species of tamarisk beetles and their associated biogeographic characteristics could be crucial to their successful utilization in biological control of tamarisk across the widely varying biogeography of the western North American tamarisk invasion. Many taxonomists consider the tamarisk beetles to comprise a single species, *D. elongata* (Brullé, 1832), with three to four subspecies ranging from North Africa and southwestern Europe to Mongolia and western China (Wilcox 1971, Riley *et al.* 2003, Bieńkowski 2004, Lopatin *et al.* 2004). However, Berti and Rapilly (1973) removed two tamarisk beetles, *D. carinata* (Faldermann, 1837) and *D. carinulata* (Desbrochers, 1870), from synonymy with one another, and by implication with *D. elongata*. Their findings were based primarily upon diagnostic differences in the male endophalli (eversible internal sacs of the aedeagi) in the holotypes of *D. carinata* and *D. carinulata*, but they did not characterize the endophallus of *D. elongata*. We characterize the endophallus of *D. elongata* and corroborate the findings of Berti and Rapilly (1973). We also find several additional diagnostic male and female genitalic characters by which to distinguish these species, remove *D. sublineata* (Lucas, 1849) from synonymy with *D. elongata*, and elevate *D. carinulata meridionalis* Berti and Rapilly (1973) to species status as *D. meridionalis* Berti and Rapilly. A complex of five fully diagnosable species of tamarisk beetles is established as forming the *Diorhabda elongata* species group: *D. elongata*, *D. carinata*, *D. sublineata*, *D. carinulata* and *D. meridionalis*. Four species of tamarisk beetles (excluding *D. meridionalis*) are recently introduced for biological control of tamarisk in the United States. We provide the first detailed distributional data for all five species of tamarisk beetles, revealing their unique biogeographic characteristics and providing a basis for further ecogeographic studies. New data on the biogeography of tamarisk beetles are used in matching each species to different regions of the North American tamarisk invasion using hand-fitted habitat suitability index models.

The Eurasian tamarisks *T. ramosissima* Ledebour, *T. chinensis* Loureiro and their hybrids (mixed populations of pure lines and hybrids all referred to as *T. ramosissima/T. chinensis*) are highly invasive in arid and semi-arid riparian areas of the western U.S. (Gaskin and Schaal 2002, 2003), where they are the second most dominant woody riparian plant after native cottonwoods (*Populus deltoides* Barton ex Marshall) (Friedman *et al.* 2005). *Tamarix parviflora* de Candolle is invasive in riparian areas of California (DiTomaso 1998, Gaskin and Schaal 2003). Populations of *T. canariensis* Willdenow/*T. gallica* Linnaeus are minor invasives along the Gulf Coast of Texas and Louisiana, and they commonly hybridize with *T. ramosissima/T. chinensis* in Texas (Gaskin and Schaal 2002, 2003; John Gaskin, USDA/ARS, Sydney, MT, pers. comm.). *Tamarix aphylla* (Linnaeus) Karsten (athel tamarisk) is an evergreen ornamental (DeLoach 1990) planted primarily in subtropical areas of the southwestern U.S. and northern Mexico where it commonly escapes vegetatively and sometimes propagates by seed and is showing the potential to become more invasive (Walker *et al.* 2006) as it is along the Finke River in Australia (Griffen *et al.* 1989). Naturalized hybrids of *T. aphylla* and *T. ramosissima/T. chinensis* have recently been found in the southwestern U.S. which could possibly contribute to the invasive potential of *Tamarix* (Gaskin and Shafroth 2005). Dominance of exotic tamarisks is facilitated by their pre-adaptation to low soil moisture riparian habitats that have widely increased due to stream flow regulation practices (Glen and Nagler 2005, Lite and Stromberg 2005, Stromberg *et al.* 2007). Tamarisks also invade unregulated river, spring, and marsh systems where they displace a variety of woody and herbaceous riparian communities, and can alter ecosystem function to the detriment of native biota, including endangered species (DiTomaso 1998, Lovich and DeGouvenain 1998, Tracy and DeLoach 1999, DeLoach *et al.* 2000, Stenquist 2000, Dudley and DeLoach 2004, Kennedy *et al.* 2005, Birken and Cooper 2006, Whiteman 2006, Whitcraft *et al.* 2007). Invasive tamarisk could cost an estimated US \$7–16 billion in lost ecosystem function in the U.S. from 2000–2055, mainly as a result of losses in hydropower (on Colorado River) and wildlife habitat (Zavaleta 2000).

Great effort and expense is being directed towards control of tamarisk to both reduce its use of water and help restore native riparian ecosystems (Hart 2003, Shafroth *et al.* 2005, Carruthers *et al.* 2008). Herbicidal treatment of individual tamarisk trees is often practiced (Duncan 2003), especially in southern California and

Arizona (Barrows 1993, Brock 2003). Large-scale control of tamarisk by aerial herbicidal application, sometimes in combination with mechanical removal or prescribed burning, is the prevalent control method in New Mexico and west Texas (Hughes 2003, McDaniel and Taylor 2003, Hart *et al.* 2005). Over 100 species of Old World tamarisk specialist arthropod herbivores that attack *T. ramosissima* in Asia (Kovalev 1995) are absent in North America, and the lack of these herbivores is an often overlooked factor contributing to the invasiveness of tamarisk and its competition against comparatively herbivore-stressed native flora (DeLoach *et al.* 2000, Dudley *et al.* 2000). The objective of classical biological control of tamarisk is to re-associate tamarisk in North America with its Old World *Tamarix*-specific natural enemies in order to reduce tamarisk populations below thresholds requiring other control methods. Tamarisk biological control can contribute to native ecosystem restoration by permanently suppressing tamarisk without collateral damage to native riparian flora, with low cost, and without need of re-application (DeLoach 1990, 1997; Gould and DeLoach 2002). The use of tamarisk beetles in biological control was recently initiated, and they are already filling a critical herbivore niche in North American riparian ecosystems by continually suppressing tamarisk over large areas in Nevada, Utah and Wyoming (DeLoach *et al.* 2004; DeLoach and Carruthers 2004a; Carruthers *et al.* 2006, 2008; Dave Kazmer, USDA/ARS, Sydney, MT, pers. comm.), allowing increase in understory vegetation, while the tamarisk beetles serve as forage for insectivorous birds (Longland and Dudley 2008) and small mammals (Dudley 2005a).

Populations of tamarisk beetles from China and Kazakhstan that we studied for biological control were initially identified as *D. elongata deserticola* Chen (1961) or “*D. elongata*” (DeLoach *et al.* 2003b; Lewis *et al.* 2003a, 2003b; Milbrath and DeLoach 2006a; Milbrath *et al.* 2007; DeLoach *et al.* in prep.). These identifications were obtained from several chrysomelid taxonomists, including Igor Lopatin (Belarus State University, Minsk, Belarus), Alexander Konstantinov (USDA-ARS SEL, Beltsville, MD), Shawn Clark (Brigham Young University, Provo, Utah), Steven Lingafelter (USDA-ARS SEL, Beltsville, MD), and Richard White (USDA-ARS SEL, retired). Permits for release of *D. elongata* in North America were first issued by USDA-Animal and Plant Health Inspections Service (APHIS) in 1999 (USDA-APHIS 1999, DeLoach *et al.* 2000). In this taxonomic revision, we synonymize *D. e. deserticola* under *D. carinulata*, the northern tamarisk beetle. Populations of northern tamarisk beetles from 44°N in northwestern China (Fukang and Turpan) and near Shelek (= Chilik), Kazakhstan, were released (as *D. elongata*) into North America for biological control of tamarisk in 2001. *Diorhabda carinulata* has established well on *T. ramosissima*/*T. chinensis* at sites north of 37°N in Nevada, Utah, Colorado, and Wyoming, defoliating large areas of tamarisk, especially in Nevada, Utah (DeLoach *et al.* 2004; Carruthers *et al.* 2006, 2008), western Colorado (Dan Bean, Colorado Department of Agriculture, Grand Junction, CO, pers. comm.), and Wyoming (D. Kazmer, pers. comm.). However, these populations of *D. carinulata* exhibit asynchrony of daylength induced diapause with seasonal changes at southern sites in New Mexico and Texas, where they initially failed to establish (DeLoach *et al.* 2004, Bean *et al.* 2007a).

Populations of tamarisk beetles that we studied from Greece, Tunisia, and Uzbekistan were originally identified as *D. elongata* by taxonomists A. Konstantinov and/or I. Lopatin. They all have diapause characteristics more adaptive to the southern U.S. (Bean and Keller in prep), they are all host specific to tamarisk (Milbrath and DeLoach 2006a, 2006b; Herr *et al.* 2006, in prep.), and they have all been released (as *D. elongata*) in North America with permits issued by USDA-APHIS for each specific population source. In this taxonomic revision, we confirm that populations of *D. elongata* from near Sfakaki (Crete) and Posidi Beach, Greece are the true *D. elongata*, the Mediterranean tamarisk beetle. *Diorhabda elongata* was established in 2004 on *T. ramosissima*/*T. chinensis* in west Texas and *T. parviflora* in northern California. But the Mediterranean tamarisk beetle has established poorly or not at all where it was released on *T. ramosissima*/*T. chinensis* in eastern New Mexico and many locations in west and north Texas from 2004–2007. The population of “*D. elongata*” we studied from near Sfax, Tunisia is here identified as *D. sublineata*, the subtropical tamarisk beetle. *Diorhabda sublineata* was first released onto *T. canariensis*/*T. gallica* in south Texas in 2005 (Patrick Moran, USDA/ARS, Weslaco, TX, pers. comm.) but it has not yet established. Further releases of *D. sublineata* from near Marith, Tunisia are planned on *T. chinensis*/*T. canariensis* in south and

west Texas in 2009. The population of “*D. elongata*” we studied from near Qarshi (= Karshi), Uzbekistan is here classified as *D. carinata*, the larger tamarisk beetle. *Diorhabda carinata* was first released on *T. ramosissima*/*T. chinensis* in north Texas in 2006 (Jerry Michels, Texas AgriLIFE Research, Bushland, TX, pers. comm.) and appeared to be establishing near Seymour, Texas in 2008 (Charles Randal, USDA/APHIS, Olney, TX, pers. comm.). A population of “*D. elongata*” studied from near Buxoro (=Buchara), Uzbekistan (Herr *et al.* in prep.) was later found to be a mixture of *D. carinata* and *D. carinulata*. *Diorhabda meridionalis*, the southern tamarisk beetle, is primarily found in extreme southern and southwestern Iran, and it is yet to be studied for its potential in biological control. The list below summarizes the correlation between the revised taxonomy for tamarisk beetles and “*D. elongata*” population/ecotype designations used in a number of reports and publications by us and others in relation to tamarisk biological control (see recent citations under “*D. elongata*” in the synonymies for each *Diorhabda* species account).

Scientific name	Proposed common name	“ <i>D. elongata</i> ”, “saltcedar leaf beetle” population/ecotype designation
<i>D. carinulata</i>	northern tamarisk beetle	Fukang and Turpan, China; Chilik, Kazakhstan; Buchara, Uzbekistan (part); <i>D. e. deserticola</i> , also “tamarisk leaf beetle”
<i>D. elongata</i>	Mediterranean tamarisk beetle	Crete (nr Sfakaki) and Posidi Beach, Greece
<i>D. sublineata</i>	subtropical tamarisk beetle	Sfax, Tunisia and southeast of Marith, Tunisia
<i>D. carinata</i>	larger tamarisk beetle	Qarshi, Uzbekistan; Buchara, Uzbekistan (part)
<i>D. meridionalis</i>	southern tamarisk beetle	south Iran (not yet introduced into USA)

Releases of tamarisk beetles in southern California, Arizona, and along the Rio Grande in western New Mexico, are currently delayed until concerns can be resolved regarding safety of tamarisk biological control to nesting habitats of the federally endangered southwestern willow flycatcher, *Empidonax traillii* Audubon subspecies *extimus* Phillips, which will nest in tamarisk (see DeLoach *et al.* 2000, Dudley and DeLoach 2004). Efforts are continuing to establish tamarisk beetles across widely varying biogeographic areas invaded by tamarisk in the western U.S, but apparent adaptation problems are still being encountered in many southern areas. A basic understanding of the native biogeography of all the species of tamarisk beetles would be valuable in identifying their potential to adapt to different regions.

Ongoing taxonomic research can be essential to the success of biological control programs. Precise species identifications are necessary to properly characterize genetic variability in biological control agents regarding: (1) risks to non-target vegetation; (2) efficacy and host preferences among target hosts; and (3) biogeographic adaptations at a variety of spatial scales (see also Schauff 1992). A recent example of the importance of ongoing taxonomic research in biological control is the discovery that a common biological control agent of exotic thistles in North America and Australia, the thistle rosette weevil, *Trichosirocalus horridus* (Panzer) (Coleoptera: Curculionidae: Ceutorynchinae), actually comprises a complex of three sibling species, each apparently differing in the thistle species preferred as hosts (Alonso-Zarazaga and Sánchez-Ruiz 2002). An inability to taxonomically distinguish similar species of candidate biological control agents has led to lengthy delays in successful implementation of biological control programs. Such delays result from not recognizing and utilizing interspecific variability in the efficacy of potential agents (Gordh and Beardsley 1999). A more accurate appreciation of the interspecific variability in tamarisk beetles, especially in regard to their biogeographic characteristics, should facilitate more timely and effective utilization of their desirable traits in biological control of tamarisk.

Our primary objectives are to clarify the number of morphologically diagnosable species of tamarisk beetles, and to stabilize their taxonomic status. To this end, we review all currently recognized specific and subspecific taxa of tamarisk-feeding *Diorhabda*. Sibling, or cryptic, species are difficult or impossible to distinguish based solely on external morphology. But, sibling species are often distinctly different in genitalic

morphology, distribution, behavior, ecology, and genetics, which is evidence of their reproductive isolation in nature. Our revision examines data on genitalic morphology, ecology, behavior and distribution, which are often the most reliable means of distinguishing sibling species, even with current genetic methods (Bull *et al.* 2006). The foundation of our revision is the geographic distribution of morphological character states of the genitalia, especially the endophallus, which are useful in distinguishing sibling species. Berti and Rapilly (1973) were among the first to use the gross morphology of the endophallus in distinguishing sibling species of Chrysomelidae in their restoration of the species *D. carinata* and *D. carinulata* from synonymy with *D. elongata*. Additional examples of taxonomic and morphological studies involving the endophallus in Chrysomelidae are given by Mann and Crowson (1996) and Flowers (1997). In the last 16 years, chrysomelid taxonomists have found the morphology of individual sclerites of the endophallus useful in distinguishing members of several sibling species complexes, including the *Galerucella nymphaeae* (Linnaeus) species group (Galerucinae) (Lohse 1989), the *Oulema melanopus* (Linnaeus) species group (Criocerinae) (Berti 1989, Siede 1991, Hansen 1994), the *Cryptocephalus flavipes* Fabricius species group (Cryptocephalinae) (Duhaldeborde 1999), and the *Cryptocephalus marginellus* Olivier species group (Sassi 2001). In addition to characterizing the endophallic sclerites of tamarisk beetles, we also characterize structures of the female genitalia that are useful in separating similar species in Galerucinae, such as internal sternite VIII (e.g., LeSage 1986), spermathecae (e.g., LeSage 1986, Biondi and D'Alessandro 2003), and vaginal palpi (e.g., Baselga and Novoa 2005).

Inaccurate identification of sibling species creates great confusion in the biological and ecological data published for these species. A current example of such confusion is seen in recent studies of sibling leaf beetle species in the *Galerucella nymphaeae* species group. Lohse (1989) used a combination of five morphological characters (including endophallic sclerites) in distinguishing four sympatric members of the *G. nymphaeae* species group in central Europe (Warchalowski 2003, Bieńkowski 2004). Application of Lohse's (1989) taxonomic characters is needed to clarify the identity of a number of these species in several biological and ecological investigations, including "*G. sagittariae* (Gyllenhal)" in Finland (Hippa and Koponen 1986; Nokkala and Nokkala 1994, 1998; Nokkala *et al.* 1998; but see Kangas 1991) (possibly *G. kerstensi* Lohse and other species), "*G. nymphaeae*" host races from Polygonaceae in the Netherlands (Pappers *et al.* 2001, 2002a, 2002b; Pappers and Ouborg 2002) (possibly Lohse's [1989] two *Polygonum* and *Rumex* host races of *G. aquatica* [Geoffroy]), and "*G. nymphaeae*" in North America (Otto and Wallace 1989, Nokkala *et al.* 1998, Cronin *et al.* 1999) (possibly one or more new species; the type locality of *G. nymphaeae* is Sweden according to Silfverberg [1974]). Similar taxonomic confusion over the identity of sibling species has sometimes clouded research in biological control programs (Schauff 1992, Clarke and Walter 1995, Schauff and LaSalle 1998). Another objective of this revision is to avoid further taxonomic confusion in future biological studies of *D. elongata* and its sibling species and to clarify the identity of these species as far as possible in the previous literature.

We provide illustrated keys to sexes and species of adults of the *D. elongata* species complex and a genitalic phenogram showing morphological groupings based on similarity in key genitalic characters. Male genitalic hybrid morphologies are characterized for progeny from laboratory crossings of *D. sublineata* × *D. elongata* (F1 hybrids) and their F1 hybrids (F2 hybrids). Extensive annotated bibliographies are included under the synonymies for each species account that clarify numerous misapplications of names in the literature for more than 100 years. Distribution maps display biomes (Olson and Dinerstein 2002), point localities for selected *Tamarix* spp., and point localities of *Diorhabda* species derived from examined specimens and literature records for which we could assign identifications based on species distribution patterns. Descriptive statistics are presented for elevation, latitude, distance to ocean (continentality) and percent distribution across biomes for field collection data of each *Diorhabda* species. We analyze similarities in biomes inhabited among the *Diorhabda* species and selected *Tamarix* species invasive in North America, providing biomic dendrograms and three dimensional biomic principal coordinate analysis scatter plots. Descriptive statistics for biogeographic variables are used to construct biomic dendrograms and hand-fitted habitat suitability index models to examine the comparative biogeography of the *D. elongata* group. We

provide geocoordinates used in the distribution maps that are essential to future development of species distribution models using climatic data. Label data from the literature and examined specimens are given. Information on the distribution, taxonomy, host plants, ecology, phenology, behavior, development, reproduction, biogeography, and potential in tamarisk biological control is reviewed for each tamarisk beetle species. New distribution and host records are reported. Finally, we summarize the implications of our research regarding biological control of tamarisk.

Materials and methods

Morphology. Genitalia are dissected (abbreviated “diss.” in material examined) from mounted specimens after first soaking the specimens in warm water for several hours to soften them before removal of the body from the pin or point. In males, the abdomen is usually removed from the body prior to extraction of the genitalia under a binocular stereoscope. Dissections are done in water over a yellow clay substrate to aid in positioning of the genitalia. Following removal of a male’s abdomen, the aedeagus is first pulled from the opening at the base of the abdomen to allow access to the endophallus (Fig. 14; END). We were unable to inflate the endophalli with a needle and pipette using a method similar to that of Silfverberg (1974). Occasionally, we everted the uninflated endophallus from the median lobe (ML) into its natural position by gently teasing the endophallus out through the distal dorsal ostium (DO, or apical orifice) of the aedeagus (Fig. 14) with a hooked minuten pin (inserted into a match stick). However, the eversion procedure is very tedious and is often unsuccessful, resulting in tearing of the endophallic membrane and sclerites, especially in older specimens. We usually employed the faster technique of dissecting out the endophallic sclerites in a non-everted (inverted) endophallus using the following procedure. An insect pin is used to first make a longitudinal slit along the entire length of the ventral membrane (VM) of the median lobe of the aedeagus (Fig. 14). The pin is then inserted through this slit at the basal foramen (BF, or basal orifice) and used to push the distal tip of the inverted endophallus out from the median lobe. Fine forceps are used to gently pull the inverted endophallus completely out of the median lobe, and the base of the inverted endophallus is carefully torn free from the membrane at the apex of the median lobe. The removed inverted endophallus is splayed open to reveal the endophallic sclerites. A hooked minuten pin is used to longitudinally slice the endophallic membrane from the torn opening at its base. Before slicing the endophallus, it is oriented such that, while the base is pointed downwards, the palmate (dorsal) endophallic sclerite (PES) is at the left and the elongate (ventral) endophallic sclerite (EES) is on the right in order to avoid damage to any linear connecting (lateral) endophallic sclerite (CES) (Figs. 14, 16). We develop terminology for endophallic sclerites of the *D. elongata* group (Figs. 14–33), and the preceding general terminology for endophallic sclerites in parentheses follows that of Mann and Crowson (1996).

Extraction of the female genitalia (Figs. 34–38) normally involves first removing the abdomen. The last abdominal tergite and the internal sternite VIII (IS VIII) are then severed from connections to other abdominal tergites and sternites and the digestive tract to allow their removal with the attached oviduct, vaginal palpi (VP), and spermatheca (SP) (Fig. 34). Occasionally the spermatheca becomes detached in the abdomen after removal of the oviduct and has to be retrieved separately with forceps. In living specimens, the stalk of internal sternite VIII can sometimes be seen as a dark Y-shaped area through the translucent last visible abdominal sternite (Lewis *et al.* 2003b, Fig. 1G). Also, in living specimens, the vaginal palpi and the apical lobe of internal sternite VIII can be seen between the last visible abdominal sternite and tergite after they are spread apart with forceps. Terminology of female genitalia (Figs. 34–43) follows that of LeSage (1986) and Konstantinov (1998). Duckett (2003, Fig. 5) illustrates the orientations of internal sternite VIII, vaginal palpi (as gonocoxae) and spermatheca with respect to one another in another galerucine beetle, *Pedilia sirena* Duckett.

Camera lucida drawings are made at 80x magnification for endophallic sclerites of males and internal sternite VIII, spermathecae and vaginal palpi of females. Following examination of dissected genitalia, they

are stored in glycerin in polyethylene genitalia vials (4 mm × 10 mm) that are placed on the pin beneath the specimens. Removed abdomens are glued to points beneath the body of the specimens. Digital photographs are made of the habitus of adults with the aid of a stereomicroscope. Dissected specimens are assigned unique numbers, and label data, species identifications, and geocoordinates are entered into a database.

Morphometrics. Only adults identified through examination of genitalia are used in measurements. Specimens measured are representative of the entire geographic range of each species, with from 15 to 61 individuals measured for each external character (Table 2) and from 12 to 29 individuals measured for each genitalic character (Tables 3 and 4). A calibrated ocular micrometer is used in making measurements of adults at 12.8x and 32x magnification and genitalia at 80x magnification. The blade or ridge of the elongate endophallic sclerite (EES) is measured as the total length of raised ridge (Figs. 14–28; LB). The extent of the blade is not as clearly distinguishable from the lateral view of the EES in *D. elongata* (Fig. 19, LB) as compared to other species of the group (Figs. 20–23). Most of the blade in *D. elongata* may be demarcated by a spindle-shaped outline (Fig. 24—Methoni,) seen from dorsal view of the EES, but the apex of the blade may be more fully demarcated by a single median dark line seen from either a certain dorso-lateral view (Fig. 24—Methoni, DLV) or the dorsal view (Fig. 24—nr Kresna). The length of the spined (or toothed) area of the blade along the EES is measured as the distance from the basal tip of the sclerite to the most apical spine (Figs. 14–28; SL). If the EES is armed with a single distal spine (as is often the case for *D. elongata*), the length of the spined area is assigned a value of 0.01 mm. Accurate measurement of the blade length and spined area length of the EES can be important in distinguishing laboratory produced *D. sublineata*/*D. elongata* hybrids. We test for significant differences in some general external and key genitalic morphometric variables, especially looking for any morphometric discontinuities between the species. Various measurements of the female genitalia, including the vaginal palpi (VP) and internal sternite VIII (IS VIII), are illustrated in Figures 34–38. The frequency distributions of a few morphometric variables (e.g., width of elytra at widest point) fail the test for normality. For consistency, all data are analyzed using the nonparametric Two-Way Kruskal-Wallis Test on ranks using ANOVA and Fisher's Protected LSD test to separate means of ranks (SAS Institute 2005). Scatter plots for measurements of the elongate endophallic sclerite are made with the Microsoft Excel Spreadsheet software.

Stenophenetic analysis. Methods of cluster analysis used in numerical taxonomy (Sneath and Sokal 1973) are employed in analyzing phenetic similarities among the *D. elongata* species group. In contrast to the standard approach in phenetic analyses in which a large number of characters (ca. 60) is selected from throughout the body of each taxonomic unit for phenogram construction, we select only characters that are informative in species diagnosis, in this case eight characters from the male and female genitalia, to construct genitalic phenograms. We narrow the characters selected for phenetic analysis in a manner similar to that used in cladistic analyses in which only characters considered to be phylogenetically informative are used (Panhurst 1991). We adopt the new term *stenophenetic analysis* to distinguish this approach from typical broader phenetic analysis. A rectangular data matrix of genitalic character state profiles is constructed with qualitative interval states for the eight key genitalic characters standardized to range from zero to one. An average taxonomic dissimilarity matrix, based on the average taxonomic distance coefficient, and a Pearson product-moment correlation similarity matrix, based on the Pearson product-moment correlation coefficient, are computed from the data matrix (NTSYSpc Interval Data [SIMINT] module [Rohlf 2006]) (see Sneath and Sokal [1973] for details on calculation of coefficients). Both the dissimilarity and similarity matrices are used in separate cluster analyses for the species with three standard clustering algorithms: unweighted pair-group method using arithmetic averages (UPGMA), complete-link method, and single-link method (NTSYSpc SAHN module). Genitalic dissimilarity and similarity phenograms are produced from each cluster analysis (NTSYSpc Tree plot module). The cophenetic correlation coefficient, r_{coph} , is calculated as a measure of goodness of fit for each phenogram to the original dissimilarity or similarity matrix from which it was derived through a particular method of cluster analysis (r_{coph} values from 0.80–0.90 indicate a good fit for the cluster analysis) (NTSYSpc Cophenetic values and Matrix Comparison Plot [MxComp] modules).

Distribution. Cities and other precise geographic features given on locality labels of examined specimens or in literature records are assigned geocoordinates and updated place names using databases of the U.S. National Geospatial-Intelligence Agency (NGA) and the U.S. Board on Geographic Names accessed from internet geoname servers such as the GEOnet Names Server (NGA 2006). Locality label data giving distances and directions from landmarks and elevations are assigned geocoordinates with the aid of global elevation grid (1 km grid resolution), stream and road map layers, and distance measuring utilities using ArcMap software. Point location data are plotted in a Miller cylindrical projection for publication using ArcMap. Precision of point geocoordinates derived from precise locality label or literature data are in the range of ca. \pm 5 km. Point geocoordinates derived from general locality data (precision much less than ca. \pm 5 km) are noted as approximate locations. Geocoordinates and updated place names for label data of examined specimens are given in brackets under the Material Examined section for each species. Specimens that we examined with previously published identifications are noted in the Material Examined and Distribution sections of each species. Specimens from collection localities with previously published identifications that we did not examine are listed with geocoordinates and their probable identities are discussed under the heading **Distribution-Unconfirmed Records** for each species.

Biogeography. *Descriptive.* The distribution of each species of *Diorhabda* is mapped and described in relation to biogeographic realms, biomes, ecoregions, elevation, latitude, distance to the ocean (continentality), and the distributions of a few selected known and potential hosts of the genus *Tamarix* (comprised of ca. 90 species; Zhang and Zhang 1990, Qiner and Gaskin 2006). Realms, biomes and ecoregions are mapped with the ecoregions Arcview shapefile map of Olson and Dinerstein (2002). Approximate elevations in meters for plotted point locations are obtained from the GLOBE 1 km base digital elevation model ArcMap grid (Hastings *et al.* 1999). Distances to ocean are measured in kilometers with ArcMap software.

Old World point distribution data for *Tamarix* spp. are obtained from a variety of regional and local floras (e.g., Post and Dinsmore 1932; Corti 1942; Rusanov 1949; Schiman-Czeika 1964; Baum 1967b, 1978, 1983; Qaiser and Ghafoor 1979; Baum and Townsend 1980; Qaiser 1983; De Martis *et al.* 1984, 1986; Browicz 1991; Boratyński *et al.* 1992; Zieliński 1994), ecological literature (e.g., Danin 1981, Hoberlandt 1981, Izco *et al.* 1984, Salinas *et al.* 2000, Omar *et al.* 2002, Kurschner 2004) and our herbarium records from Kazakhstan and western China (DeLoach unpublished). Data from published “dot” distribution maps are scanned, georeferenced according to their projection, and the geocoordinates queried using ArcMap software. For example, maps of Baum (1978) and Zieliński (1994) are in the Miller Cylindrical projection while those of Rusanov (1949) and Boratyński *et al.* (1992) are in the Bonne projection. Most North American locality data on *T. ramosissima/T. chinensis* are from Friedman *et al.* (2005). Additional North American *Tamarix* spp. locality data are primarily from online herbarium databases (e.g., Calflora, Seinet, and Tropicos) and our own herbarium specimens. Mexican locality data are less certain regarding both species identifications and possible ornamental status of *T. ramosissima/T. chinensis* (possibly confused with *T. canariensis/T. gallica*) at some locations, and data are included from De León González and Vásquez Aldape (1991).

Primary habitats for each *Diorhabda* spp. are identified based upon frequency of collections, relative abundance with regard to sibling species, and reports of damage to *Tamarix*. Areas with possibly distinct climatypes (climatic ecotypes; Turesson 1925) that have potential use in biological control of tamarisk are identified and discussed in detail under the heading **Potential in Tamarisk Biological Control** for each species and in the concluding section, **Implications Regarding Biological Control of Tamarisk** (see for further explanation). Our assessments of the suitability of various biomes/elevation/latitude/distance to ocean combinations for *Diorhabda* spp. should be viewed with caution because the evenness of sampling effort across differing habitats and for differing species with presence-only distribution data are not controlled. Additional analyses are in progress with climatic data to produce presence-only species distribution models.

Biomic Analysis. Methods of cluster analysis and principal coordinate analysis (PCoA) used in numerical ecology (Legendre and Legendre 1998) are employed in analyzing similarities in biomic occurrence state profiles (biomic profiles) among species of the *D. elongata* group and *Tamarix* spp. invasive in North

America. Rectangular data matrices of biomic profiles are constructed with semiquantitative states standardized to range from zero to one that indicate the degree of indigenous occurrence in various biomes: 0 - no record; 0.5 - single record (minor presence); 1 - multiple records (major presence). In view of the lack of systematic surveys for *Diorhabda* and *Tamarix* species in each biome, we consider more than one locality record as representing potentially more than a minor presence within a biome. We also calculate the biomic specialization index (BSI) (Hernández Fernández and Vrba 2005), which is the number of biomes inhabited by a given species, a low BSI indicating the highest biomic specialization. We modify BSI to represent the sum of biomic occurrence states for each species and use biomes as classified by Olson and Dinerstein (2002).

From biomic profiles for *Diorhabda* species and *Diorhabda* and *Tamarix* species, we calculate biomic dissimilarity matrices and dendrograms with associated r_{coph} values using NTSYSpc (Rohlf 2006) in a manner similar to that described above for construction of the genitalic phenograms. However, the data matrices of biomic profiles are first normalized with the transformation $\log(x + 1)$ (NTSYSpc Transformation module) and biomic Bray-Curtis dissimilarity matrices are then constructed using the Bray-Curtis (percentage difference) distance coefficient (NTSYSpc Interval Data [Simint] module), which eliminates double zero values from being counted as similarities in habitats (for details on calculation of Bray-Curtis coefficient, see distance coefficient D_{14} in Legendre and Legendre [1998]). The biomic Bray-Curtis dissimilarity matrix and the genitalic average taxonomic dissimilarity matrix (discussed previously) for the five *Diorhabda* species are analyzed for a positive correlation using a one-tailed Mantel test in which the significance level of the normalized Mantel statistic, r_M , is determined using a Monte Carlo randomization procedure with 9,999 permutations (NTSYSpc, Matrix Comparison Plot [MxComp] module; test for probability random $r_M \geq$ observed r_M , including observed r_M with random values in test).

PCoA analysis is used to visualize biomic relationships among *Diorhabda* and *Tamarix* species. First, eigenvectors and eigenvalues are computed (NTSYSpc Eigen module) from the double centered biomic Bray-Curtis dissimilarity matrix (NTSYSpc Dcenter module). (A lack of negative PCoA axis eigenvalues did not necessitate using the square-root transformation for values in the Bray-Curtis dissimilarity matrix.) Eigenvalues of species along the first three PCoA eigenvector axes are displayed in a three dimensional biomic PCoA scatter plot (NTSYSpc Mod3D module). Loadings of the biomes on the first six PCoA axes are computed *a posteriori* using Spearman rank-order coefficients (Proc Corr; SAS Institute 2005) for ranks of the species in biomes versus ranks of the species in PCoA eigenvector axes.

Habitat Suitability Index Models. Habitat suitability index (HSI) models estimate the habitat suitability of geographic areas for a given species based upon the subjectively or objectively appraised value of habitat indicator variables (suitability indices). HSI models were originally developed in the 1980's to assess habitat suitability for various wildlife species by USDI Fish and Wildlife Service (1980, 1981) and were later coupled with GIS at a landscape level (e.g., Larson *et al.* 2003). We develop hand-fitted HSI models (5 minute grid resolution) to depict a first rough approximation of the relatively most suitable tamarisk beetle species for a given area. Four variables or biogeographic descriptors that we consider as encompassing intangible life requisites related to bioclimatic suitability for each *Diorhabda* species are employed in our HSI models: biome, latitude, elevation and distance to the ocean (continentality). Variable parameters employed in the model are from descriptive statistics of field collection data for each *Diorhabda* species assembled in this revision (locality data from specimens dissected in 2008 are not included in the models).

ArcMap, ArcInfo and the above mentioned elevation and biome grids are used to create ArcGIS grids for each of the four HSI model variables and *Diorhabda* field collection data at 5 minute (0.08333 degree) grid cell resolution to facilitate computer processing and to approximate the level of precision in the less precise *Diorhabda* locality data. ArcInfo is used to calculate a grid of distance to ocean (continentality) using an Euclidean distance function between 5 minute resolution ocean grid cells (including the Black Sea and Mediterranean Sea) and land grid cells derived from the above mentioned 1 km resolution elevation grid. A program macro for ArcMap is made to calculate a latitude grid using a point shapefile made from elevation land grid cells. Distribution points of *Diorhabda* that fall into 5 minute grid cells of incorrect values (e.g.,

ocean grid cells or incorrect biome grid cells) in the generalized biome and elevation grids are moved to adjacent grid cells of the appropriate value. The adjusted distribution points of each *Diorhabda* species are then converted into 5 minute *Diorhabda* locality grids used to query or sample values from the 5 minute grids of each of the four variables using ArcInfo. The resulting tables of 5 minute *Diorhabda* grid cell locations and grid cell values for each variable are used in calculating descriptive statistics in the form of schematic box plots for continuous variables (Proc Boxplot [Boxstyle = Schematic]; SAS Institute 2005) and frequency percentages for distribution of each *Diorhabda* species across eight biomes (Proc Freq; SAS Institute 2005; biome frequency percentage equals the number collections of a *Diorhabda* species within a biome divided by total numbers of collections for the species across all biomes). Descriptive statistics used in calculating habitat suitability indices are plotted using the Microsoft Excel Spreadsheet software. Lack of absence data and lack of even sampling across ranges of variables in native habitats precludes detailed statistical comparisons of means or frequencies.

From descriptive statistics for the above four 5-minute variable grids, a total of four suitability index (SI₁–SI₄) grids and one biomic relative suitability index (SI₅) grid are calculated for each species. The biomic relative suitability index calculates the percent presence in a biome relative to data for other *Diorhabda* species in the biome and provides extra weighting for the biome variable in the model. A final HSI value is calculated as the geometric mean ($[X_1 \times X_2 \times \dots \times X_n]^{1/n}$) of these five grids, giving a final HSI value of zero if any single SI variable is zero (Larson *et al.* 2003). Modeled values of the five suitability indices for each species are plotted against corresponding environmental variables using Microsoft Excel Spreadsheet software and the conditional statements and equations used in Arc Macro Language of ArcInfo for calculating HSI model grids are given below:

Suitability index (SI) grids	Calculation per 5 minute grid cell for each <i>Diorhabda</i> species ^a
latitudinal suitability index (SI ₁)	if within species interquartile range for latitude, then = 1; else if between max/min and 1% of range, linear decrease from 1 to 0; otherwise = 0
elevational suitability index (SI ₂)	if within species interquartile range for elevation, then = 1; else if between max/min and 10% of range, linear decrease from 1 to 0; otherwise = 0
continentality suitability index (SI ₃)	if within species interquartile range for distance to ocean, then = 1; else if between max/min and 20% of range, linear decrease from 1 to 0; otherwise = 0
biomic suitability index (SI ₄)	= (percent presence of species in biome)/(highest percent presence of species in any biome) (ranges 0.01–1; values less than 0.01 are set to 0.01 ; 1 for biome with highest percent presence for the species)
biomic relative suitability index (SI ₅)	= (percent presence of species in biome)/(percent presence of most common species in biome) (ranges 0.01–1; values less than 0.01 are set to 0.01 ; 1 when most common species in biome)
habitat suitability index (HSI)	= (SI ₁ × SI ₂ × SI ₃ × SI ₄ × SI ₅) ^{1/5} (ranges 0 to 1)

^aValues for max/min range, interquartile range, and percent presence of species in a biome used in calculating SI₁–SI₅ are given in the inset tables of Figures 51–52. Values in bold are subjectively adjusted model parameters.

The values for five hand-fitted parameters of the HSI model (bold figures in above table) are used to assign marginal suitability to areas in which variable values (e.g., elevation) are outside of the range at which the species were found in the field in the Old World. Values for these five parameters are adjusted and various formulations for calculating HSI are evaluated (e.g., weighted arithmetic means; with or without SI₅) in a

series of preliminary models of all five tamarisk beetles in order to minimize visually assessed errors regarding estimations of where several species are common in sympatry or where single species dominate in areas of either sympatry or nonsympatry in the final HSI models for both the Old World and New World (where introduced). The influence of various suitability indices and the inclusion of the biomic relative suitability index (SI_5) on the sensitivity and elasticity of HSI models is analyzed using the following formulae to calculate sensitivity (S) and elasticity (E) (after Mitchell *et al.* 2002):

$$S = \frac{\sum_{i=1}^n \left(|HSI_i - \overline{HSI}| \right)}{n}, \text{ and } E = \frac{\sum_{i=1}^n \left(\left| 1 - HSI_i / \overline{HSI} \right| \right)}{n},$$

where \overline{HSI} is the mean HSI value from a series of $n = 8$ values of HSI_i for which the value of a given suitability index ranges from 0.0 to 1.0 while all other suitability indices are held constant at 0.5. Suitability indices contributing to greater sensitivity and elasticity of HSI might be more important to include in the HSI model. A composite map displays where each *Diorhabda* spp. scores within the top 15% of the maximum HSI value of any *Diorhabda* species for a given grid cell (where $HSI > 0.01$).

Coden	Institution
AMA	Azerbaijan Milli Akademiyasi, Baku, Azerbaijan
BMNH	Natural History Museum, London, United Kingdom
CABP	Commonwealth Agricultural Bureau Institute Bioscience Pakistan Centre, Rawalpindi, Pakistan
DEI	German Entomological Institute, Müncheberg, Germany
HNHM	Hungarian Natural History Museum, Budapest, Hungary
MNMS	National Natural Science Museum, Madrid, Spain
IRNSB	Institut Royal des Sciences Naturelles de Belgique, Belgium, Brussels
IZAS	Institute of Zoology, Chinese Academy of Sciences, Beijing, China
MRSN	Regional Museum of Natural Science, Torino, Italy
MSNM	Civic Museum of Natural History, Milano, Italy
MZHF	Zoological Museum, University of Helsinki, Helsinki, Finland
MZLU	Museum of Zoology, Lund University, Sweden
NHMB	Natural History Museum, Basel, Switzerland
NHRS	Swedish Museum of Natural History, Stockholm, Sweden
NMPC	National Museum, Prague, Czech Republic
NMSU	New Mexico State University, Las Cruces, New Mexico, USA
TAU	Tel Aviv University, Tel Aviv, Israel
USNM	National Museum of Natural History, Washington D.C., USA
ZMAN	Zoololical Museum Amsterdam, Amsterdam, Netherlands
ZMUH	Universität von Hamburg, Zoologisches Institut und Zoologisches Museum, Hamburg, Germany
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
	Individuals
EGRC	Edward G. Riley, College Station, Texas
IAET	Irfan A. Aslan, Erzurum, Turkey
MBPF	Michel Bergeal, Versailles, France
RBCN	Ron Beenen, Nieuwegein, Netherlands

Label Data. All original label data from dissected and examined specimens are given under the listings of material examined for each species. Label data are ordered in a consistent manner; date formats are standardized and taxa on determination labels are abbreviated where appropriate. Additional information not on the labels, such as updated place names (from the GEOnet Names Server; NGA 2006) and geocoordinates are given in brackets. We also add in brackets the unique specimen label numbers placed on each dissected specimen and entered into a database of label data. An example of our specimen number label is “USDA USNM 2003-01”, where “USDA” is the name of our umbrella institution which is placed on each label (“USDA” is omitted from the label numbers in the lists), “USNM” represents an abbreviation designating the source collection, “2003” represents the year the specimen was dissected, and “01” represents a specimen number in our database. Data for examined voucher specimens from laboratory colonies are listed by their source field collection locations and includes receiver identifier codes (e.g., GSWRL-1999-8 [Temple, TX]) from invertebrate shipment records with foreign/overseas sources referenced in the USDA Agricultural Research Service (ARS) Germplasm Resources Information Network’s (GRIN) Releases of Beneficial Organisms (ROBO) database (USDA ARS 2006) under Invertebrate Germplasm information.

Specimens. Most of the over 2,392 specimens examined (of which 784 were dissected) for this revision were loaned from the collections of the listed 21 institutions and four individuals.

Vouchers of specimens from the USDA Grassland, Soil and Water Research Laboratory, Temple, Texas (GSWRL) are deposited at the USNM with the USDA-ARS Systematics Entomology Laboratory (SEL) under lot numbers GSWRL-2005-02 (for shipment and experimental vouchers) and GSWRL-2009-01 (North American field vouchers and general overseas collections).

Taxonomy

Genus *Diorhabda* Weise, 1883

Diorhabda Weise, 1883:316 (Type species: *Galeruca elongata* Brullé, 1832, by original designation).

Radymna Reitter, 1912:135 (Type species: *Diorhabda rickmersi* Weise, 1900, by monotypy).

Prophyllis Reitter, 1912:135 (Type species not designated [undetermined hairy species]).

Diorrhabda: Rusanov, 1949:118 (unjustified emendation).

Diagnosis. A future revision of the entire genus *Diorhabda* is needed, and it will probably involve additional transfers of current member species to other closely related genera of the tribe Galerucini Latreille (1802) (Galerucinae: Chrysomelidae), such as *Galerupipla* Maulik (1936) (see discussions below and under *D. elongata* group). After membership in the genus *Diorhabda* is stabilized, a description of distinguishing generic morphological characters can be made in comparison with other related genera.

Included species. As of this revision, 14 species are recognized from the genus *Diorhabda* in Europe, Africa, Asia and Australia (New Guinea) (Ogloblin 1936; Wilcox 1971, 1975; Berti and Rapilly 1973; Lopatin 1977a; Medvedev 1999). These 14 species are listed in the below discussion of information on their host plants under **Biology. Discussion. Taxonomy.** *Galeruca elongata* Brullé (1832) was made the type species for the genus *Diorhabda* by Weise (1883). *Galerupipla persica* (Faldermann, 1837) and *G. fisheri* (Faldermann, 1837), both of which attack *Alhagi maurorum* Medikus (Fabaceae) (Ogloblin 1936, Medvedev and Roginskaya 1988), were transferred from *Diorhabda* by Aslam (1972) without comment (see also Wilcox 1975), and this transfer has been widely overlooked (Lopatin 1977a, Mirzoeva 2001, Aslan *et al.* 2000, Lopatin *et al.* 2003, Warchalowski 2003, Gök and Duran 2004, Bieńkowski 2004, Lopatin *et al.* 2004). Other species transferred from *Diorhabda* include *Menippus clarki* Jacoby (1884; as *D. robusta* Jacoby [1899], Aslam 1972) and *M. brevicornis* (Jacoby, 1889) (Medvedev 1999). Both the genera *Diorhabda* and *Galerupipla* are in need of taxonomic revision. Our present revision is limited to treating the taxonomy of the five species of the *Tamarix*-feeding *Diorhabda elongata* group.

TABLE 1. Host plant associations of the *Diorhabda elongata* group.^a

Species	Host Plant	Location	Citation	
<i>Diorhabda elongata</i>	<i>Tamarix gallica</i>	Italy	Lundberg <i>et al.</i> 1987, present study	
	<i>T. smyrnensis</i>	Greece (Crete), Turkey	Regalin 1997; Gerling and Kugler 1973; Gök and Çilbıroğlu 2003, 2005; Gök and Duran 2004	
	<i>T. hampeana</i>	Greece	present study	
	<i>T. parviflora</i>	Greece, United States (California)	present study; R. Carruthers, pers. comm.	
	<i>T. chinensis</i> × <i>T. canariensis</i> / <i>T. gallica</i>	United States (Texas)	present study	
	<i>T. sp.</i>	Cyprus, Bulgaria, Greece	Georghiou 1977, Tomov 1979, present study	
<i>D. carinata</i>	<i>T. ramosissima</i>	Georgia, Tajikistan, Kazakhstan, Turkmenistan	Lozovoi 1961, Kulinich 1962, present study	
	<i>T. ramosissima</i> / <i>T. chinensis</i>	United States (Texas)	present study	
	<i>T. smyrnensis</i> (as <i>T. hohenackeri</i>)	Georgia, Azerbaijan	Lozovoi 1961, Samedov and Mirzoeva 1985	
	<i>T. arceuthoides</i>	Tajikistan	Kulinich 1962	
	<i>T. hispida</i>	Tajikistan	Kulinich 1962	
	<i>T. aphylla</i>	Pakistan	Habib and Hasan 1982, present study	
	<i>T. meyeri</i>	Azerbaijan	Samedov and Mirzoeva 1985	
	<i>T. c.f. indica</i> (as <i>T. cf. troupii</i>)	Pakistan	present study	
	<i>T. aralensis</i>	Turkmenistan	present study	
	<i>T. aucheriana</i>	Turkmenistan	present study	
	<i>T. sp.</i>	Pakistan, Azerbaijan, Uzbekistan	Habib and Hasan 1982, Samedov and Mirzoeva 1985, present study	
	<i>D. sublineata</i>	<i>T. africana</i>	Algeria, Morocco	Peyerimhoff 1926, Jolivet 1967
		<i>T. boveana</i> (as <i>T. bounopaea</i>)	Algeria	Peyerimhoff 1926
		<i>T. gallica</i>	France, Spain	Laboissière 1934, Hopkins and Carruth 1954
<i>T. senegalensis</i>		Senegal	present study	
<i>T. aphylla</i>		Tunisia	A. Kirk, pers. comm.	
<i>T. spp.</i>		Egypt, Tunisia, Algeria, Morocco	Boehm 1908; Alfieri 1976; S. Doguet, pers. comm.; present study	
<i>Diorhabda carinulata</i>	<i>T. ramosissima</i>	Uzbekistan, Kazakhstan, China, United States (Nevada, Utah, Wyoming, Colorado)	Sinadsky 1968; Mityaev and Jashenko 1998, 2007; DeLoach <i>et al.</i> 2003b; DeLoach <i>et al.</i> 2004	
	<i>T. hispida</i> var. <i>hispida</i>	Uzbekistan, China, Kazakhstan	Sinadsky 1968; Sha and Yibulayin 1993; Mityaev and Jashenko 1998, 2007; DeLoach <i>et al.</i> 2003b	

continued.

TABLE 1. (continued)

Species	Host Plant	Location	Citation
<i>Diorhabda carinulata</i> (cont.)	<i>T. laxa</i>	China, Kazakhstan	Sha and Yibulayin 1993; Mityaev and Jashenko 1998, 2007; DeLoach <i>et al.</i> 2003b
	<i>T. elongata</i>	China, Kazakhstan	Sha and Yibulayin 1993; Mityaev and Jashenko 1998, 2007; DeLoach <i>et al.</i> 2003b
	<i>T. arceuthoides</i>	China	Sha and Yibulayin 1993, DeLoach <i>et al.</i> 2003b
	<i>T. gracilis</i>	China, Kazakhstan	Sha and Yibulayin 1993; Mityaev and Jashenko 1998, 2007
	<i>T. smyrnensis</i> (as <i>T. hohenackeri</i>)	China	Sha and Yibulayin 1993, DeLoach <i>et al.</i> 2003b
	<i>T. leptostachya</i>	Kazakhstan, China	Mityaev and Jashenko 1998, 2007; present study
	<i>T. kansuensis</i>	China	Sha and Yibulayin 1993
	<i>T. androssowii</i>	China	Sha and Yibulayin 1993
	<i>T. chinensis</i>	China, United States (Colorado)	Sha and Yibulayin 1993, DeLoach <i>et al.</i> 2004
	<i>T. hispida</i> var. <i>karelinii</i>	China	DeLoach <i>et al.</i> 2003b
	<i>T. aralensis</i>	Turkmenistan	present study
	poss. <i>T. kotschyi</i> (as <i>T. leptopetela</i>) ^b	Iran	present study
	<i>T. parviflora</i>	United States (Nevada)	Dudley <i>et al.</i> 2006; Dudley <i>et al.</i> in prep.
	<i>T. sp.</i>	Kazakhstan, Mongolia, China	Mityaev 1958; Kulenova 1968; Lopatin 1970; Medvedev and Voronova 1977a, 1977b, 1979; Medvedev 1982; Tian <i>et al.</i> 1988; Bao 1989; Ishkov 1996; Mityaev and Jashenko 1997, 1999, 2007; Li <i>et al.</i> 2000
	<i>Myricaria alopecurooides</i>	Mongolia	Medvedev and Voronova 1979
	<i>M. sp.</i>	Mongolia, Kazakhstan	Medvedev 1982; Mityaev and Jashenko 1997, 2007
<i>D. meridionalis</i>	<i>T. sp.</i>	Iran	Berti and Rapilly 1973
	poss. <i>T. dioica</i> ^b	Iran	present study

^aAll species referred to in previous citations as *D. elongata*, *D. e. deserticola* (China and Kazakhstan), or *D. carinulata meridionalis* (Iran). See text for each *Diorhabda* species under **Distribution** for discussion of data supporting corrected species identities. See **Material Examined** and **Biology-Host Plants** sections for details of new host records from the present study. Authors of plant names are given at their first mention in the text.

^bPossible hosts based on list of *Tamarix* and other plant species present at collection sites for the expedition (Hoberlandt 1981) with which *Diorhabda* we examined were collected.

Biology. Host Plants. The plant families attacked by different *Diorhabda* spp. range across the two subclasses Carophyllidae and Rosidae (plant taxonomic groupings according to Spichiger *et al.* 2004). Five species feed upon *Tamarix* (Carophyllidae: Tamaricaceae): *D. elongata*, *D. carinata*, *D. sublineata*, *D. carinulata* and *D. meridionalis* (Table 1). *Diorhabda carinulata* additionally feeds upon *Myricaria*, also of the Tamaricaceae. Five other *Diorhabda* species also feed on plants of one or two closely related genera. *Diorhabda rickmersi* Weise (1900) feeds on *Rumex* sp. (Ogloblin 1936) and *Rheum* sp. (Medvedev and Roginskaya 1988) (both of Carophyllidae: Polygonaceae); *D. lusca* Maulik (1936) feeds on *Celtis australis* Linnaeus (Rosidae: Ulmaceae) (Maulik 1936); *D. trirakha* Maulik (1936) feeds on *Ulmus wallichiana*

Planchon (Ulmaceae) (Maulik 1936); *D. rybakowi* Weise (1890), which includes *D. koltzei* Weise (1900) as a junior synonym (Ogloblin 1936, Lopatin 1977a), feeds on *Nitraria* spp. (Carophyllidae: Nitrariaceae) (Medvedev and Voronova 1977b); and *D. tarsalis* Weise (1889) feeds on *Glycyrrhiza uralensis* Fischer et de Candolle (Rosidae: Fabaceae) (Medvedev and Voronova 1978). Hosts are unknown for four species of *Diorhabda*: *D. inconspicua* Jacoby (1894), *D. nigrifrons* Laboissière (1914), *D. octocostata* Gahan (1896), and *D. yulensis* Jacoby (1886).

***Diorhabda elongata*-Group**

tamarisk beetles

Diagnosis. The following diagnostic characters for tamarisk beetles are partly based upon keys to *Diorhabda* species for central Asia (Gressitt and Kimoto 1963a, Lopatin 1977a) and the Mediterranean region (Warchalowski 2003), and descriptions of certain south Asian *Diorhabda* species (Jacoby 1886, 1894; Maulik 1936). Tamarisk beetles may be distinguished from other species of *Diorhabda* by the following combination of characters: (1) the pronotum and elytra are glabrous or with very sparse setae, except for the pubescence of the epipleura; (2) the lateral borders of the prothorax are narrow, not flattened, with the posterior angles obtuse and distinct, not rounded or quadrate; (3) the elytral punctation is denser and finer than that of the pronotum; and (4) the elytron bears only a distinct lateral carina extending from the humeral calus. The description of external characters for adult *D. carinulata* (as *D. e. deserticola*) by Lewis *et al.* (2003b) applies generally to all species in the group, excepting measurements and coloration, which are discussed below in each species account along with genitalia.

Included species. We recognize five sibling genitalic morphospecies of tamarisk beetles as forming the *D. elongata* group: *D. elongata*, *D. carinata*, *D. sublineata*, *D. carinulata* and *D. meridionalis* (Figs. 1–45).

Distribution. The *D. elongata* species group is broadly distributed over the majority of the distribution of *Tamarix* from North Africa, southern Europe to central Asia (Map 1). Although tamarisk is also native to southern Africa, Israel and Palestine, and Southeast Asia (India, Bangladesh, and Burma) (Baum 1978), tamarisk beetles are unreported from these areas. Detailed distribution data with maps are discussed under the heading **Distribution** in each species account.

Discussion. Taxonomy. *Diorhabda elongata* Brullé (as *Galeruca*) was originally described from the Pelopónnisos peninsula of Greece in 1832 (Brullé 1832). From 1858 to 1893, four other species described under *Galeruca* were synonymized under *D. elongata* (Reiche and Saulcy 1858, Weise 1893): (1) *D. carinata* (Faldermann, 1837) (of the Transcaucasus), (2) *Galeruca sublineata* (Lucas, 1849) (of Annaba, Algeria), which has been regarded as the subspecies *D. e. sublineata* (Lucas) (Gressitt and Kimoto 1963a), (3) *D. carinulata carinulata* (of Sarepta, Russia), and (4) *G. costalis* (Mulsant, 1852) (of southwest Turkey). We compare specimens of these four taxa collected from the vicinity of type localities to literature descriptions of type specimens. We similarly studied specimens corresponding to the subspecific taxa *D. e. deserticola* Chen (1961) (of Yuli, China; also examined paratypes), *D. carinulata meridionalis* Berti & Rappilly (of Minab, Iran), and *D. e. carinata* (Faldermann) (from central Asia) as regarded by Bechyné (1961). We characterize the variability of the genitalia and some external characters (size and elytral markings) for each taxon using specimens from the type localities (topotypes) where possible. We compare and match specimens of tamarisk beetles from throughout southern Europe, Africa and west and central Asia with the various taxa above, providing data on variability in genitalia across the entire distribution of each taxon.

In our comparisons of the above taxa of tamarisk beetles, we examined male and female genitalia of 784 specimens from 37 countries. We distinguish five qualitatively distinct endophallic morphotypes based on endophallic sclerites. We also find geographically corresponding female genitalic morphotypes with distinct differences in internal sternite VIII and vaginal palpi. These five fully diagnosable genitalic morphotype pairs have additional nondiscrete differences in ranges of body length for each sex and, in some cases, striping of the elytra. Intermediate forms between these species are not seen in the extensive material examined, even in

several instances of sympatry and syntopy (sharing individual tamarisk trees as habitat). Most species appear to be at least parapatric or marginally sympatric and some are moderately sympatric. Among species with overlapping or abutting geographic ranges, the absence in nature of intermediate hybrid genitalic forms along a geographic cline towards areas of range contact constitutes a morphological hiatus that is inconsistent with a status of interbreeding subspecies (see Krysan *et al.* 1980, Patten and Unitt 2002) or geographic races. Although additional material would be desirable in the areas of abutting ranges of certain species such as in western Italy and central Turkey, we believe the data available sufficiently document the lack of intermediate forms between species. The numbers of diagnostic genitalic differences between the few allopatric species are comparable with the number of diagnostic differences seen between moderately sympatric species. Consequently, a status of potentially interbreeding subspecies or races is also inconsistent for the few species living in allopatry (see Helbig *et al.* 2002). The maintenance of distinguishing genitalic characteristics in four species in culture under identical laboratory conditions is contraindicative of a status of intraspecific morphs, such as might occur in cases of genitalic polymorphism (e.g., Jocqué 2002) or phenotypic plasticity (e.g., Agrawal 2001). Distinct qualitative differences and morphometric discontinuities in genitalic structures distinguishing species are evidence of strong reproductive isolation in nature (Helbig *et al.* 2002). We find that these morphotype pairs are a complex of five fully diagnosable sibling genitalic morphological species (morphospecies) of *Diorhabda*. Further evidence for reproductive isolation between the four species *D. elongata*, *D. carinata*, *D. sublineata*, and *D. carinulata* is also found in differences in component ratios of putative aggregation pheromones (discussed below under **Biology-Aggregation Pheromones**) and reduced laboratory F2 hybrid egg viability (discussed below under *Experimental Hybridization*).

We characterize the genitalia of *D. elongata* and corroborate the restoration of the species *D. carinata* and *D. carinulata* and their removal from synonymy with *D. elongata* by Berti and Rapilly (1973). Specimens identified by Bechyné as *D. e. carinata* are conspecific with *D. carinata*. The following four taxonomic changes are made: (1) *Galeruca sublineata* Lucas is removed from synonymy with *D. elongata* and restored as the species *D. sublineata* (Lucas); (2) *D. e. deserticola* Chen is synonymized under *D. carinulata*; (3) *D. koltzei* ab. *basicornis* Laboissière is synonymized under *D. carinulata*; and (4) *D. carinulata meridionalis* Berti & Rapilly is elevated to species status as *D. meridionalis* Berti & Rapilly. The color variant *D. e.* ab. *bipustulata* Normand is synonymized under *D. sublineata*. Five sibling species (with no subspecies) are recognized as forming the *D. elongata* group: *D. elongata*, *D. carinata*, *D. sublineata*, *D. carinulata* and *D. meridionalis*. Each species of tamarisk beetle exhibits some degree of sympatry with at least one of the other species. Four of these five tamarisk beetle species were originally described in the 1800's and one was described as a subspecies, but all have been identified and published under the name *D. elongata* by various workers (e.g., Wilcox 1971, Riley *et al.* 2003, Warchalowski 2003, Bieńkowski 2004, Lopatin *et al.* 2004).

The five species of the *D. elongata* group may be distinguished by a combination of eight discrete, or near discrete, genitalic characters, involving the forms of the male endophallic sclerites and female vaginal palpi (Table 5), and the additional genitalic character of the form of female internal sternite VIII. Males of all species are distinguishable by the forms of one or more of three endophallic sclerites (PES, EES, and CES; Figs. 14–33). A combination of characters involving the forms of the vaginal palpi (VP) and internal sternite VIII (IS VIII) can be used to distinguish between females of three species, *D. elongata*, *D. carinulata* and *D. meridionalis* (Figs. 34–43). Females of two species, *D. carinata* and *D. sublineata*, are distinguished from the three other species by these same characters, but only in some cases are they distinguishable from one another, and only by the form of internal sternite VIII (Figs. 40–41). We find no differences in the morphology of the spermatheca (Figs. 34–38; SP) or median lobe (Figs. 14–18; ML) and tegmen (not shown) of the aedeagus that are sufficient for species diagnosis.

Significant patterns in clinal geographic variation in the five species are not seen and, therefore, no subspecies are recognized. We provide keys for the sexing of adults, followed by keys to species for each sex based upon the genitalia.

We are unable to distinguish the five sibling species of the *D. elongata* group solely on the basis of external characters. The presence of elytral vittae that extend into the basal half of the elytra (SMV and SSV; Figs. 5, 9) can be used to eliminate an identification of *D. elongata*, in which the elytral vittae, if present, are confined to the apical half of the elytra (Fig. 1). Differences in ranges of body length for each sex (Table 2) can aid in species identification of some individuals when used with distribution data (Map 1). Further investigation might reveal obscure external characters useful in separating some species such as external setation (e.g., Konstantinov and Lopatin 2000).

TABLE 2. External morphometrics ($\bar{x} \pm SD$ [range], mm) of field collected material for the *Diorhabda elongata* species group.

Species	n	Length body ^a	Length left elytron (LE) ^a	Width elytra (WE) ^{b,c}	Ratio WE/LE ^a
Males					
<i>Diorhabda elongata</i>	61	5.96 ± 0.38 b (5.33–6.78)	4.63 ± 0.27 b (4.08–5.26)	2.58 ± 0.19 c (1.56–3.04)	0.56 ± 0.04 bc (0.33–0.63)
<i>D. carinata</i>	49	6.29 ± 0.50 a (5.12–7.34)	5.01 ± 0.41 a (4.01–5.81)	2.73 ± 0.21 b (2.28–3.11)	0.55 ± 0.03 a (0.48–0.60)
<i>D. sublineata</i>	45	5.98 ± 0.50 b (4.98–6.92)	4.67 ± 0.39 b (3.74–5.47)	2.63 ± 0.31 c (1.52–3.18)	0.56 ± 0.05 c (0.29–0.62)
<i>D. carinulata</i>	47	5.31 ± 0.35 c (4.63–6.09)	4.16 ± 0.26 c (3.74–4.84)	2.31 ± 0.21 d (1.66–2.83)	0.55 ± 0.05 b (0.36–0.61)
<i>D. meridionalis</i>	14	5.12 ± 0.40 c (4.15–5.61)	3.90 ± 0.32 c (3.11–4.29)	2.18 ± 0.17 d (1.73–2.42)	0.56 ± 0.03 bc (0.52–0.63)
Females					
<i>D. elongata</i>	32	6.60 ± 0.47 b (5.80–7.68)	5.23 ± 0.38 b (4.71–6.09)	2.96 ± 0.18 a (2.70–3.32)	0.57 ± 0.02 bc (0.52–0.60)
<i>D. carinata</i>	31	6.76 ± 0.72 a (5.05–8.44)	5.46 ± 0.59 a (4.15–6.71)	2.97 ± 0.43 a (1.63–3.74)	0.54 ± 0.06 a (0.28–0.62)
<i>D. sublineata</i>	24	6.52 ± 0.60 b (4.91–7.40)	5.16 ± 0.46 b (4.01–5.81)	2.94 ± 0.23 a (2.49–3.39)	0.57 ± 0.03 c (0.50–0.62)
<i>D. carinulata</i>	23	5.80 ± 0.51 c (4.98–6.99)	4.60 ± 0.49 c (3.60–5.88)	2.53 ± 0.37 c (1.28–3.25)	0.55 ± 0.04 b (0.37–0.61)
<i>D. meridionalis</i>	15	5.81 ± 0.44 c (4.77–6.37)	4.51 ± 0.47 c (3.60–5.67)	2.58 ± 0.19 c (2.15–2.84)	0.58 ± 0.04 bc (0.46–0.62)

^a Ranks of values followed by the same letter within the same column for each sex are not significantly different. The ranks of values for females are significantly larger than those of males with no sex by species interactions ($P > 0.05$; Two-Way Kruskal-Wallis Tests on ranks using PROC GLM-LSMEANS test; SAS Institute 2005).

^b Species by sex interaction is significant and ranks of values followed by the same letter within the same column (including both sexes) are not significantly different ($P > 0.05$; Two-Way Kruskal-Wallis Tests on ranks using PROC GLM-LSMEANS test; SAS Institute 2005).

^c Combined width of both elytra at widest point.

The endophalli (END) of the *D. elongata* group consist of an elongated tubular sac bearing one to three sclerites and various characteristic bulgings (Figs. 14–18). The sacs widen distally in *D. elongata*, *D. carinata* and *D. sublineata*, but narrow distally in *D. carinulata* and *D. meridionalis* (see Fig. 19d–e of Berti and Rapilly 1973 for an illustration of the fully exerted narrow tip of the endophallus in *D. meridionalis*). All species have a conspicuous palmate shaped dorsal sclerite, the palmate endophallic sclerite (PES), at the base of the sac that is armed subdistally or distally with one to several spines (or teeth) (Figs. 29–33). All species

also have an elongate shaped ventral sclerite, the elongate endophallic sclerite (EES), which runs along most of the length of the sac. The elongate sclerite also bears a raised blade which is armed with one to several spines (or teeth) (Figs. 19–23). The shapes of these two sclerites and the arrangement of the spines are useful in species diagnosis. Only *D. sublineata* possesses a third lateral sclerite that connects the palmate and elongate sclerites, the connecting endophallic sclerite (Figs. 16, 21, 31; CES). Our illustrations (Figs. 14–18) are of uninflated endophalli. Studies of inflated endophalli, such as obtained from mating pairs freshly killed by hot water, could reveal that the conformations of bulgings of the endophallus are also useful in species diagnosis. Scanning electron micrography is being done for the endophallic sclerites of the *D. elongata* species group by Jessica Perez, Roxana Reyna-Islas, and Dave Thompson at NMSU using some of our dissected material.

Silfverberg (1974) found characters of the endophallic sclerites useful in helping differentiate between the genera *Galerucella*, *Pyrrhalta*, and *Xanthogaleruca* in the tribe Galerucini. Endophalli in the *D. elongata* group closely resemble those of several *Galerucella* spp. (Figs. 1a, 4, 5 of Silfverberg 1974) which are also in the form of a tubular sac. Endophalli of *Galerucella* differ in bearing only a dorsal sclerite which is elongate, not palmate, in shape. The endophallus of *D. lusca* with its large serrated flagellum (Fig. 97 of Mann and Crowson 1996) is strikingly different from those in both the *D. elongata* group and *Galerucella*, and the placement of *D. lusca* in the genus *Diorhabda* should be reviewed. Spermathecae of the *D. elongata* group (Figs. 34–38; SP) more closely resemble those of some *Galeruca* spp. (Figs. 1d, 2d of Beenen 1999) than the more slender spermathecae of some *Galerucella* spp. (Fig. 6 of Hippa and Koponen 1986), but differ from both in bearing a pointed appendage at the distal tip (similar to that in North American *Ophraella*, but more prominent; LeSage 1986). Additional studies are needed of the morphology of the endophalli and its sclerites and the female genitalia (vaginal palpi, spermathecae and internal sternite VIII; Figs. 34–38) in other species of *Diorhabda* and related genera. Such genitalic studies should be useful in any reviews of subtribal, generic, or specific classifications within the tribe Galerucini.

Experimental Hybridization. D. C. Thompson *et al.* (in prep.) have conducted laboratory crossing studies between *D. elongata* and each of the three sibling species *D. carinulata*, *D. sublineata*, and *D. carinata*, and between *D. carinulata* and *D. carinata* (also Dave C. Thompson and Beth Peterson, New Mexico State University, Las Cruces, NM, pers. comm.). Additional crossing studies between *D. elongata* and *D. carinulata* have been conducted by some of us (DeLoach and Tracy unpublished data) and Julie Keller and Dan Bean (pers. comm.). These experiments are the subject of pending publications and involve interspecific pure line crossings, hybrid crossings, and concurrent pure line conspecific control crossings of laboratory reared virgin adult male and female beetles in no choice situations confined in vials with fresh tamarisk leaves for food ($n = \text{ca. ten}$ replications per type of cross). The mean percent viability of the F1 eggs produced from crossing the parental females and viability of the F2–F3 eggs from crossing progeny of the parental females were recorded. *Diorhabda* colonies used in these studies were found to be free of *Wolbachia* bacterial infections (D. Kazmer pers. comm.) that can reduce fertility in crosses between chrysomelid subspecies, such as is seen in the subspecies of *Diabrotica virgifera* LeConte (Giordano *et al.* 1997).

In a no-choice laboratory environment, matings readily occurred between pure line *D. elongata* and the three other *Diorhabda* spp. (*D. carinulata*, *D. carinata*, and *D. sublineata*) and between *D. carinulata* and *D. carinata*, producing F1 hybrid eggs with 50–100% viability of control crosses, depending on parental species and their sex. In ♀ *D. carinata* × ♂ *D. carinulata* crossings, F1 hybrid egg viability was reduced by over 50% from that of pure line control crosses. But no F1 eggs were viable from ♀ *D. carinulata* × ♂ *D. carinata* crossings in which 90% of females died in copulo. A high incidence of female death in copulo also occurred in ♀ *D. carinulata* × ♂ *D. elongata* crossings and was associated with a 30% reduction in F1 egg viability over that of controls, but percent F1 egg viability was normal for ♀ *D. elongata* × ♂ *D. carinulata* crossings. Most surviving females failing to produce viable eggs in interspecific crosses probably failed to mate, but fertilization could also have produced inviable eggs. The larger size of male *D. carinata* and *D. elongata*, along with the larger more prominent distal basal facing spines of their palmate endophallic sclerites (Figs. 14–18), may be a factor in their observed difficulty disengaging from copulation with female *D. carinulata* and the associated high in copulo death rate for female *D. carinulata*.

Reductions in F2 egg viability of ca. 50–100% from that of controls were found in at least one of the male/female crossing combinations for all interspecific hybrid/hybrid progeny crosses. Observed reductions in F1 and/or F2 hybrid egg viabilities is a form of hybrid breakdown (the opposite of hybrid vigor) providing further evidence for reproductive isolation between all the crossed *Diorhabda* species. Laboratory hybridization studies between the most morphologically similar species, *D. sublineata* and *D. carinata*, have not yet been conducted. However, these species strongly and asymmetrically differ with respect to the F1 and F2 hybrid egg viabilities resulting from the two combinations of male/female crosses of each species with *D. elongata* (D.C. Thompson and B. Peterson, pers. comm.), providing additional evidence of reproductive isolation. For example, in ♀ *D. elongata* × ♂ *D. sublineata* crosses, F1 egg viabilities are close to that of control crosses, but in ♀ *D. elongata* × ♂ *D. carinata* crosses, no F1 egg are viable.

D. Thompson and B. Peterson (pers. comm.) found that hybrid breakdown in the form of reduced egg viability over that of controls is much less apparent in F2 and F3 progeny of laboratory produced hybrid/hybrid crosses of *D. sublineata* × *D. elongata* (0–60% reductions) compared to that of F2 progeny produced from other hybrid/hybrid crosses in the *D. elongata* group (90% reductions). For example, egg viability of F2 *D. elongata* × *D. carinulata* hybrids is reduced by ca. 90–100% over that of pure line controls. However, egg viability of ♀ *D. sublineata* × ♂ *D. elongata* hybrids is reduced by about 60% from that of pure line controls for the F2 generation and it is reduced by about 50% for the F3 generation. In ♀ *D. elongata* × ♂ *D. sublineata* hybrids, egg viability is about the same as pure line controls in the F2 generation, but is reduced by about 25% in the F3 generation, possibly as a result of additional hybrid breakdown between generations. Colonies of *D. sublineata* × *D. elongata* hybrids can be easily maintained for at least six generations in the laboratory (D. C. Thompson and B. Peterson, pers. comm.) and F1 and F2 hybrids can have diagnostic anomalous hybrid character combinations (see *D. sublineata* × *D. elongata* **Hybrid Morphology** under species account for *D. sublineata*). Egg viability has never been measured in F4 or later generation hybrids, and, over several more generations of hybrid inbreeding, additional hybrid breakdown might lead to severe reductions in egg viability. Egg viability in backcross *D. sublineata*/*D. elongata* hybrids has not yet been characterized. With *D. carinulata*/*D. elongata* hybrids, egg viability appears normal when hybrid females are backcrossed with pure line males but there is no egg viability when hybrid males are backcrossed with pure line females (DeLoach and Tracy unpublished data). Additional forms of hybrid breakdown may occur in field situations (discussed below).

Reduced F2 egg viability is also seen in laboratory hybrids of the chrysomelids *Altica carduorum* Guerin-Meneville and *A. cirsiicola* Ohno (Laroche *et al.* 1996). The chrysomelids *Diabrotica longicornis* (Say) and *D. virgifera* will also hybridize in the laboratory and produce fertile F1 and F2 hybrids. However, interspecific matings between these *Diabrotica* spp. are very rare in the field and prezygotic reproductive isolation apparently is operating through differences in adult feeding habits, pheromones, and phenologies (Hintz and George 1979). Interspecific laboratory crossings of sympatric populations of *Galerucella nymphaeae* and “*G. sagittariae*” from different host plants in Finland produce fertile F1 hybrids, but there is no cytological evidence of hybridization in nature (Nokkala and Nokkala 1998). The production of laboratory hybrids able to reproduce for several generations is not evidence for extensive hybridization and gene flow in nature (see Helbig *et al.* 2002). We have seen no morphological intermediates in nature that give evidence of hybridization between any species of the *D. elongata* group (for further discussion and characterization of male genitalia in laboratory produced hybrids, see *D. sublineata* × *D. elongata* **Hybrid Morphology** under *D. sublineata* species account). In addition, the genitalic morphology of laboratory produced male hybrids of *D. sublineata* and *D. elongata* cannot be attributable to other known species of *Diorhabda*. The lack of intermediate genitalic morphotypes between these species in nature, especially in areas of sympatry and parapatry, is strong evidence of reproductive isolation.

Reproductive isolation in sympatric *Diorhabda* is probably maintained by prezygotic isolating mechanisms such as differing mate-recognition systems which may be reinforced by differences in aggregation pheromones (see **Biology – Aggregation Pheromones** below). It is possible that some of these *Diorhabda* species may hybridize rarely in nature and have limited flow between certain genes, as is seen in

some other closely related animal species (Helbig *et al.* 2002, Mallet 2005, Bull *et al.* 2006). For example, several species of passion-vine butterflies, *Heliconius* (Lepidoptera: Nymphalidae: Heliconiinae), will interbreed and produce fertile hybrids in hybrid zones, but genetic analyses reveal strong barriers to interspecific gene flow, probably as a result of differing mate recognition systems (Jiggins *et al.* 1997, Bull *et al.* 2006). A limited amount of interspecific hybridization resulting in fertile hybrids also occurs between natural populations of some sympatric nonsibling Hawaiian species of *Drosophila* fruit flies (Diptera: Drosophilidae) which are strongly reproductively isolated by differing mate-recognition systems (Ahearn and Templeton 1989). The natural phenomenon of uncommon interspecific hybridization leading to fertile offspring is becoming more widely known among a variety of animal taxa (Mallet 2005).

Diorhabda hybrids in the field might exhibit hybrid breakdown in areas additional to reduced egg viability, including behavioral disruptions in foraging (e.g., Godoy-Herrera *et al.* 1994) and pheromonal communication as a result of changes in hybrid pheromone composition (e.g., Wee and Tan 2005) and response (e.g., Lanier 1970). Laboratory or cage produced *Diorhabda* hybrids should not be considered as candidates for tamarisk biological control because of known and potential problems of hybrid breakdown in the field which would probably lead to low persistence and low efficacy. Further investigation is needed with genetic techniques to search for various types of hybrids and backcross hybrids and genetic introgression between *Diorhabda* species in the Palearctic.

Morphometrics. Ranges for variables of all the external measurements overlap among males and females of all species in the *D. elongata* group (Table 2). Certain individuals of extremely small or large size can be identified as being of one or two species. For example, only females of *D. carinata* reach over 8.0 mm in length. Several significant differences in mean ranks of morphometric variables are seen. The mean lengths of the body and left elytron are significantly greater in females than males in each of the five species in the group. Mean lengths of the body and left elytron of both males and females of *D. carinata* are significantly greater than those of all other species in the *D. elongata* group (Table 2). Mean length of the body and left elytron are significantly smaller in males and females of *D. carinulata* and *D. meridionalis* compared to all other members of the *D. elongata* group. The combined width of the elytra at the widest point is significantly greater in females of *D. elongata*, *D. sublineata*, and *D. carinata*, than in females of *D. carinulata* and *D. meridionalis* and males of all species. The width of the elytra is significantly greater in male *D. carinata* compared to males of all other species and females of *D. carinulata* and *D. meridionalis*. The mean ratio of the width of the elytra to the length of the left elytron is significantly smallest in *D. carinata* making it the most elongate species in the group. Additional external morphometric variables are being evaluated for use in classification of the *D. elongata* group (Joaquin Sanabria, International Fertilizer Development Center [IFDC], Muscle Shoals, AL, pers. comm.).

Milbrath and DeLoach (2006b) found the mean lengths of the left elytron (mm) in *D. elongata* (from Crete) reared on *T. ramosissima* × *T. chinensis* (4.57 ± 0.05 in 29 males, 5.19 ± 0.04 in 47 females) are slightly but significantly larger than that of individuals reared on *T. aphylla* (4.46 ± 0.04 in 42 males, 5.09 ± 0.05 in 33 females). These mean values for the length of the left elytron were similar to those observed for field material of *D. elongata* in this revision (Table 2), but the standard deviations they observed were much smaller than we observed. The wide geographic range of specimens measured in our revision probably accounts for the wider variability in measurements.

Significant interspecific differences are seen in ranks of measurements of male endophallic sclerites (Table 3) and female vaginal palpi and internal sternite VIII (Table 4). All species of the *D. elongata* group significantly differ in the mean values of three variables: (1) the length of the blade of the elongate endophallic sclerite, (2) the ratio of the length of the blade of the elongate sclerite to the total length of the elongate sclerite, and (3) the width of the stalk of female internal sternite VIII. We find nine instances of discrete breaks or near breaks in size ranges of genitalic structures between species of the group, some of which are used in the keys to species (below): (1) both the range in width and width to length ratio of the palmate endophallic sclerite is nearly separate between *D. carinulata* and *D. meridionalis*, (2) the length of the elongate sclerite is largest in *D. carinata* and the range separates *D. carinata* from *D. carinulata* and *D.*

meridionalis (see also scatter plot of Fig. 48); (3) the ratios of both the blade length and length of the spined area of the blade to the length of the elongate sclerite is smallest in *D. elongata* and the range separates *D. elongata* from all other species (see also scatter plot of Fig. 48), (4) the range in the ratio of the blade length to the length of the elongate sclerite separates *D. carinulata* and *D. meridionalis* (Fig. 48B); (5) both the range of width and width to length ratio of the vaginal palpus in *D. carinulata* and *D. meridionalis* is nearly separate from all other species in the group; (6) the range in width of the stalk of female internal sternite VIII separates *D. meridionalis* from all other members of the group except *D. elongata*; (7) the range in ratio of the width of stalk to width of apical lobe of female internal sternite VIII separates *D. meridionalis* from all other members of the group except *D. elongata*; and (8) the width of the lobe of the stalk in female internal sternite VIII separates *D. meridionalis* and *D. carinata*.

TABLE 3. Male genitalic morphometrics ($\bar{x} \pm$ SD [range], mm) of field collected material for the *Diorhabda elongata* species group.^a

Species	n	Palmate Endophallic Sclerite			Elongate Endophallic Sclerite			SpinedArea Length (SL)	Ratio SL/L
		Width (W)	Length (L)	Ratio W/L	Length (L)	Blade Length (LB)	Ratio LB/L		
<i>Diorhabda elongata</i>	27	0.31 ± 0.04 c (0.22–0.37)	0.51 ± 0.08 c (0.38–0.73)	0.61 ± 0.09 b (0.44–0.85)	1.09 ± 0.06 c (0.96–1.23)	0.37 ± 0.05 e (0.27–0.44)	0.34 ± 0.05 e (0.24–0.42)	0.05 ± 0.06 d (0.01–0.18)	0.05 ± 0.05 c (0.01–0.16)
<i>D. carinata</i>	21	0.40 ± 0.04 a (0.32–0.46)	0.74 ± 0.07 a (0.59–0.87)	0.54 ± 0.07 c (0.40–0.69)	1.34 ± 0.08 a (1.17–1.52)	0.67 ± 0.07 b (0.57–0.82)	0.50 ± 0.05 d (0.43–0.63)	0.58 ± 0.07 a (0.46–0.68)	0.43 ± 0.05 b (0.34–0.52)
<i>D. sublineata</i>	22	0.33 ± 0.04 b (0.27–0.40)	0.66 ± 0.06 b (0.53–0.75)	0.50 ± 0.05 d (0.42–0.63)	1.21 ± 0.10 b (1.06–1.41)	0.62 ± 0.05 c (0.52–0.72)	0.52 ± 0.03 c (0.48–0.56)	0.52 ± 0.06 b (0.38–0.64)	0.43 ± 0.05 b (0.31–0.51)
<i>D. carinulata</i>	23	0.34 ± 0.04 b (0.28–0.43)	0.45 ± 0.04 d (0.38–0.55)	0.77 ± 0.10 a (0.61–1.02)	0.99 ± 0.07 d (0.87–1.14)	0.56 ± 0.05 d (0.46–0.63)	0.57 ± 0.05 b (0.49–0.66)	0.44 ± 0.06 c (0.34–0.54)	0.45 ± 0.05 b (0.33–0.52)
<i>D. meridionalis</i>	13	0.23 ± 0.02 d (0.19–0.29)	0.49 ± 0.04 c (0.41–0.56)	0.47 ± 0.07 d (0.35–0.63)	1.03 ± 0.07 d (0.87–1.12)	0.77 ± 0.06 a (0.65–0.86)	0.75 ± 0.03 a (0.67–0.79)	0.57 ± 0.08 a (0.40–0.70)	0.55 ± 0.05 a (0.46–0.64)

^aRanks of values followed by the same letter within the same column are not significantly different ($P > 0.05$; Two-Way Kruskal-Wallis Tests on ranks using PROC GLM-LSMEANS test; SAS Institute 2005) (see Figs. 14–33 for illustrations of measured structures; see Fig. 48 for scatter plots of measurements of the elongate endophallic sclerite).

TABLE 4. Female genitalic morphometrics ($\bar{x} \pm$ SD [range], mm) of field collected material for the *Diorhabda elongata* species group.

Species	n	Vaginal palpi			Internal sternite VIII			
		Length (LP)	Width (WP)	Ratio LP/WP	Width stalk (WST)	Width apical lobe (WAL)	Ratio WST/WAL	Width lobe of stalk (WLS) ^b
<i>Diorhabda elongata</i>	29	0.16 ± 0.02 b (0.11–0.19)	0.20 ± 0.01 b (0.17–0.23)	0.78 ± 0.11 b (0.52–0.94)	0.37 ± 0.06 d (0.22–0.51)	0.70 ± 0.08 b (0.52–0.84)	0.53 ± 0.10 c (0.35–0.81)	0.08 ± 0.01 c (0.06–0.11)
<i>D. carinata</i>	21	0.16 ± 0.02 ab (0.12–0.20)	0.22 ± 0.02 a (0.19–0.26)	0.74 ± 0.12 bc (0.50–0.89)	0.56 ± 0.07 b (0.42–0.68)	0.82 ± 0.08 a (0.70–1.00)	0.68 ± 0.10 b (0.53–0.86)	0.14 ± 0.02 a (0.11–0.17)
<i>D. sublineata</i>	19	0.17 ± 0.02 a (0.12–0.20)	0.24 ± 0.03 a (0.18–0.30)	0.71 ± 0.09 c (0.46–0.85)	0.61 ± 0.07 a (0.52–0.77)	0.79 ± 0.08 a (0.63–0.94)	0.78 ± 0.06 a (0.62–0.87)	0.12 ± 0.03 b (0.08–0.18)
<i>D. carinulata</i>	20	0.17 ± 0.01 a (0.14–0.19)	0.16 ± 0.01 c (0.14–0.18)	1.06 ± 0.11 a (0.94–1.36)	0.46 ± 0.07 c (0.36–0.57)	0.71 ± 0.05 b (0.60–0.81)	0.64 ± 0.09 b (0.49–0.77)	0.14 ± 0.03 ab (0.07–0.22)
<i>D. meridionalis</i>	12	0.18 ± 0.02 a (0.14–0.19)	0.16 ± 0.02 c (0.13–0.17)	1.13 ± 0.10 a (1.00–1.31)	0.28 ± 0.03 e (0.22–0.33)	0.68 ± 0.04 b (0.61–0.76)	0.41 ± 0.05 d (0.33–0.48)	0.06 ± 0.02 c (0.04–0.09)

^aRanks of values followed by the same letter within the same column are not significantly different ($P > 0.05$; Two-Way Kruskal-Wallis Tests on ranks using PROC GLM-LSMEANS test; SAS Institute 2005). See Figs. 34–38 for illustrations of measured structures.

^bWidth of widest lobe.

TABLE 5. Genitalic character state profiles for eight discrete, or near discrete, multi-state characters used in taxonomic keys of the *Diorhabda elongata* species group.^a

Genitalic character	Species				
	<i>Diorhabda elongata</i>	<i>D. carinata</i>	<i>D. sublineata</i>	<i>D. carinulata</i>	<i>D. meridionalis</i>
Elongate endophallic sclerite					
Increasing proportion of blade length (length blade/length EES)	0 (0.24–0.42)	0.5 (0.43–0.63)	0.5 (0.48–0.56)	0.5 (0.49–0.66)	1 (0.67–0.79)
Presence of hooked apex (1); absence (0)	0	0	0	0	1
Palmate endophallic sclerite					
Increasing spination of distal margin (spination) ^b	0.5 (1–6 [commonly 2–4] usually subdistal spines, maximum 2 spines distal)	1 (2–6 [commonly 4–5] usually distal spines, maximum 1 spine subdistal)	1 (2–6 [commonly 3–4] usually distal spines, maximum 1 spine subdistal)	0 (1–2 subdistal spines)	0 (1–2 subdistal spines)
Increasingly narrowing distal margin ^b	0.33 (usually broadly rounded, rarely truncate serrate)	0 (truncate serrate)	0 (truncate serrate)	0.67 (acutely rounded)	1 (narrowly rounded)
Presence of lateral appendage (1); absence (0)	0	1	1	0	0
Connecting endophallic sclerite					
Absent (0) vs. present (1)	0	0	1	0	0
Vaginal palpi					
Broadly rounded (0) vs. narrowly rounded (1)	0	1	1	0	0
Increasing elongation of vaginal palpi (length palpi/width palpi) ^c	0 (0.52–0.94)	0 (0.50–0.89)	0 (0.46–0.85)	1 (0.94–1.36)	1 (1.00–1.31)

^aIncreasing degree or presence of a character state is denoted by a higher number. For details on diagnostic genitalic character states, see illustrated taxonomic keys, genitalic characters under each species, and Tables 2, 3 and 4. Character states are standardized to range from zero to one. Differences in character states between species are discrete with the exceptions noted below for three characters with near discrete differences for separating *D. elongata* from some species.

^bDifferences in spination and narrowing of the palmate endophallic sclerite are near discrete between *D. elongata* and the two species *D. carinata* and *D. sublineata*.

^cDifferences in elongation of vaginal palpi are near discrete between *D. elongata* and *D. carinulata* (difference is discrete if used in combination with width of widest lobe of female internal sternite VIII).

TABLE 6. Genitalic average taxonomic dissimilarity matrix (upper right) and genitalic Pearson product-moment correlation similarity matrix (lower left, shaded) for the *Diorhabda elongata* species group (from Table 5).^a

Species	Species				
	<i>Diorhabda elongata</i>	<i>D. carinata</i>	<i>D. sublineata</i>	<i>D. carinulata</i>	<i>D. meridionalis</i>
<i>D. elongata</i>	0/1	0.571	0.672	0.449	0.680
<i>D. carinata</i>	0.200	0/1	0.354	0.746	0.884
<i>D. sublineata</i>	0.048	0.745	0/1	0.825	0.952
<i>D. carinulata</i>	-0.007	-0.506	-0.703	0/1	0.412
<i>D. meridionalis</i>	-0.115	-0.674	-0.944	0.728	0/1

^a Matrices produced with NTSYSpc Interval Data (SIMINT) module (Rohlf 2006).

Stenophenetic Analysis. The data matrix of genitalic character state profiles for the *D. elongata* group is shown in Table 5 and the derived average taxonomic dissimilarity matrix and a Pearson product-moment correlation similarity matrix are shown in Table 6. The genitalic dissimilarity and similarity phenograms produced from these matrices using the UPGMA clustering method (Figs. 49–50) were of the highest quality having the greatest r_{coph} values of 0.817 and 0.885, respectively. Genitalic phenograms produced from complete-linkage clustering and single-linkage clustering (not shown) have lower r_{coph} values of 0.745 and 0.811, respectively, for dissimilarity phenograms, and 0.882 and 0.862, respectively, for similarity phenograms. The genitalic similarity phenograms produced from any of the three clustering methods are of higher quality (have higher r_{coph} values) than genitalic dissimilarity phenograms produced from any of the clustering methods. Both UPGMA dissimilarity and similarity phenograms (Figs. 49–50) reveal *D. carinata* and *D. sublineata* are the most similar in genitalia, sharing seven of eight genitalic character states. *D. carinata* and *D. sublineata* form a group separate from the other three species in the genitalic dissimilarity phenogram while they form a group with *D. elongata* in the genitalic similarity phenogram. *Diorhabda carinulata* and *D. meridionalis* share five of eight genitalic character states and form a group with *D. elongata* in the genitalic dissimilarity phenogram but are separate from the other three species in the genitalic similarity phenogram. Similarities in genitalia among these *Diorhabda* species that are seen in the genitalic phenograms may or may not be correlated with genetic similarity.

Berti and Rapilly (1973) originally described *D. meridionalis* as a subspecies of *D. carinulata*. *Diorhabda sublineata* differs from *D. carinata* by only a single genitalic character in each sex. Therefore, we suspect the *D. carinulata*/*D. meridionalis* and *D. carinata*/*D. sublineata* groupings do represent genetic similarity. The placement of *D. elongata* with either *D. carinulata*/*D. meridionalis* or *D. carinata*/*D. sublineata* has less support. A morphometric phenogram for the *D. elongata* group based upon external and genitalic data are in preparation (J. Sanabria, pers. comm.). Studies of genetic similarity in mitochondrial and nuclear DNA among *D. elongata*, *D. sublineata*, *D. carinata*, and *D. carinulata* are in progress (D. Kazmer, pers. comm.).

Common Name. The vernacular name “tamarisk leaf beetle” has been applied in the Bulgarian, Russian and North American biological literature to *D. elongata* (Tomov 1974) as well as *D. carinulata* (as *D. elongata*: Sinadsky 1957, 1963, 1968; as *D. e. deserticola*: Bean *et al.* 2007b). The name “elongate tamarisk leaf beetle” was applied by Lozovoi (1961) to *D. carinata* (as *D. elongata*) in Georgia. The name “saltcedar leaf beetle” has been applied in North American biological control literature primarily to both *D. elongata* and *D. carinulata* (as *D. elongata*; DeLoach and Carruthers 2004b, Dudley and DeLoach 2004, Dudley 2005a, USDA Animal and Plant Health Inspection Service 2005, Carruthers *et al.* 2006, Dudley *et al.* 2006, Herr *et al.* 2006, DeLoach *et al.* in prep., Moran *et al.* in press), but also to *D. carinata* and *D. sublineata* (as *D. elongata*; DeLoach and Carruthers 2004b). We propose the term “tamarisk beetles” to refer to all five species of the *D. elongata* group. Because *Diorhabda* are Old World species, in the common name we conserve the term “tamarisk”, used for the entire genus *Tamarix* in much of its native distribution (Baum 1978) and often in North America (e.g., Baum 1967a, Birken and Cooper 2006). In contrast, the competing term “saltcedar” is generally confined to use in the United States where it applies to certain weedy deciduous species (*T. ramosissima*/*T. chinensis*, *T. canariensis*/*T. gallica*, and *T. parviflora*; DiTomaso 1998). Members of the *D. elongata* group are probably the most important coleopterous defoliators of tamarisk, making this group worthy of the general name “tamarisk beetle”. Consequently, the term “leaf” is dropped from the group vernacular name in order to shorten proposed common names for each species. Species common names are formed by adding a term referring to some unique intrinsic biogeographical or morphological characteristic before the term “tamarisk beetle”. Other species of the numerous beetles specializing on tamarisk outside the tribe Galerucini (Kovalev 1995) could be distinguished in their common name from “tamarisk beetle” by a name referring to their differing tribe (e.g., “tamarisk flea beetle” for Alticini), subfamily (e.g., “tamarisk casebearer” for Cryptocephalinae) or family (e.g., “tamarisk weevil” for Curculionidae). Vernacular names are listed following the Latin names in the section header for each species account.

Biology. *Host Plants.* Only shrubs and trees of the Old World family Tamaricaceae (order Tamaricales), including *Tamarix* and *Myricaria*, serve as hosts for any of the five species of tamarisk beetles (Table 1). Among tamarisks in North America, *T. aphylla* (Linnaeus) Karsten (athel tamarisk) is considered a non-target for biological control by *Diorhabda* because of its value as a shade tree and for windbreaks in parts of the southwestern U.S. and northern Mexico (DeLoach 1990; Map 7) and because it is only a minor invasive. However, *T. aphylla* is a major invasive along the Finke River in Australia (Griffin *et al.* 1989), and could potentially become more invasive in North America, where it is now known to invade by seed propagation in addition to vegetative propagation in southern Nevada (Walker *et al.* 2006) and northern Mexico (unpublished data; Map 7). *Tamarix aphylla* is a natural, but probably minor, host for *D. carinata* in Pakistan and *D. sublineata* in Tunisia (Table 1). In no-choice, small field cages, *D. elongata*, *D. carinata*, and *D. sublineata*, accepted *T. aphylla* for oviposition to the same degree as they accepted *T. ramosissima* × *T. chinensis* (Milbrath and DeLoach 2006b). In more sensitive multiple-choice, field cages studies, *D. sublineata* and *D. carinulata* generally prefer other North American tamarisks to *T. aphylla* for oviposition (egg-laying). However, *D. elongata* and *D. carinata* selected *T. aphylla* equally as well as other *Tamarix* species for oviposition in some tests, but oviposited on *T. aphylla* significantly less in other tests (Milbrath and DeLoach 2006a, 2006b), laying only ca. 22–30% as many eggs on *T. aphylla* as on some other tamarisks. In open field multiple-choice tests, *D. elongata* preferred ovipositing on *T. chinensis* × *T. canariensis*/*T. gallica* when compared with *T. aphylla* (Moran *et al.* in press). *Tamarix aphylla* appears to be at low to moderate risk to damage by the four tested *Diorhabda* spp. in the field. Potential damage by these *Diorhabda* to *T. aphylla* in a no-choice open field setting (especially where other *Tamarix* spp. are absent) is difficult to predict (Milbrath and DeLoach 2006b). The degree of potential damage to *T. aphylla* is still under investigation in field studies.

Frankenia spp. (family Frankeniaceae) subshrubs and herbs are also in the order Tamaricales and occur throughout the native range of the *D. elongata* group (Jäger 1992) and in western North America (Whalen 1987). Native North American *Frankenia* spp. are of major concern as non-targets of tamarisk biological control whose safety must be insured (Lewis *et al.* 2003a; Milbrath and DeLoach 2006a; Herr *et al.* 2006, in prep.). *Frankenia* spp. can serve as a suitable but generally less favorable host in development from larvae to adult for *D. elongata*, *D. carinata*, *D. sublineata* and *D. carinulata* in caged no-choice studies (further discussed later; DeLoach *et al.* 2003b; Lewis *et al.* 2003a; Milbrath and DeLoach 2006a; Herr *et al.* 2006, in prep.). However, *Frankenia* spp. are never reported to serve as a hosts for any *Diorhabda* spp. under natural conditions in the open field (Table 1), even in specific surveys of *Frankenia* adjacent to where *Diorhabda* is found in Tunisia (DeLoach *et al.* 2003b). Three North American *Frankenia* spp., *F. salina* (Molina) I.M. Johnston, *F. johnstonii* Correll, and *F. jamesii* Torrey ex. A. Gray, provide almost no attraction for oviposition compared to *Tamarix* in field cage multiple-choice studies with *D. carinulata* (Lewis *et al.* 2003a, Milbrath and DeLoach 2006a) and *D. elongata*, *D. carinata*, and *D. sublineata* (Milbrath and DeLoach 2006a). In field cage no-choice studies with *D. carinulata*, *D. sublineata* and *D. carinata*, oviposition on *F. jamesii* and *F. johnstonii* was not different from non-host coyote willow (*Salix exigua* Nuttall) and adults experienced increased mortality compared to *T. ramosissima* × *T. chinensis* treatments (Milbrath and DeLoach 2006a). However, in laboratory cage no-choice tests, differences in oviposition by *D. elongata* on *F. salina* (inland variety) and *T. ramosissima*, *T. parviflora*, and *T. aphylla* were not significant (Herr *et al.* 2006). In open field testing of *Frankenia salina* transplanted among stands of *Tamarix* in Nevada and Wyoming, *D. carinulata* did not oviposit on *F. salina* which only sustained light (<4%) foliage loss from feeding of *Diorhabda* larvae that had crawled from nearby *Tamarix* (Dudley and Kazmer 2005). In open field tests with *F. salina*, *T. ramosissima*/*T. chinensis* and *T. aphylla* transplanted together in the field at Big Spring, Texas, *D. elongata* oviposited only a single egg mass on *F. salina* compared with hundreds on *T. chinensis* × *T. canariensis*/*T. gallica* (Herr *et al.* 2006). Lewis *et al.* (2003a) and Milbrath and DeLoach (2006a) concluded that *Frankenia* is at very low risk of damage from any of the four tested *Diorhabda* species. Attack on non-preferred host plants by insect biological control agents is generally reduced as distance to the preferred host increases (Blossey *et al.* 2001). Consequently, we expect that damage by these four *Diorhabda* species to both *Frankenia* and *T. aphylla* is more unlikely the further away these plants are growing from preferred *Tamarix*

spp. hosts. Host preferences of *D. meridionalis* remain to be studied. Further information on the host range of the *D. elongata* group as well as additional biological data are reviewed later for each species.

Phenology. *Diorhabda carinulata* has two to four generations from April through September and overwinter as adults in ground cover in western China and central Asia (Sinadsky 1968; Tian *et al.* 1988; Bao 1989; Sha and Yibulayin 1993; Mityaev and Jashenko 1998, 2007; Chen *et al.* 2000; Li *et al.* 2000). *Diorhabda carinulata* has two generations north of 38° in North America (DeLoach and Carruthers 2004b). *Diorhabda elongata*, *D. carinata*, and *D. sublineata* can have up to five generations from March to October in field cages at Temple, Texas (Milbrath *et al.* 2007). Five generations have also been observed for *D. carinata* (as *D. elongata*) at Ashgabat, Turkmenistan from March to September (Myartseva 1999). *Diorhabda sublineata* is collected from mid-January to mid-December in Tunisia (from examined material), where it may have more than five generations. The voltinism of *D. meridionalis* is yet to be studied, but adults are found from March to October in southern Iran (from examined material).

Bean *et al.* (2007a) found the critical photoperiod (inducing diapause in 50% of the population) for adult *D. carinulata* from Fukang, China (44°N) is ca. 14 hours 55 minutes at 28°C. In comparison to *D. carinulata* from Fukang, the critical photoperiod for diapause induction is more influenced by temperature and much shorter in *D. elongata* from Crete (35°N), *D. carinata* from Qarshi, Uzbekistan (38°N), and *D. sublineata* from Sfax, Tunisia (35°N) (*D. sublineata* having the shortest critical photoperiod) (Bean and Keller in prep.).

Bean and Keller (in prep.) also found intraspecific differences in critical photoperiod between two populations of *D. carinulata* from a similar latitude but widely varying elevations in China. *Diorhabda carinulata* from a low elevation at Turpan (42.8°N, -3 m elevation) have a critical photoperiod ca. 1 hr shorter than populations from Fukang (44.2°N, 552 m elevation) under laboratory conditions of ca. 25°C. These populations may represent two climatypes of *D. carinulata* adapted to differing seasonal progressions as influenced by elevation. Climatypes with intraspecific differences in critical daylength as influenced by seasonal differences across wide latitudinal and elevational gradients can probably be found among all the species of the *D. elongata* group. Additional observations on phenology are discussed in the species accounts.

Aggregation Pheromones. Cossé *et al.* (2005) identified a male-produced aggregation pheromone in *D. carinulata* (as *D. elongata*) in laboratory and field studies. The pheromone consists of two components, the aldehyde (2*E*,4*Z*)-2,4-heptadienal and the alcohol (2*E*,4*Z*)-2,4-heptadien-1-ol. Robert Bartelt (USDA/ARS, Peoria, IL, pers. comm.) found that these same chemical components are also emitted by males of *D. elongata*, *D. carinata* and *D. sublineata*, but that the ratios of aldehyde to alcohol are not necessarily the same as in *D. carinulata*. In species other than *D. carinulata*, these chemicals are considered as putative pheromones until they can be field tested. The component ratio of alcohol to aldehyde in the putative pheromone of *D. elongata* of Sfakaki, Crete, Greece, is almost identical to that of *D. carinulata*. However, field testing revealed the *D. carinulata* pheromone is ineffective for *D. elongata* established at Big Spring, Texas (Allen Knutson, The Texas AgriLIFE Extension Service, Dallas, TX, pers. comm.). *Diorhabda elongata* from Posidi Beach, Greece are unusual in producing a higher proportion of alcohol in the pheromone, up to ca. 4 times higher than in the Crete population, as more pheromone is released. It is unclear whether the Crete *D. elongata* population may also be able to release higher amounts of pheromone under the proper conditions and prove to be more similar in pheromone composition to the Posidi Beach population than to *D. carinulata* (R. Bartelt, pers. comm.). If the Crete *D. elongata* pheromone is more similar to that of the Posidi Beach *D. elongata*, this would explain why the *D. carinulata* pheromone was ineffective for *D. elongata*. Proportions of alcohol in putative pheromones of *D. carinata* were intermediate between those of *D. elongata* from Crete and Posidi Beach. The proportion of alcohol in the putative pheromone of *D. sublineata* is about 10 to 20 times higher than that found in *D. carinata*, *D. elongata* from Crete, and *D. carinulata*, and about 5 times higher than that found in *D. elongata* from Posidi Beach. In some sympatric and syntopic species of bark beetles (Coleoptera: Scolytidae), pheromones of one species may disrupt conspecific pheromonal response of another species (Poland and Borden 1998), and the possibility of such competitive interactions between some sympatric and syntopic species of tamarisk beetles may warrant investigation.

TABLE 7. Biogeographic characteristics in the *Diorhabda elongata* species group.

Characteristic	<i>Diorhabda elongata</i>	<i>D. carinata</i>	<i>D. sublineata</i>	<i>D. carinulata</i>	<i>D. meridionalis</i>
Elevation (m) (location)					
Maximum	1,720 (Velez Planina, Bosnia Herzegovina)	2,903 (Sare Gearbid Mt., Afghanistan)	2,606 (Tacchedirt, Morocco)	1,834 (Bogda Shan Mts., 80 km NW Urumqi, China)	1,102 (Sekand, 27 km ENE, Iran)
Minimum	1 (Lido di Volano, Italy) ^a	-15 (Sabirabad, Azerbaijan)	1 (LeBarcares, France) ^a	-55 (Turpan Botany Station, China)	18 (Bilal, Iran)
Latitude (°N) (location)					
Maximum	45.64 (Trieste environs, Italy)	43.60 (Shelek environs, Kazakhstan)	43.60 (Montpelier, France)	48.55 (Ynderbor, Kazakhstan)	36.20 (Halab, Syria)
Minimum	30.05 (Al Qahirah, Egypt)	29.53 (Borazjan, 30 km NNE, Iran)	16.15 (Ndiol Nar, Senegal)	29.32 (Abareq, Iran)	25.73 (Bahukalat, Iran)
Distance from ocean (km) (location)					
Maximum	255 (Malatya, Turkey)	2,328 (Charyn River by Chundzha, Kazakhstan)	503 (Baghdad, Iraq)	2,282 (Burenhayran, Mongolia)	293 (Jolow Gir, Iran)
Minimum	0 (Lido di Volano, Italy) ^a	37 (Omidiyeh, 34 km SE, Iran)	0 (LeBarcares, France) ^a	266 (Abareq, Iran)	8 (Bilal, Iran)
Major biomes inhabited (percentage of field collections) ^b					
	Mediterranean Forests, Woodlands & Scrub (79.0%); Temperate Broadleaf & Mixed Forests (19.0%)	Deserts & Xeric Shrublands (37.0%); Temperate Grasslands, Savannas & Shrublands (31.5%); Temperate Broadleaf & Mixed Forests (16.3%)	Mediterranean Forests, Woodlands & Scrub (73.2%); Flooded Grasslands & Savannas (14.6%)	Deserts & Xeric Shrublands (62.7%); Temperate Grasslands, Savannas & Shrublands (20.5%)	Deserts & Xeric Shrublands (62.5%); Temperate Broadleaf & Mixed Forests (25.0%)
Biogeographic descriptors ^c					
	maritime temperate warm Mediterranean woodlands/ broadleaf forests	continental temperate warm deserts/ grasslands/ broadleaf forests	maritime subtropical Mediterranean woodlands /flooded grasslands	continental temperate cold and warm deserts/ grasslands	maritime subtropical deserts/ broadleaf forests

^aOne of several coastal locations with minimum values (See Figs. 51–52 for descriptive statistics of biogeographic characteristics summarized over 5 minute resolution grids).

^bBiomes ordered by percentage collections; biomes listed until cumulative percentage of collections from biomes equals at least 80% (Fig. 52B).

^cBased on descriptive statistics of biogeographic characteristics (Figs. 51–52).

Biogeography. *General.* The native range of the *D. elongata* species group is primarily restricted to the Palearctic realm (Map 1). However, *D. sublineata* extends marginally into the Afrotropical realm in Senegal and Yemen and *D. carinata* extends marginally into the Indo-Malayan realm in northern Pakistan. All species of the *D. elongata* group are at least marginally sympatric with at least one other species in the group (Map 1; Table 8). *Diorhabda carinulata* and *D. carinata* are the most widely sympatric among the group, overlapping in distribution over a large portion of central Asia. The *D. elongata* group is distributed from 48°N in Kazakhstan (*D. carinulata*) to 16°S in Africa (*D. sublineata*) (Map 1, Table 7, Fig. 51B). *Diorhabda carinulata* is primarily found further north than all other species in the group while *D. meridionalis* is primarily found further south than all other species. The primary distributions of *D. elongata*, *D. carinata*, and

D. sublineata are intermediate in latitude within the *D. elongata* group, but *D. sublineata* is primarily found further south than *D. elongata* and *D. carinata* (Map 1, Fig. 51B). All species may be found at or below sea level and *D. carinata* and *D. sublineata* can range to 2,903 and 2,606 m elevation, respectively (Table 7, Fig. 51A). *Diorhabda elongata*, *D. sublineata*, and *D. meridionalis* are primarily found at elevations below 400 m and in maritime regions. In contrast, *D. carinata* and *D. carinulata* are primarily found above 400 m and are more continental in distribution, occurring the furthest inland from the oceans (Map 1, Table 7, Figs. 51A, 52A).

TABLE 8. Biogeographic and habitat relationships among the *Diorhabda elongata* species group.^a

Species pair ^b	Closest known points of range contact	Closest distance	Biogeographic/habitat relationship
<i>Diorhabda elongata</i> / <i>D. carinata</i>	S. Turkey (Adana)–N. Syria (Halab)	186 km ^c	marginal sympatry ^c
<i>D. elongata</i> / <i>D. sublineata</i> *	Egypt (Cairo), S. Spain, Portugal, Algeria	0 km	marginal sympatry
<i>D. elongata</i> / <i>D. carinulata</i> *	S. Russia (Dagestan Republic)	0 km? ^d	marginal sympatry
<i>D. elongata</i> / <i>D. meridionalis</i>	S. Turkey (Adana)–N. Syria (Halab)	186 km	parapatry
<i>D. carinata</i> */ <i>D. sublineata</i>	Iraq (Baghdad)	0 km	marginal sympatry
<i>D. carinata</i> **/ <i>D. carinulata</i> **	Azerbaijan, Turkmenistan, N. Iran, S. Uzbekistan, Tajikistan, S. Kazakhstan, Kyrgyzstan, W. China	0 km	moderate sympatry, partial syntopy
<i>D. carinata</i> **/ <i>D. meridionalis</i> **	W. Iran, Syria	0 km	partial sympatry, partial syntopy
<i>D. sublineata</i> / <i>D. carinulata</i>	S. Azerbaijan (Ordubad)–C. Iraq (Baghdad)	635 km	allopatry
<i>D. sublineata</i> / <i>D. meridionalis</i>	W. Iran (Shush)–C. Iraq (Baghdad)	385 km	allopatry
<i>D. carinulata</i> / <i>D. meridionalis</i>	S. Iran (Abareq–Sabzvaran)	102 km	parapatry

^a Closest point of range contact and distance are based upon examined material. In the text, we list locations where sympatric species were collected in close proximity, locations where syntopic species were collected from the same tamarisk trees or within the same series, and additional probable areas of range contact. See Map 1 for display of combined ranges of species.

^b Species with a single asterisk are dominant in known areas of weak or marginal sympatry with the other species in a pair. Species with two asterisks are sometimes dominant or sometimes less abundant than the other species in a pair, depending on the area (see text).

^c Actual closest distance between *D. elongata* and *D. carinata* may be zero based upon probable range contact between these species in E. Turkey (see text).

^d Approximate location (Dagestan Republic) of *D. elongata* specimen precludes measurement.

Eight desert, grassland and forest biomes characterize the biogeography of differing *Diorhabda* species (Table 9, Maps 2–6, Fig. 52B). Within these biomes, *Diorhabda* are most likely to be found in the primarily riparian, spring and maritime habitats of their host *Tamarix* species. The biomes inhabited vary widely among *Diorhabda* and host *Tamarix* species (Tables 9 and 11; Fig. 52B). *Diorhabda elongata* is usually collected in Mediterranean and Temperate Broadleaf forest biomes, and it is not reported from desert or grassland biomes as are many other species in the *D. elongata* group. The bioclimatic conditions to which *D. elongata* is adapted for Mediterranean maritime and riparian habitats are likely very different from conditions found in riparian habitats of the desert biome in which *D. carinulata* and *D. meridionalis* are primarily found.

TABLE 9. Biomic occurrence state profiles for degree of indigenous occurrence in eight biomes by country in the *Diorhabda elongata* species group.^a

Biome	<i>Diorhabda elongata</i>	<i>D. carinata</i>	<i>D. sublineata</i>	<i>D. carinulata</i>	<i>D. meridionalis</i>
Deserts & Xeric Shrublands	0	1 (Afghanistan, Azerbaijan, Georgia, Iraq, Iran, Kazakhstan, Pakistan, Tajikistan, Turkmenistan, Uzbekistan)	1 (Algeria, Egypt, Iraq, Tunisia)	1 (Azerbaijan, China, Iran, Kazakhstan, Russia, Mongolia, Tajikistan, Turkmenistan, Uzbekistan)	1 (Iran, Pakistan)
Temperate Grasslands, Savannas & Shrublands	0	1 (Armenia, Azerbaijan, Kazakhstan, Kyrgyzstan, Tajikistan, Turkey, Uzbekistan)	0	1 (Azerbaijan, Kazakhstan, Kyrgyzstan, Russia, Uzbekistan)	0
Montane Grasslands & Shrublands	0	1 (Afghanistan, Pakistan, Tajikistan, Turkmenistan)	0.5 (Morocco)	1 (China, Iran)	0.5 (Iran)
Mediterranean Forests, Woodlands & Scrub	1 (Croatia, Cyprus, Greece, Italy, Lebanon, Macedonia, Spain, Turkey)	0.5 (Syria)	1 (Algeria, France, Morocco, Spain, Tunisia)	0	0.5 (Syria)
Temperate Broadleaf & Mixed Forests	1 (Bosnia Herzegovina, Bulgaria, Italy, Macedonia, Turkey)	1 (Azerbaijan, Georgia, Iran, Turkey)	0	0.5 (Iran)	1 (Iran)
Temperate Conifer Forests	0.5 (Turkey)	1 (Iran, Turkey, Pakistan)	0	0.5 (Iran)	0
Flooded Grasslands & Savannas	0.5 (Egypt)	0	1 (Algeria, Tunisia, Egypt)	0	0
Tropical & Subtropical Grasslands, Savannas & Shrublands	0	0	0.5 (Senegal)	0	0
Biomic Specialization Index (BSI)	3.0	5.5	4.0	4.0	3.0

^aBiomes of Olson and Dinerstein (2002). States of occurrence in biome: 0—no record; 0.5—single record (minor presence); 1—multiple records (major presence).

Similarly, desert riparian habitats and grassland riparian habitats differ in bioclimatic and biogeographic characteristics. For instance, different salicaceous trees and shrubs generally characterize North American grassland riparian habitats, such as plains cottonwood (*Populus deltoides* Barton ex Marshall subsp. *monilifera* [Aiton] Eckenwalder), and black willow (*Salix nigra* Marshall), and various desert riparian habitats, such as Fremont cottonwood (*P. fremontii* Watson subsp. *fremontii*), Meseta cottonwood (*P. fremontii* Watson subsp. *mesetae* Eckenwalder), Rio Grande cottonwood (*P. deltoides* Barton ex Marshall subsp.

wislizenii [Watson] Eckenwalder), and Goodding willow (*S. gooddingii* Ball) (Eckenwalder 1977, Powell 1998). *Diorhabda carinata* is also most often found in the desert biome but it occurs in the temperate grassland biome to a higher degree than other species of the *D. elongata* group. Like *D. elongata*, *D. sublineata* is also most common in the Mediterranean biome, but it also is common in the desert biome in which *D. elongata* is absent and has a strong presence in the Flooded Grasslands and Savannas biome in which *D. elongata* is uncommon (Fig. 52B). *Diorhabda elongata* and *D. meridionalis* occur in the fewest biomes and are the most stenobiomic species with low biomic specialization index (BSI) values of 3.0 (Table 9). *Diorhabda carinata* occurs in the largest number of biomes and is the most eurybiomic species, with the largest BSI value of 5.5.

TABLE 10. Biomic Bray-Curtis dissimilarity matrix for the *Diorhabda elongata* species group (from Table 9).^a

Species	Species				
	<i>Diorhabda elongata</i>	<i>D. carinata</i>	<i>D. sublineata</i>	<i>D. carinulata</i>	<i>D. meridionalis</i>
<i>D. elongata</i>	0	-	-	-	-
<i>D. carinata</i>	0.504	0	-	-	-
<i>D. sublineata</i>	0.568	0.555	0	-	-
<i>D. carinulata</i>	0.681	0.145	0.620	0	-
<i>D. meridionalis</i>	0.500	0.276	0.409	0.409	0

^a Matrix produced with NTSYSpc Interval Data (SIMINT) module (Rohlf 2006). Raw data matrix normalized with log (x + 1) transformation before dissimilarity matrix calculated.

Our knowledge of the biogeographic characteristics of the *D. elongata* group is limited by potentially under-collected areas such as eastern Turkey, Syria, Pakistan, Afghanistan and the Arabian Peninsula. Additional comparative and descriptive information on the biogeography of each *Diorhabda* species, including the primary ecoregions they inhabit and their biogeographic associations with indigenous host *Tamarix* species, is discussed under the heading **Biogeography** in the species accounts.

As an aid to matching *Diorhabda* species to target tamarisk species in North America, we compare the similarities in biomic profiles of the *D. elongata* group with those of tamarisk species invasive in North America below (see *Biomic Analysis*). Among these tamarisk species, *T. aphylla* and *T. ramosissima* are the most eurybiomic with BSI values of 8.0 and 6.0, respectively (Table 11). *Tamarix chinensis* and *T. parviflora* are the most stenobiomic tamarisks with BSI values of 1 and 2.5, respectively.

Tamarix austromongolica is closely related to *T. chinensis* (Zhang 2004), and our comparison of the native ranges and biomic profiles of these tamarisks prompted us to examine the potential presence of *T. austromongolica* in North America. *Tamarix chinensis* is widely cultivated throughout China, but it is indigenous only to eastern China (Zhang and Zhang 1990), east of 115°E in the Temperate Broadleaf and Mixed Forests biome. *Tamarix chinensis* has long been considered as widely invasive in the western U.S. (Baum 1967a; Gaskin and Schaal 2002, 2003), but the native biomic profile of *T. chinensis* does not include desert and grassland biomes from which it is reported in the western U.S. (Table 11). However, the native biomic profile of *T. austromongolica* does include desert and grassland biomes to which it is indigenous in the area between Lanzhou and Hohhot in north central China (Ma and Liu 1988; DeLoach, unpublished data; Zhang, Peng-yun, Lanzhou University, Lanzhou, China, pers. comm.; Map 5). *Tamarix austromongolica* was once considered a subspecies of *T. chinensis* (Zhou 1989), but recent studies support its status as a separate species (Hua *et al.* 2004, Zhang 2004). In response to our interest in the potential presence of *T. austromongolica* in North America, J. Gaskin haplotyped intron 4 of the nuclear phosphoenolpyruvate carboxylase (pepC) gene (Gaskin and Schaal 2002) from specimens of cultivated *T. austromongolica* from China and found that some genetically match that of common *T. chinensis* and *T. ramosissima*/*T. chinensis* hybrids (J. Gaskin, pers. comm.). The fairly narrow distribution of *T. austromongolica* from ca. 103–112°E in

TABLE 11. Biomic occurrence state profiles for degree of indigenous occurrence in nine biomes by countries for *Tamarix* spp. invasive in North America.^a

Biome	<i>Tamarix ramosissima</i>	<i>T. chinensis</i>	<i>T. austro-mongolica</i> ^b	<i>T. parviflora</i>	<i>T. gallica</i>	<i>T. canariensis</i>	<i>T. aphylla</i> ^c
Deserts & Xeric Shrublands	1 (Afghanistan, Azerbaijan, China, Georgia, Iran, Iraq, Kazakhstan, Kyrgyzstan, Mongolia, Pakistan, Russia, Saudi Arabia, Turkmenistan, Uzbekistan)	0	1 (China)	0	0	1 (Algeria, Morocco, Tunisia)	1 (Afghanistan, Algeria, Egypt, Ethiopia, India, Iran, Iraq, Israel, Jordan, Kuwait, Lebanon, Libya, Oman, Pakistan, Saudi Arabia, Syria, Tunisia, Yemen)
Temperate Grasslands, Savannas & Shrublands	1 (Azerbaijan, China, Iran, Iraq, Kazakhstan, Kyrgyzstan, Romania, Russia, Tajikistan, Turkmenistan, Ukraine, Uzbekistan)	0	1 (China) ^d	0	0	0	0
Montane Grasslands & Shrublands	1 (China, Kazakhstan, Kyrgyzstan)	0	1 (China)	0	0	0	1 (Afghanistan, Ethiopia, Pakistan)
Mediterranean Forests, Woodlands & Scrub	0	0	0	1 (Albania, Algeria, Croatia, France, Greece, Italy, Libya, Portugal, Spain, Turkey)	1 (Algeria, France, Italy, Morocco, Spain)	1 (Algeria, France, Italy, Libya, Morocco, Portugal, Spain, Tunisia)	1 (Egypt, Israel, Lebanon, Libya, Morocco, Palestine, Tunisia)
Temperate Broadleaf & Mixed Forests	1 (Armenia, Azerbaijan, China, Georgia, Iran, Iraq, Russia, Turkey)	1 (China)	0	1 (Greece, Italy, Portugal)	1 (France, Italy, Spain, United Kingdom)	1 (Spain)	1 (Iran)
Temperate Conifer Forests	1 (China, Kazakhstan, Kyrgyzstan, Pakistan)	0	0	0.5 (Turkey)	0.5 (Morocco)	0	1 (Afghanistan, Iran, Pakistan)
Flooded Grasslands & Savannas	1 (Iraq)	0	0	0	0	0.5 (Libya)	1 (Egypt, Iraq, Tunisia)
Tropical & Subtropical Grasslands, Savannas & Shrublands	0	0	0	0	0.5 (Senegal)	0	1 (Ethiopia, Somalia, Sudan)
Tropical and Subtropical Dry Broadleaf Forests	0	0	0	0	0	0	1 (India)
Biomic Specialization Index (BSI)	6	1	3	2.5	3	3.5	8

^aBiomes of Olson and Dinerstein (2002). States of occurrence in biome: 0—no record; 0.5—single record (minor presence); 1—multiple records (major presence).

^bInvasiveness in North America requires further confirmation.

^cCurrently minor invasive.

^dDistribution based on hand-drawn map of Zhang Peng-yun (pers. comm.).

China is situated at the eastern edge of the distribution of *T. ramosissima* and approaching the westernmost edge of the distribution of *T. chinensis* (115°E) where a *T. ramosissima*/*T. chinensis* hybrid zone would be expected to occur (Map 5). In view of the biomic profile, DNA data, and distribution of *T. austromongolica*, the possibilities that this species may be a *T. ramosissima*/*T. chinensis* hybrid and that it is contributing to the genome of invasive *T. ramosissima*/*T. chinensis* in western North America warrant further investigation.

Biomic Analysis. The biomic profile for the *D. elongata* species group (Table 9) is used to generate a biomic Bray-Curtis dissimilarity matrix (Table 10) in order to compare similarities in biomic profiles within the group. Of the several clustering methods used to generate biomic dissimilarity dendrograms from the dissimilarity matrix, the UPGMA clustering method produces the biomic dendrogram with the greatest r_{coph} value of 0.879 (Fig. 53). Biomic dendrograms produced from complete-linkage clustering and single-linkage clustering (not shown) have lower r_{coph} values of 0.850 and 0.855, respectively. In the UPGMA biomic dendrogram, *D. carinata* and *D. carinulata* are the most similar in biomic profiles. The close relationship in biomes inhabited by *D. carinata* and *D. carinulata* can be related to these species having the greatest degree of sympatry and syntopy in the *D. elongata* group (Table 8, Map 1). *Diorhabda meridionalis* is partially sympatric with *D. carinata* and is grouped next followed by *D. sublineata*. *Diorhabda elongata* is grouped separately from all other tamarisk beetles.

We also test for a positive correlation in the dissimilarities in biomic profiles of the *D. elongata* group (Table 10) to dissimilarities in key morphological characters of the genitalia (Table 6, discussed previously). The biomic Bray-Curtis dissimilarity matrix of the *D. elongata* group (Table 10) is not significantly positively correlated with the genitalic average taxonomic dissimilarity matrix (Table 6) ($r_M = -0.40559$, $P[\text{random } r_M \geq \text{observed } r_M] = 0.9211$ with 9,999 permutations, Mantel Test; NTSYS Matrix Comparison Plot [MXCOMP] module [Rohlf 2006]). In other words, we find no significant positive correlation between the similarity in biomes inhabited by the five *Diorhabda* species and similarities in their genitalia. Instead, genitalic similarity tends to be negatively correlated with biomic similarity. This negative correlation is seen in species pairs such as *D. carinata*/*D. carinulata*, which are similar in biomic profiles but dissimilar in genitalic character profiles, and *D. carinata*/*D. sublineata*, which are different in biomic profiles, but similar in genitalic character profiles (Figs. 49 and 52; see **Discussion—Stenophenetic Analysis** above). An exception to genitalic similarity more greatly differing biomically is found in the species pair *D. carinulata*/*D. meridionalis*, which are both common in the Deserts and Xeric Shrublands biome. However, *D. carinulata* and *D. meridionalis* are parapatric (Map 4), and the apparent biogeographic distinctiveness of these species probably results from different preferences for latitude and distance to the ocean within the desert biome (discussed later; see Figs. 51–52). Further ecogeographic studies in the *D. elongata* group should include testing for a negative correlation between morphological similarity and a profile of a variety of climatic variables.

The combined biomic profiles of the *D. elongata* group (Table 9) and tamarisks invasive in North America (Table 11) are used to generate a Bray-Curtis dissimilarity matrix (Table 12) in order to assess similarities in biomic profiles among *Diorhabda* and *Tamarix* together. Two biomic dissimilarity dendrograms from the dissimilarity matrix that are produced using the UPGMA clustering method have the greatest r_{coph} value of 0.881 (one dendrogram is shown in Fig. 54). Several biomic dendrograms produced from complete-linkage clustering and single-linkage clustering (not shown) have lower r_{coph} values of 0.841 and 0.808, respectively. The two UPGMA biomic dendrograms differ only in alternating the places of *T. gallica* and *D. elongata* (Fig. 54). In these dendrograms, *D. carinulata*, *D. carinata*, *T. ramosissima*, and *T. austromongolica* form a group similar in biomic profiles. *Diorhabda elongata*, *T. parviflora*, and *T. gallica* also form a group associated with *T. chinensis*. *Diorhabda meridionalis* and *T. canariensis* form a group from which *D. sublineata* occurs next up the tree.

In order to display spatial relationships in biomic profiles among the *Diorhabda* and *Tamarix* species, a three dimensional principle coordinate analysis (PCoA) scatter plot (Fig. 55) is computed from the biomic Bray-Curtis dissimilarity matrix for *Diorhabda* and *Tamarix* (Table 12). Visual groupings of the *Diorhabda* and *Tamarix* species generally coincide with relationships in the biomic dissimilarity dendrogram

(Fig. 54). The two groupings of *D. elongata*/*T. gallica*/*T. parviflora* and *D. meridionalis*/*T. canariensis* are the most distinct in the biomic PCoA scatter plot. The group of *D. carinata*/*T. ramosissima*/*D. carinulata*/*T. austromongolica* is also evident, but less distinct. The taxa of *D. sublineata* and *T. aphylla* are more isolated as in the biomic dendrogram. The influence or loadings of the different biomes on PCoA axes are computed as Spearman rank-order coefficients (Table 13—Spearman rank-order correlation coefficients) for ranks of species in biomes (from Tables 9 and 11) versus ranks of species in PCoA axes (from Table 13—Eigenvectors). The *D. elongata*/*T. gallica*/*T. parviflora* group has high eigenvectors along PCoA axis one (Table 13—Eigenvectors, Fig. 55) which is strongly negatively correlated with the Desert and Xeric Shrublands, Temperate Grasslands, Savannas and Shrublands, and Montane Grasslands and Shrublands biomes (Table 13- Spearman rank-order correlation coefficients), but positively correlated for Mediterranean and Temperate Broadleaf and Mixed Forests biomes. In other words, deserts and grasslands are strongly contraindicative for the presence of species favoring Mediterranean and Temperate Broadleaf and Mixed Forests biomes, such as *D. elongata*, *T. gallica* and *T. parviflora*. In contrast, eigenvectors for *D. carinulata*, *D. carinata*, *T. ramosissima*, and *T. austromongolica*, are very low along axis one as these species have a strong presence in deserts and temperate and montane grasslands. Eigenvectors for *T. aphylla* and *D. sublineata* are highest along PCoA axis two which is strongly positively correlated with Flooded Grasslands and Savannas. The eigenvector for *D. carinata* is the highest along axis three which is strongly positively correlated with the Temperate Conifer Forests biome.

TABLE 12. Biomic Bray-Curtis dissimilarity matrix for the *Diorhabda elongata* species group and invasive North American *Tamarix* species (From Tables 9 and 11).^a

Species	Species											
	<i>D. elongata</i>	<i>D. carinata</i>	<i>D. sublineata</i>	<i>D. carinulata</i>	<i>D. meridionalis</i>	<i>T. ramosissima</i>	<i>T. chinensis</i>	<i>T. austromongolica</i>	<i>T. parviflora</i>	<i>T. gallica</i>	<i>T. canariensis</i>	<i>T. aphylla</i>
<i>Diorhabda elongata</i>	0.000											
<i>D. carinata</i>	0.188	0.000										
<i>D. sublineata</i>	0.184	0.217	0.000									
<i>D. carinulata</i>	0.213	0.116	0.189	0.000								
<i>D. meridionalis</i>	0.149	0.154	0.154	0.143	0.000							
<i>Tamarix ramosissima</i>	0.209	0.142	0.197	0.116	0.188	0.000						
<i>T. chinensis</i>	0.130	0.224	0.201	0.188	0.130	0.224	0.000					
<i>T. austromongolica</i>	0.239	0.174	0.170	0.083	0.159	0.174	0.201	0.000				
<i>T. parviflora</i>	0.059	0.179	0.206	0.205	0.137	0.288	0.116	0.232	0.000			
<i>T. gallica</i>	0.083	0.188	0.197	0.213	0.149	0.236	0.130	0.239	0.059	0.000		
<i>T. canariensis</i>	0.116	0.183	0.143	0.197	0.093	0.205	0.154	0.209	0.130	0.143	0.000	
<i>T. aphylla</i>	0.209	0.201	0.188	0.232	0.209	0.201	0.265	0.265	0.228	0.209	0.205	0.000

^a Matrix produced with NTSYSpc Interval Data (SIMINT) module (Rohlf 2006). Raw data matrix normalized with log (x + 1) transformation before dissimilarity matrix calculated.

Habitat Suitability Index Models. Descriptive statistics of the four biogeographic variables (biome, latitude, elevation and distance to ocean) for each *Diorhabda* species are displayed in Figures 51–52. These four descriptive statistics are used in calculating the five suitability indices (SI₁–SI₅; Figs. 56–58), and the final habitat suitability index (HSI; the geometric mean of SI₁–SI₅) in hand-fitted HSI models for each *Diorhabda* species. We subjectively adjusted parameters of the suitability indices in preliminary HSI models

(not shown) to reduce the visually assessed overall error in the final models (see **Materials and Methods**). Our sensitivity and elasticity analysis of the five suitability indices revealed that the categorical biomic indices SI_4 alone and both SI_4 and SI_5 together produce significantly higher model elasticities than do the continuous linear variable indices SI_1 , SI_2 , and SI_3 (Table 14).

TABLE 13. Data from principal coordinate analysis (PCoA) of biomic Bray-Curtis dissimilarity matrix (Table 12) for species of *Diorhabda* and *Tamarix*.^a

Category	Principal Coordinate Eigenvector Axis					
	1	2	3	4	5	6
Species	Eigenvectors					
<i>Diorhabda elongata</i>	0.093	0.010	0.020	0.025	0.020	0.031
<i>D. carinata</i>	-0.062	0.015	0.086	-0.053	0.003	0.019
<i>D. sublineata</i>	-0.021	0.032	-0.116	0.007	-0.006	0.037
<i>D. carinulata</i>	-0.102	-0.047	0.026	0.003	-0.015	-0.009
<i>D. meridionalis</i>	0.008	-0.029	-0.023	-0.046	0.017	-0.046
<i>T. ramosissima</i>	-0.105	0.027	0.040	0.063	0.049	0.002
<i>T. chinensis</i>	0.069	-0.083	-0.011	0.048	-0.009	-0.040
<i>T. austromongolica</i>	-0.111	-0.078	-0.038	-0.010	-0.034	0.015
<i>T. parviflora</i>	0.098	-0.020	0.039	-0.005	-0.010	0.015
<i>T. gallica</i>	0.100	0.004	0.027	-0.001	-0.042	0.012
<i>T. canariensis</i>	0.050	0.007	-0.042	-0.038	0.061	-0.003
<i>T. aphylla</i>	-0.017	0.163	-0.008	0.006	-0.034	-0.033
Eigenvalue	0.074	0.045	0.030	0.014	0.011	0.008
% Axis Loading	39.992	24.415	16.155	7.355	6.111	4.438
% Cumulative Axis Loading	39.992	64.407	80.561	87.916	94.028	98.881
Biome	Spearman rank-order correlation coefficients for ranks of species in biomes (from Tables 9 and 11) versus ranks of species in PCoA axes (from above eigenvectors)					
Deserts & Xeric Shrublands	-0.819*	0.307	-0.256	-0.307	0.205	-0.154
Temperate Grasslands, Savannas & Shrublands	-0.819*	-0.102	0.410	-0.102	-0.051	0.102
Montane Grasslands & Shrublands	-0.899*	0.238	0.185	-0.079	-0.159	-0.079
Mediterranean Forests, Woodlands & Scrub	0.618*	0.473	0.191	-0.366	0.069	0.321
Temperate Broadleaf & Mixed Forests	0.580*	0.161	0.470	-0.023	0.354	-0.304
Temperate Conifer Forests	-0.112	0.551	0.834*	0.156	-0.052	0.138
Tropical and Subtropical Dry Broadleaf Forests	-0.044	0.480	-0.044	0.131	-0.306	-0.306
Flooded Grasslands & Savannas	-0.181	0.816*	-0.225	0.524	0.402	0.189
Tropical & Subtropical Grasslands, Savannas & Shrublands	0.170	0.557	-0.184	0.198	-0.479	0.078

^a PCoA eigenvectors and eigenvalues computed (NTSYSpc Eigenvectors [EIGEN] module; Rohlf 2006) from double centered symmetric dissimilarity matrix (not shown; NTSYSpc Dcenter module). Spearman rank-order correlation coefficients with asterisk are significant ($P < 0.05$; Proc Corr; SAS Institute 2005). See Figure 55 for biomic PCoA scatter plot of the first three axes.

Our final HSI models for the *D. elongata* group in the Palearctic (Maps 8 and 9) are generally accurate in estimating the optimal native range for each *Diorhabda* species. However, the models overestimate the optimal native ranges in some cases such as for *D. elongata* in France, Spain, and northwest Africa where *D. sublineata* dominates (Map 8a) and for *D. sublineata* in southeastern Europe from which only *D. elongata* is known (Map 8c). The domination of either *D. elongata* or *D. sublineata* in parapatric areas of similar suitability could be related to potentially strong competitive interactions between these species.

TABLE 14. Sensitivity and elasticity ($\bar{x} \pm SD$) of habitat suitability indices (HSI) for the *Diorhabda elongata* species group as influenced by suitability indices (SI) for HSI models with and without the biomic relative suitability index (SI₅).^a

Suitability index	n	Sensitivity		Elasticity	
		HSI models without SI ₅	HSI models with SI ₅	HSI models without SI ₅	HSI models with SI ₅
SI ₁ , SI ₂ or SI ₃ (<i>D. elongata</i> group)	8	0.131 ± 0.132 a	0.122 ± 0.134 a	0.303 ± 0.306 a	0.281 ± 0.310 a
SI ₄ or SI ₄ /SI ₅					
<i>Diorhabda elongata</i>	8	0.118 ± 0.087 a	0.163 ± 0.118 a	0.435 ± 0.322 b	0.686 ± 0.495 b
<i>D. carinata</i>	8	0.127 ± 0.082 a	0.184 ± 0.090 a	0.328 ± 0.211 b	0.490 ± 0.238 b
<i>D. sublineata</i>	8	0.118 ± 0.076 a	0.154 ± 0.113 a	0.404 ± 0.258 b	0.556 ± 0.409 b
<i>D. carinulata</i>	8	0.133 ± 0.065 a	0.190 ± 0.084 a	0.433 ± 0.210 b	0.652 ± 0.289 b
<i>D. meridionalis</i>	8	0.123 ± 0.082 a	0.181 ± 0.109 a	0.395 ± 0.264 b	0.650 ± 0.391 b
Total ^b	160	0.129 ± 0.114 a	0.135 ± 0.122 a	0.311 ± 0.279 a	0.363 ± 0.340 a

^a Means of a given variable and the same sample size followed by the same letter are not significantly different ($P > 0.05$; Fisher's Protected LSD Test using PROC GLM-LSMEANS test; SAS Institute 2005). Sensitivities and elasticities are calculated across eight possible values ranging from 0.0 to 1.0 for the analyzed suitability index while the other indices are held constant at 0.5. For the continuous variables SI₁, SI₂ and SI₃, eight values are chosen at equal intervals of 0.125 (0.0, 0.125, 0.250, ... 1.0) and these do not vary between species. For the categorical variables SI₄ and SI₅, the eight fixed possible values (from Figs. 57B and 58) vary between species, and SI₄ and SI₅ vary directly with one another and are considered together in calculating sensitivity and elasticity.

^b Total sample size (n) = five species × four indices × eight values per index = 160.

The estimated North American ranges of the various *Diorhabda* spp. vary widely (Maps 10 and 11). The HSI model for *D. elongata* correctly predicts both the high suitability of the Cache Creek, California site and the low suitability of the Artesia, New Mexico and Lake Meredith, Texas sites. However, our *D. elongata* HSI model underestimates the suitable habitat at sites in west Texas at Big Spring, Imperial, and Pecos, where *D. elongata* has established well but where the model continentality suitability index and biomic suitability indices are near zero (Map 10a). The HSI model for *D. carinulata* correctly predicts the high suitability of northern desert habitats in Nevada, Colorado and Wyoming, and additionally predicts suitable habitat in the northern Chihuahuan Desert. Our HSI models estimate that *D. carinata* should have the widest area of suitable habitat in North America (Map 10b), while *D. elongata* is estimated to have the smallest area (Map 10a). The wider area of suitability for *D. carinata* is related to its being the most eurybiomic species (see **Biogeography**—*General* above), giving it a wide tolerance in the biomic suitability indices (Figs. 57B and 58), and having a relatively wide tolerance in both the elevational and continentality suitability indices (Figs. 56B and 57A). The smaller estimated area of suitability for *D. elongata* in North America is related to it being among the most stenobiomic species, giving it a smaller tolerance for the biomic suitability indices (Fig. 57B and 58), and having a very narrow tolerance in the continentality index. *D. sublineata* is estimated to have a similar area of optimal suitability to *D. elongata* in Mediterranean biome along the Pacific coast, but has a

higher suitability for southern desert biomes (Map 10c). *D. meridionalis* is predicted to have the highest suitability in southern maritime desert habitats such as the Sonoran Desert and Tamaulipan Mezquital in southern Texas (Map 11b).

The composite maps displaying which *Diorhabda* spp. score within the top 15% of the maximum HSI value of any *Diorhabda* spp. are generally accurate in estimating which single species or multiple species dominate in any given area of their native range (Map 12). For example, both the dominance of *D. carinulata* in China and the northern part of its range, and the dominance of *D. carinata* in some grasslands of Central Asia are depicted fairly accurately. The composite HSI maps fail to depict the dominance of *D. sublineata* in France, Spain, and the coast of northwest Africa and the dominance of *D. elongata* in the northeastern Mediterranean, instead depicting both species as equally dominant in these areas.

The composite HSI maps for the *D. elongata* group for North America (Map 13) estimate *D. carinulata* as dominant or co-dominant with *D. carinata* in areas where it has established well above 38°N in temperate cold deserts such as the Great Basin Shrub Steppe, Colorado Plateau Shrublands and Wyoming Basin Shrub Steppe. *Diorhabda carinulata* and *D. carinata* are estimated as potentially dominating or co-dominating in temperate warm desert areas below 38°N such as the northern Mojave Desert, southern Colorado Plateau Shrublands, and the Trans-Pecos region of the Chihuahuan Desert. *Diorhabda carinata* is estimated to dominate in large areas of temperate grasslands in the Great Plains, such as the Western Short Grasslands (including where *D. carinulata* has established at Pueblo, Colorado) and Central and Southern Mixed Grasslands, and in temperate conifer forests, such as the Arizona Mountains Forests in Arizona and New Mexico (Map 13). Although *D. carinulata* is established in the Western Short Grasslands at Pueblo, Colorado, our model predicts that *D. carinata* is better suited to this habitat for which it is in a more optimal range in terms of biome (being a grassland), latitude, and distance to the ocean. Pueblo, Colorado falls within the HSI environmental envelope suitability score (SI_5) for *D. carinulata*, but the model map only displays *D. carinata* for Pueblo because this species is more than 15% higher in the overall optimality (SI_{10}) score. Introduction of southern climatypes of *D. carinulata* and *D. carinata* may speed their adaptation to areas south of 34°N (see further discussion in species accounts under **Potential in Tamarisk Biological Control**). *Diorhabda elongata* is correctly estimated as dominating the Mediterranean biome of northern California, including where it is established vigorously at Cache Creek. However, our models estimate that areas of west Texas, where *D. elongata* has also established well, are more suitable for *D. carinata* and *D. carinulata*. West Texas falls outside the environmental envelope suitability scoring (SI_5) for *D. elongata* in both biome (being in temperate grasslands) and distance to ocean limits (over 600 km from ocean versus a 255 km limit) (Table 7, Fig. 52). The environmental envelope suitability score portion of our HSI model underestimates the potential range of *D. elongata* in grasslands and desert of west Texas, but our overall HSI model score may still be accurate in predicting that *D. carinata* and *D. carinulata* are better suited to these areas. *Diorhabda sublineata* is estimated as dominating in the Mediterranean biome in California below 37°N and the Chihuahuan Desert below 29°N. *Diorhabda meridionalis*, a species with a higher preference for maritime subtropical deserts between 26–31°N, is estimated as dominating over most of the southern Sonoran desert and Tamaulipan Mezquital xeric shrubland.

We consider the estimations of these hand-fitted HSI models as first rough approximations of the optimal tamarisk beetle species for various Old World and New World tamarisk habitats. The descriptive statistics used in calculating HSI grids could change substantially for some *Diorhabda* species with additional distribution data from under-collected areas. Complex interactions of the biogeographic variables we examined between both one another and unexamined bioclimatic variables probably occur, especially near environmental extremes for each species or in novel environments such as North America. Bioclimatic variables are among the best predictors of species distributions and further studies of the distributions of tamarisk beetles are planned using climatic data with species distribution models designed for presence-only data (e.g., Elith *et al.* 2006).

More detailed comparisons of the descriptive statistics for biogeographic variables among *Diorhabda* species are found in the species accounts below under the heading *Biogeography - Comparative*. Discussion of these results regarding biological control of tamarisk appear under the heading *Potential in Tamarisk Biological Control* for each species and in the concluding section, *Implications Regarding Biological Control of Tamarisk*

Key to the Sexes of the *Diorhabda elongata* Group: Adult External Characters

1. Distinct apical notch present on last visible abdominal sternite (Fig. 10). Third bi-lobed tarsomere of foretarsus 0.48–0.65 times the length of the fifth (final) tarsomere (Fig. 12) male
- Apical notch absent on last visible abdominal sternite (Fig. 11). Third bi-lobed tarsomere of foretarsus 0.28–0.44 times the length of the fifth tarsomere (Fig. 13) female

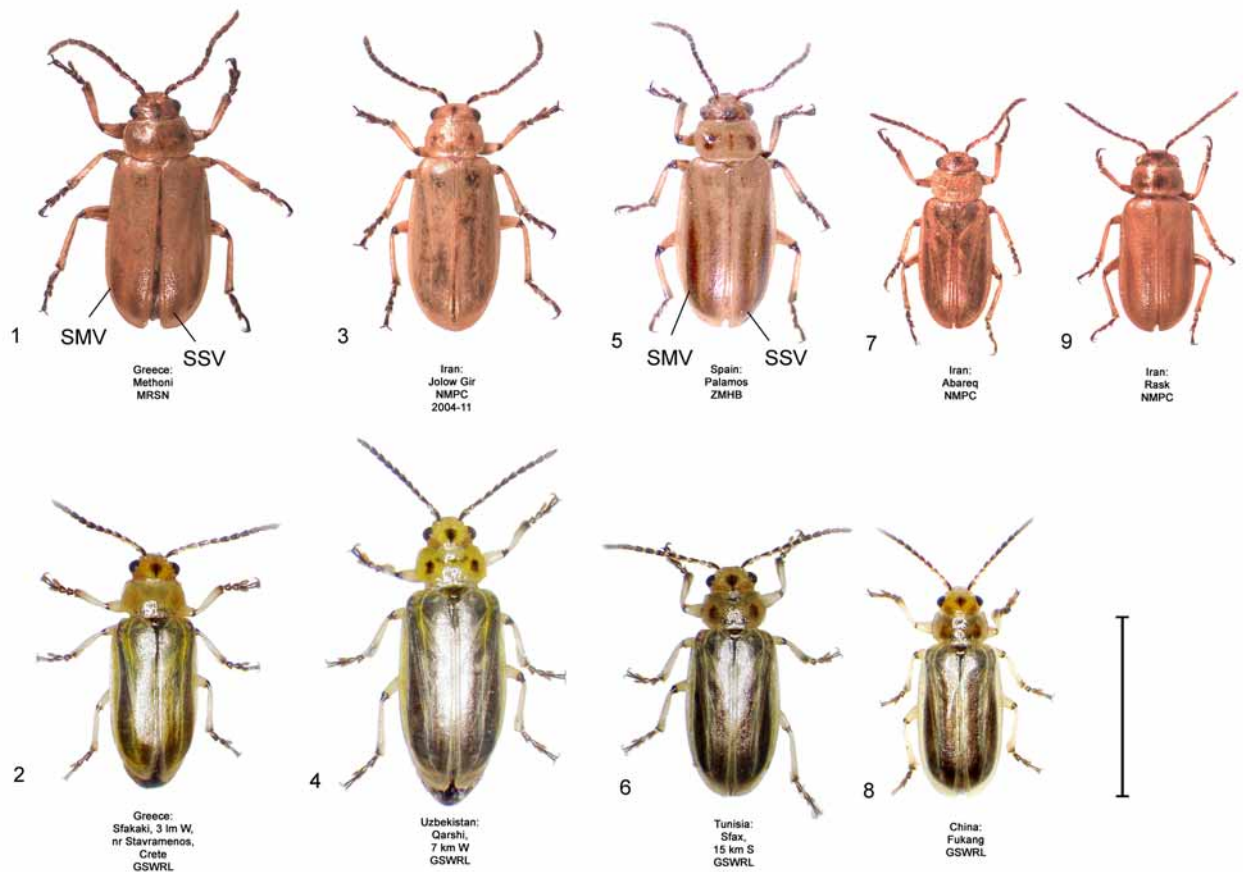
Key to the Species of the *Diorhabda elongata* Group: Adult Males

1. Elongate (ventral) endophallic sclerite (EES) armed with spines on blade (SL) extending over an area less than or equal to 0.16 times (or less than about one fifth) the length of the sclerite, and blade (LB) extending less than or equal to 0.42 times the total length of the sclerite; EES never bearing a lateral appendage, lateral notch (pointed basally), or hooked apex (Figs. 14, 19, 24). Palmate (dorsal) endophallic sclerite (PES) with distal margin usually broadly rounded and with one to six (commonly two to four) usually subdistal spines (SDS) (maximum of two distal spines, DS), and no lateral appendage (rarely with a lateral notch, LN) (Figs. 14, 29). Subsutural (SSV) and submarginal elytral vittae (SMV), if present, never extending from apical half of elytra into the basal half (Fig. 1). Length 5.3–6.8 mm. Circummediterranean, Portugal, Bulgaria, Macedonia, S. Russia (Dagestan Republic), W. North America (introduced), commonly collected from coastal C. Turkey to Italy *elongata* (Brullé)
- Elongate endophallic sclerite armed with spines on blade extending over an area greater than or equal to 0.31 times (or greater than about one third) the length of the sclerite, with blade extending greater than or equal to 0.43 times the total length of the sclerite; EES sometimes bearing a lateral appendage (LA), lateral notch (LN, pointed basally) or hooked apex (HA) (Figs. 15–18, 20–23, 25–28). Palmate endophallic sclerite with distal margin truncate serrate and with two to six (commonly three to five) usually distal spines (maximum one spine subdistal) and a lateral appendage (Figs. 15–16, 30–31), or with distal margin narrowly or acutely rounded and one or two small subdistal spines and no lateral appendage (sometimes with lateral notch) (Figs. 17–18, 32–33). Subsutural and submarginal elytral vittae, if present, often extending from apical half of elytra into the basal half (Figs. 5, 9). Length 4.2–7.3 mm. Portugal, Spain, France, N. Africa, Senegal, Yemen, S. Ukraine, S. Russia, Turkey, Syria, Transcaucasus, Iraq, Iran, C. Asia, Pakistan, N.W. and N.C. China, S.W. Mongolia, W. North America (introduced) 2
- 2(1). Palmate endophallic sclerite bearing a strong lateral appendage and its distal margin truncate-serrate with two to six (commonly three to five) usually distal spines (maximum one spine subdistal) (Figs. 15–16, 30–31). Elongate endophallic sclerite with spines along blade often irregularly spaced with conspicuous gaps (Figs. 15–16, 20–21). Length 5.0–7.3 mm. Portugal, Spain, France, N. Africa, Senegal, Yemen, S. Ukraine, Turkey, Syria, Transcaucasus, C. Asia (east to N.W. China and Pakistan), Iraq, Iran, W. North America (introduced) 3
- Palmate endophallic sclerite never bearing a lateral appendage (rarely bearing a lateral notch) and its distal margin narrowly or acutely rounded, with one or two small subdistal spines that may project beyond the distal margin (Figs. 17–18, 32–33). Elongate endophallic sclerite with spines usually evenly and closely spaced along blade (Figs. 17–18, 22–23). Length 4.2–6.1 mm. S. Russia, Transcaucasus, Syria, Iran, C. Asia, Pakistan, N.W. and N.C. China, S.W. Mongolia, W. North America (introduced) 4
- 3(2). Lateral appendage (LA) of elongate endophallic sclerite always present and connected to lateral appendage of palmate endophallic sclerite by thin linear connecting (lateral) endophallic sclerite (CES) (Figs. 16, 21, 31) (in some weakly sclerotized specimens, the lateral appendage of the elongate endophallic sclerite and the connecting endophallic sclerite may be faint and appearing to evanesce). Length 5.0–6.9 mm. Portugal, Spain, France, N. Africa, Senegal, Yemen, Iraq, W. North America (introduced) *sublineata* (Lucas)
- Lateral appendage of elongate endophallic sclerite usually absent or very weak and never connected to lateral appendage of palmate endophallic sclerite by a linear connecting endophallic sclerite (Figs. 15, 20, 30) (in some darkly sclerotized specimens, a faint line connecting the lateral appendages of the palmate and elongate

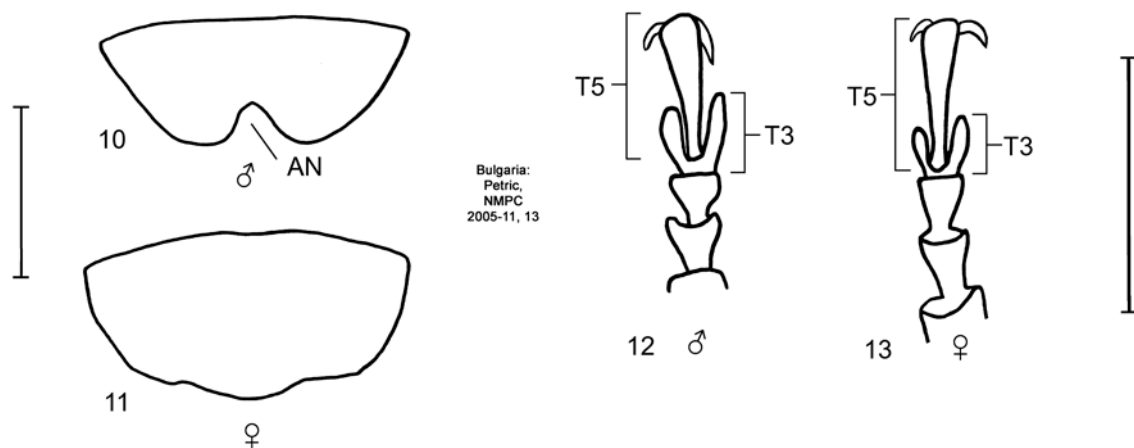
- endophallic sclerites should not be interpreted as a developed connecting endophallic sclerite). Length 5.1–7.3 mm. S. Ukraine, Turkey, Syria, Transcaucasus, C. Asia (east to N.W. China and Pakistan), Iraq, Iran, W. North America (introduced)..... *carinata* (Faldermann)
- 4(2). Apex of elongate endophallic sclerite not hooked in dorsal aspect, but often bearing a lateral notch (Fig. 27; LN); blade of elongate endophallic sclerite extending from 0.48–0.66 times the total length of the sclerite (Figs. 17, 22; LB). Ratio of width to length of palmate sclerite ranging from 0.61–1.02; distal margin of palmate endophallic sclerite acutely rounded (Figs. 17, 32). Length 4.6–6.1 mm. S. Russia, Transcaucasus, Iran, C. Asia, N.W. and N.C. China, S.W. Mongolia, W. North America (introduced) *carinulata* (Desbrochers)
- Apex of elongate endophallic sclerite strongly hooked in dorsal aspect (Fig. 28; HA); blade of elongate endophallic sclerite extending from 0.67–0.84 times the total length of the sclerite (Figs. 18, 23). Ratio of width to length of palmate sclerite ranging from 0.35–0.63; distal margin of palmate endophallic sclerite narrowly rounded (Figs. 18, 33). Length 4.2–5.6 mm. Syria, Iran, Pakistan *meridionalis* Berti & Rapilly

Key to the Species of the *Diorhabda elongata* Group: Adult Females

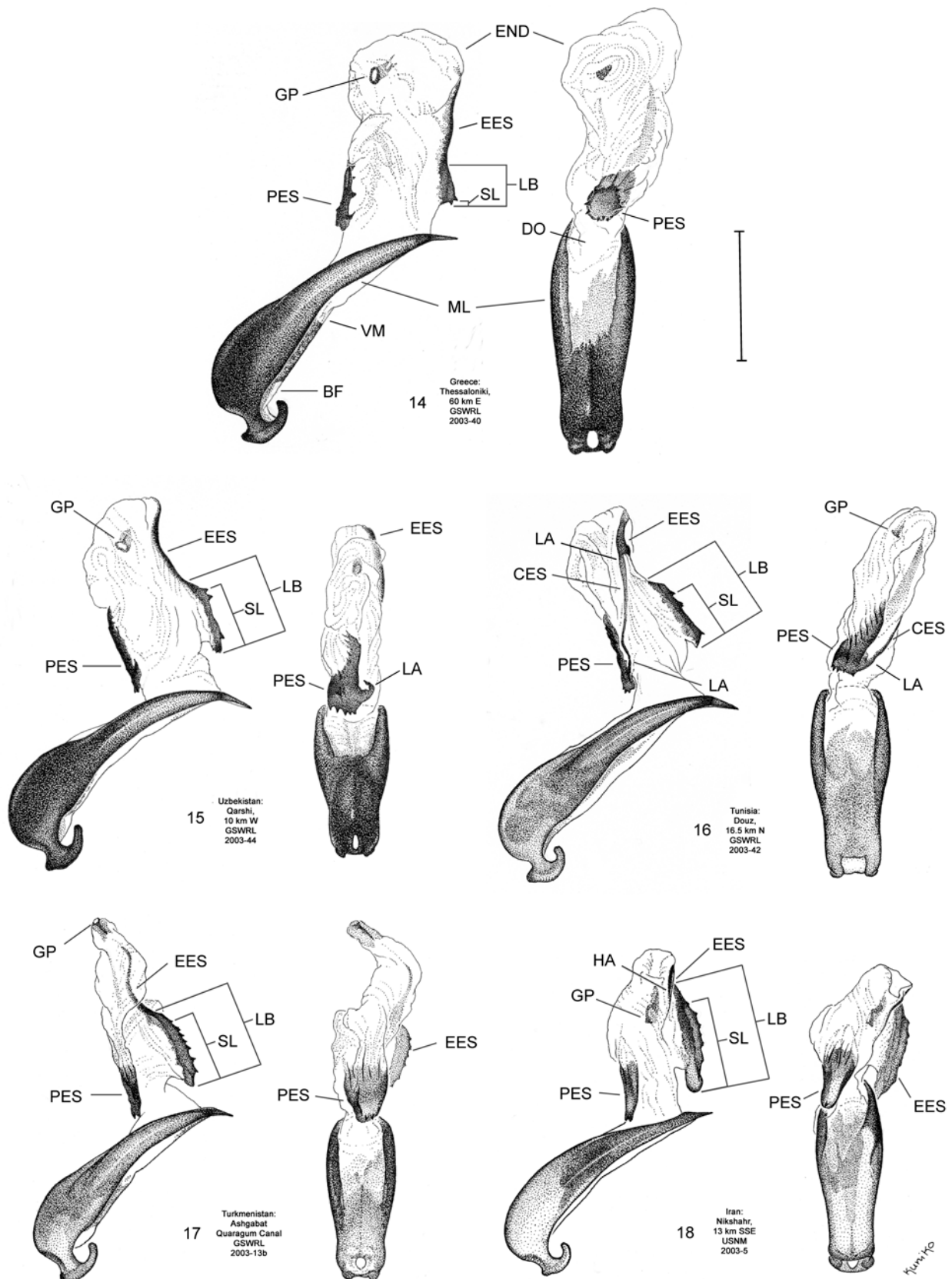
1. Vaginal palpi (VP) wider than long, with a width to length ratio (LP/WP) of 0.46–0.94 (Figs. 34–36). If width to length ratio of vaginal palpus 0.94, then the width of the widest lobe on the stalk (WLS) of internal sternite VIII (IS VIII) less than or equal to 0.10 mm (Figs. 34, 39). Length 4.9–8.4 mm. Circummediterranean, Senegal, Yemen, Portugal, Bulgaria, Macedonia, S. Ukraine, Turkey, Syria, Transcaucasus, C. Asia (east to Kazakhstan and Pakistan), Iraq, Iran, W. North America (introduced) 2
- Vaginal palpi about as long as wide or longer, with a width to length ratio of 0.94–1.36 (Figs. 37, 38). If width to length ratio of vaginal palpus 0.94, then the width of the widest lobe on the stalk of internal sternite VIII greater than or equal to 0.11 mm (Figs. 37, 42). Length 4.8–7.0 mm. S. Russia, Transcaucasus, Syria, Iran, C. Asia, Pakistan, N.W. and N.C. China, S.W. Mongolia, W. North America (introduced) 5
- 2(1). Vaginal palpi (VP) broadly rounded (Fig. 34). Width of the widest lobe on the stalk (WLS) of internal sternite VIII (IS VIII) from 0.06–0.11 mm (Fig. 34, 39). Subsutural (SSV) and submarginal elytral vittae (SMV), if present, never extending from apical half of elytra into the basal half (Fig. 1). Length 5.8–7.7 mm. Circummediterranean, Portugal, Bulgaria, Macedonia, S. Russia (Dagestan Republic), W. North America (introduced), commonly collected from coastal C. Turkey to Italy..... *elongata* (Brullé)
- Vaginal palpi triangulate, narrowly rounded (Figs. 35–36). Width of the widest lobe on the stalk of internal sternite VIII from 0.08–0.18 mm (Figs. 35–36, 40–41). Subsutural and submarginal elytral vittae, if present, often extending from apical half of elytra into the basal half (Fig. 5). Length 4.9–8.4 mm. Portugal, Spain, France, N. Africa, Senegal, Yemen, S. Ukraine, Turkey, Syria, Transcaucasus, C. Asia (east to N.W. China and Pakistan), Iraq, Iran, W. North America (introduced) 3
- 3(2). Stalk of internal sternite VIII (IS VIII) with tips of both lobes (TL) strongly curved inward away from apical lobe, and tips of lobes rounded or pointed, not quadrate (Fig. 40—Baghdad, Ashgabat, and Pul-e Charki). Length 5.1–8.4 mm. S. Ukraine, Turkey, Syria, Transcaucasus, C. Asia (east to N.W. China and Pakistan), Iraq, Iran, W. North America (introduced)..... *carinata* (Faldermann)
- Stalk of internal sternite VIII with tip of at least one lobe not strongly curved inward away from apical lobe, and tips of lobes rounded, quadrate or pointed (Figs. 35–36, 40 – Lagodekhi and Ardanuc, 41 – Biskra, Tamri, Ndiol, and Perpignan) 4
- 4(3). Stalk of internal sternite VIII (IS VIII) with tips of lobes (TL) either not curved or curved outward towards apical lobe, and tips of lobes rounded or quadrate, not pointed (Fig. 41- Ndiol, Perpignan, Kom Ombo). Length 4.9–7.4 mm. Portugal, Spain, France, N. Africa, Senegal, Yemen, Iraq, W. North America (introduced) *sublineata* (Lucas)
- Stalk of internal sternite VIII with tip of at least one lobe curved at least slightly inward away from apical lobe, and tips of lobes rounded, quadrate or pointed (Figs. 35–36, 40 – Lagodekhi and Ardanuc, 41 – Biskra and Tamri). Length 4.9–8.4 mm. (Iraq is area of range overlap) *carinata* (Faldermann) and *sublineata* (Lucas)
- 5(1). Width of stalk (WST) of internal sternite VIII (IS VIII) 0.36–0.57 mm and this width 0.49–0.77 times the width of the apical lobe (WAL) (Figs. 37, 42). Length 5.0–7.0 mm. S. Russia, Transcaucasus, Iran, C. Asia, N.W. and N.C. China, S.W. Mongolia, W. North America (introduced) *carinulata* (Desbrochers)
- Width of stalk of internal sternite VIII 0.22–0.33 mm and this width 0.33–0.48 times the width of apical lobe (Figs. 38, 43). Length 4.8–6.4 mm. Syria, Iran, Pakistan *meridionalis* Berti & Rapilly



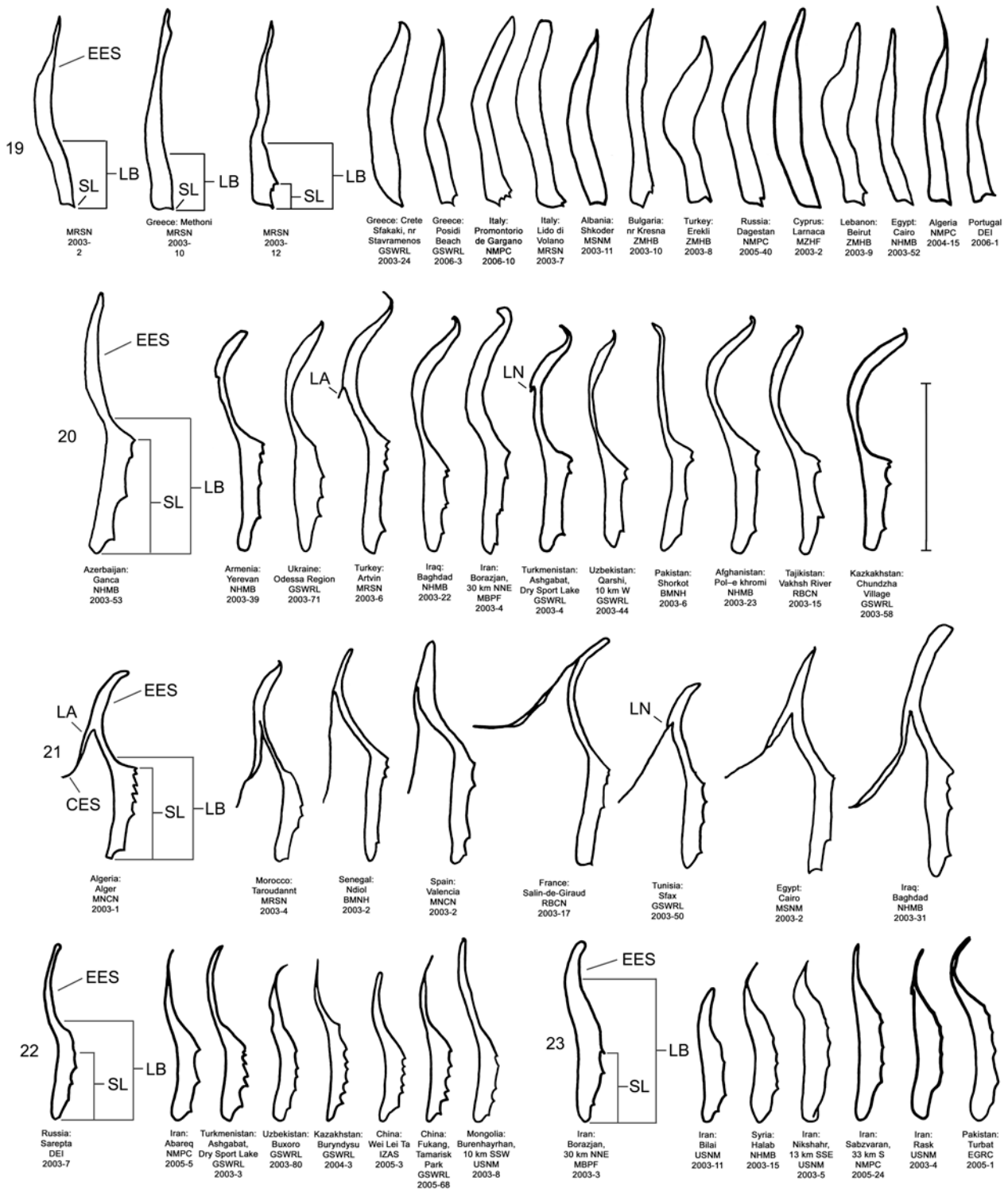
FIGURES 1–9. Dorsal habitus of males (dead - top row, living - bottom row) of the *Diorhabda elongata* species group (tamarisk beetles): 1–2—*D. elongata* (Mediterranean tamarisk beetle), 3–4—*D. carinata* (larger tamarisk beetle), 5–6—*D. sublineata* (subtropical tamarisk beetle), 7–8—*D. carinulata* (northern tamarisk beetle), 9—*D. meridionalis* (southern tamarisk beetle). SSV—subsutural elytral vitta, SMV—submarginal elytral vitta. Scale bar 5.0 mm.



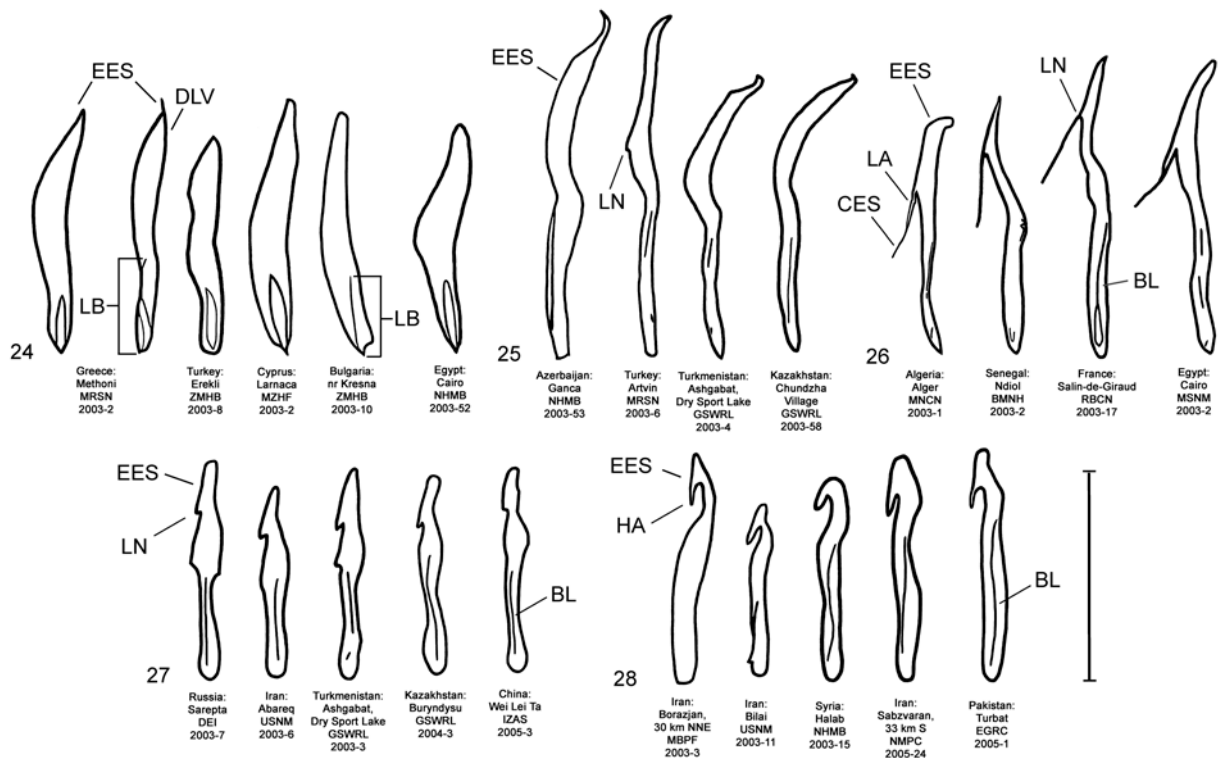
FIGURES 10–13. Sexual dimorphism in *Diorhabda elongata*: 10—male last visible sternite, 11—female last visible sternite, 12—male foretarsus, 13—female foretarsus. AN—apical notch, T3—third bi-lobed tarsal segment, T5—fifth tarsal segment. Scale bars 1.0 mm.



FIGURES 14–18. Male genitalia: median lobe (ML) of aedeagus with everted endophallus (END; uninflated) (lateral and dorsal views). 14—*Diorhabda elongata*, 15—*D. carinata*, 16—*D. sublineata*, 17—*D. carinulata*, 18—*D. meridionalis*. BF—basal foramen (or basal orifice), CES—connecting endophallic sclerite, DO—dorsal ostium (or apical orifice); EES—elongate endophallic sclerite, GP—gonopore, LA—lateral appendage, LB—length of blade, PES—palmate endophallic sclerite, SL—length of spined area of blade, VM—ventral membrane. Scale bar 1.0 mm.



FIGURES 19–23. Elongate (ventral) endophallic sclerite (lateral view) with connecting (lateral) endophallic sclerite (dorsal view, when present). 19—*Diorhabda elongata*, 20—*D. carinata*, 21—*D. sublineata*, 22—*D. carinulata*, 23—*D. meridionalis*. CES—connecting endophallic sclerite, EES—elongate endophallic sclerite, LA—lateral appendage, LB—length of blade, LN—lateral notch, SL—length of spined area of blade. Scale bar 1.0 mm.



FIGURES 24–28. Elongate (ventral) endophallic sclerite (dorsal views and a single dorso-lateral view [DLV]). 24—*Diorrhabda elongata*, 25—*D. carinata*, 26—*D. sublineata*, 27—*D. carinulata*, 28—*D. meridionalis*. BL—blade, HA—hooked apex, CES—connecting endophallic sclerite (partial), EES—elongate endophallic sclerite, LA—lateral appendage, LB—length blade, LN—lateral notch. Scale bar 1.0 mm.

***Diorrhabda elongata* (Brullé, 1832)**

Mediterranean tamarisk beetle

(Figs. 1, 2, 10–13, 14, 19, 24, 29, 34, 39, 44)

Galeruca elongata Brullé, 1832:271 (Type locality: Morée [Pelopónnisos peninsula, Greece]; Reiche and Saulcy, 1858:42 (part, France, Italy, Greece, Turkey, Syria, Lebanon [then under Syria], Egypt, Algeria, as *Galleruca*); Joannis, 1866:83 (part, Greece, Cilicia [Turkey], Lebanon [then under Syria], as *Galleruca*).

Galeruca costalis Mulsant, Mulsant and Wachanru, 1852:176 (Type locality: Cilicia [in southwest Turkey], as *Galleruca*); Reiche and Saulcy, 1858:42 (established synonymy, as *Galleruca*); Wilcox, 1971:63 (world catalog).

Diorrhabda elongata: Weise, 1883:316 (part); 1893:635 (part; Italy, coastal env. Trieste), 1893:1132 (part, taxonomy), 1924:78 (part, world catalog, coastlands of Mediterranean Sea), 1925:225 (part, Egypt, area of Mediterranean Sea); Heyden *et al.*, 1891:375 (part, catalog for Europe and Caucasus, southern Europe); Bedel, 1892:158 (part, France, as *Dirrhabda*); Winkler, 1924–1932 (part, Palearctic catalog, Mediterranean region); Corrêa de Barros, 1924:9 (part, Portugal); Peyerimhoff, 1926:359 (part, Algeria, hosts); Laboissière, 1934:53 (part, France); Porta, 1934:317 (taxonomic keys, Italy); Ogloblin, 1936:79 (part, Italy [Trieste], Greece, Turkey, Syria, Lebanon [Palestine], S. Russia); Kerville, 1939:107 (Turkey, env. Smyrna); Hopkins and Carruth, 1954:1129 (part, Spain, host); Pavlovskii and Shtakelberg, 1955:566 (part, Mediterranean region, southwest Russia, as *Dirrhabda*); Torres Sala, 1962:327 (part, Comunidad Valenciana, Spain); Lopatin, 1967:441 (Lebanon, dunes south of Beirut); Tomov, 1969:181 (Bulgaria), 1979:165 (biology, Bulgaria), 1984:377 (part, Turkey); Jolivet, 1967:331 (part, Mediterranean, hosts); Zocchi, 1971:86 (part, Italy); Wilcox, 1971:63 (part, world catalog); Gerling and Kugler, 1973:20 (Israel [sic; should read Turkey]); Warchalowski, 1974:509 (Bulgaria, as *Dirrhabda*), 2003:328 (part, taxonomic keys, Mediterranean region, Caucasus); Tomov and Gruev, 1975:146 (Turkey); Georghiou, 1977:47 (Cyprus); Lundberg *et al.*, 1987b:126 (Sicily); Petitpierre, 1988:93 (part, Spain); Regalin, 1997:69 (Crete); Gruev and Tomov, 1986:103 (Bulgaria), 1998:70 (part, Bulgaria, Mediterranean); Biondi *et al.*, 1995:12 (Italy); Kovalev, 1995:78 (part, southwest Palaeartic); Campobasso *et al.*, 1999:145 (part, host, Europe and Middle East); Lair and Eberts, 2001:1 (introduction plans, north Texas); Aslan *et al.* 2000:30 (part, Turkey); Anonymous, 2001:52N (part, southern Europe); Chatenet, 2002:223 (part, Italy, France, Spain, Algeria); DeLoach *et al.*, 2003a:229 (part, Greece), 2003b:126 (part, host range,

ecology, Italy, Crete, Turkey), (2008, in prep.) (part, Greece); Gök and Çilbırođlu 2003:66 (Turkey), 2005:14 (Turkey); Milbrath *et al.*, 2003:225 (part, Greece); Riley *et al.*, 2003:69,189 (part, catalog North America [introduced]); Bieńkowski, 2004:76 (part, keys, eastern Europe [Southern Russia]); DeLoach and Carruthers, 2004a:13, 2004b:311 (part, Greece); Gök and Duran, 2004:17 (part, Turkey); Lopatin *et al.*, 2004:127 (part, Mediterranean); Dudley, 2005a:13, 2005b:42N (part, biological control, ex: Greece); Carruthers *et al.* 2006:71, 2008:262 (part, biological control, ex: Greece); Herr *et al.* 2006:148 (host specificity, Crete); Milbrath and DeLoach, 2006a:32, 2006b:1379 (part, host specificity, Crete); Milbrath *et al.*, 2007 (part, host specificity, biology, Crete); Dudley *et al.*, 2006:137 (releases in California, Crete); Everitt *et al.* (2007) (remote sensing, Texas, Crete); Hudgeons *et al.*, 2007a:157 (establishment in Texas, Crete), 2007b:215 (tamarisk damage in Texas, ex: Crete); Mityaev and Jashenko, 2007:145 (biological control, ex: Greece); DeLoach (2008); Moran *et al.* (in press) (host range in Texas, Crete); Bean and Keller (in prep.) (diapause induction, Crete); Dalin *et al.* (in press) (host range; Crete); Thompson *et al.* (in prep.) (part, laboratory hybridization, Crete).

Diorhabda elongata ab. *carinata*: Porta, 1934:317 (keys, Italy).

Male. Genitalia. *Diorhabda elongata* can be distinguished from all other members of the *D. elongata* group by the following combination of characters, the first two of which are unique among the tamarisk beetles: (1) the length of the spined area of the blade (SL) (armed with one to six [commonly one to three] spines) of the elongate endophallic sclerite (EES) is less than or equal to 0.16 times (or less than about one fifth) the length of the EES (Table 3; Figs. 14, 19, 48B); (2) the length of the blade of the EES (LB) is less than or equal to 0.42 times the length of the EES (Table 3; Figs. 14, 19, 24, 48A); (3) the EES lacks a lateral notch (pointed basally), lateral appendage or hooked apex (Figs. 14, 19); (4) the palmate endophallic sclerite (PES) lacks a lateral appendage, it is usually broadly rounded distally, and the one to six (commonly two to four) spines are usually subdistal with no more than two distal spines (Figs. 14, 29); and (5) the connecting endophallic sclerite is lacking. In the other four species of the *D. elongata* group, the length of the spined area of the EES (SL) (armed with three to seven spines) is greater than or equal to 0.31 times (or greater than about one third) the length of the EES (Table 3; Figs. 20–23, 48B), and the length of the blade of the EES is greater than or equal to 0.43 times the length of the EES (Table 3; Figs. 15–18, 20–23, 25–28, 48A). In *D. sublineata*, and sometimes *D. carinata*, the EES bears a lateral notch (pointed basally) or lateral appendage. In *D. meridionalis* the EES bears a hooked apex (Figs. 25–28). The PES always bears a lateral appendage and the distal margin is truncate serrate with usually more than two distal spines in *D. carinata* and *D. sublineata* (Figs. 15–16, 30–31). In *D. carinulata* and *D. meridionalis*, the distal margin of the PES differs from that of *D. elongata* in being narrowly or acutely rounded with one or two small subdistal spines (Figs. 17–18, 32–33). *Measurements.* See Tables 2 and 3.

Female. Genitalia. Female *D. elongata* may be distinguished from all other members of the *D. elongata* group by the following combination of characters in the vaginal palpi (VP) and internal sternite VIII (IS VIII): (1) the vaginal palpi are both broadly rounded and wider than long with a width to length ratio (LP/WP) of 0.52–0.94 (Fig. 34, Table 4), and (2) if the width to length ratio of the vaginal palpi is 0.94, then the width of the widest lobe of the stalk (WLS) of IS VIII is less than or equal to 0.10 mm (Fig. 34). In contrast to *D. elongata*, the vaginal palpi in *D. carinulata* (Fig. 37) and *D. meridionalis* (Fig. 38) are about as long as wide or longer with a width to length ratio of 0.94–1.36 (Table 4). If the width to length ratio of the vaginal palpus is 0.94 in *D. carinulata*, then the width of the widest lobe of IS VIII is greater than or equal to 0.11 mm (Fig. 37). The vaginal palpi of *D. carinata* and *D. sublineata* differ in being narrowly rounded and triangulate (Figs. 35–36). In addition, the width of the widest lobe of the stalk of IS VIII is generally smaller in *D. elongata* (range 0.06–0.11 mm; Fig. 34) compared to *D. carinata* (range 0.11–0.17; Fig. 35) and *D. sublineata* (range 0.08–0.18 mm; Fig. 36) (Table 4).

Measurements. See Tables 2 and 4.

Coloration. *Diorhabda elongata* commonly lacks elytral vittae, but submarginal and subsutural vittae in the apical half of the elytra (evanescent toward the basal half) are not uncommon (Fig. 1). In all other members of the *D. elongata* group, elytral vittae, when present, often extend into the basal half of the elytra (Figs. 5, 9). Live specimens of *D. elongata* possess greenish-yellow tinting along veins of the elytra, probably as a result of yellow hemolymph as seen in live inflated endophalli, and this gives adults an overall olivaceous

hue (Fig. 2). Living *D. carinata* have a lesser degree of greenish-yellow tinting (Fig. 4). Living *D. sublineata* (Fig. 6) and *D. carinulata* (Fig. 8) lack greenish-yellow tinting, probably as a result of white hemolymph seen in live inflated endophalli (also seen in *D. carinata*), and they appear more tannish-yellow in hue.

Type material. Brullé's collection from his expedition to Morée (= Pelopónnisos peninsula, Greece), which should include the type specimen(s) for *D. elongata*, was deposited in the Muséum National d'Histoire Naturelle in Paris, France (MNHN) (Groll 2006). A curator at MNHN communicated intent to inform us of the status of the type material and perhaps lend it for examination, but after four years, we have not heard of the status of the Brullé type material. Once it can be ascertained that the type material is lost, a neotype should be designated using a dissected male specimen from the type locality of Pelopónnisos, Greece. We studied the original description by Brullé (1832), based on an unspecified number of specimens, with the included color habitus illustration, and topotypes from the Pelopónnisos peninsula, Greece.

The location of type specimens of *Galeruca costalis* Mulsant (Mulsant and Wachanru 1852) is uncertain. Remaining portions of E. Mulsant's collection "Natural History of the Coleoptera of France" should be located at the l'Institution Sainte-Marie de Saint-Chamond (Loire), France (Groll 2006). We studied the original descriptions of *G. costalis* by Mulsant (Mulsant and Wachanru 1852) and topotypes from the Cilicia region of Turkey.

Material examined. 157♂♂ dissected (diss.), 85♀♀ diss., 127♂♂, 164♀♀. **ALBANIA:** 1♂ diss., Durazzo [41.32305°N, 19.44138°E], Lona-Rav., *Diorhabda elongata* det. Burlini 1967, MSNM [2003-08]; 1♂ diss., 1♂, 1♀, Elbasan [41.11250°N, 20.08222°E], *D. elongata*, USNM [2003-10]; 1♂ diss., Medua [Shengjin, San Giovanni di Medva; 41.81366°N, 19.5939°E], Matzenaver, *D. elongata* det. V. Zonfal, NMPC [2004-51]; 1♂ diss., Srutari [Shkoder; 42.0675°N, 19.5131°E], *D. elongata* det. Burlini 1967, MSNM [2003-11]; 1♀ diss., Scutari [Shkoder], Heyrevsky, NMPC [2006-06]; 1♂ diss., 1♀, Valona [Vlore; 40.46666°N, 19.48972°E], [19]08, H. Hopp, ZHMB [2003-04]; **ALGERIA:** 1♂ diss., [specific locality not given], Reitter, NMPC [2004-15]; **BOSNIA & HERZEGOVINA:** 1♂ diss., Veleš Planina [Velez Planina; 43.33°N, 18.0044°E], Herzegovina, 1879, Reitter, *D. elongata*, HNHM [2003-05]; **BULGARIA:** 1♂ diss., 1♂, 1♀, Burgas [42.5°N, 27.4667°E], 16-VII-1975, Vašárhelyi, *D. elongata* det. V. Tomov 1983, HNHM [2003-06]; 1♀ diss., Gara Pirin [Kresna; 41.7333°N, 23.1500°E], Kresna defile [Kresnenska Klisura or Kresna defile (gorge)], B. Kouřil, *Diorhabda* det. B. Kouřil, P9/46/62, NMPC [2005-25]; 1♂ diss., 1♀, Gara Sandanski [Sandanski; 41.5667°N, 23.2833°E], Struma [river], 20-VII-1956, L. Hoberlandt, NMPC [2006-04]; 1♂ diss., Kresna [41.7333°N, 23.1500°E], environs, Struma [river], 29-V-1984, U. Göllner, *D. elongata* det. V. Tomov, ZMHB [2003-10]; 1♂ diss., 1♂, 1♀, Kresnicko Def. [Kresnenska Klisura or Kresna defile (gorge); 41.8°N, 23.16667°E], VII-1932, Mac, Mař et Táb, NMPC [2006-05]; 1♀ diss., Kritschin [Krichim; 42.05°N, 24.4667°E], NHMB [2003-41]; 1♂ diss., Melnik [41.5167°E, 23.4°E], 23-V-1973, St. Gruszka & A. Warchalowski, GSWRL [2003-41]; 2♂♂ diss., 1♀ diss., Petric [42.6°N, 24.01667°E], 1932, D. Putkyně, *D. elongata* det. Sterba, NMPC [2004-24, 2005-11, 13]; 1♀ diss., Pomorie [42.55°N, 27.65°E], 9-V-1970, B. Gruev, *D. elongata* det. V. Tomov 1997, GSWRL [2003-46]; 1♂ diss., 3♂♂, 2♀♀, Sandanski [41.5667°N, 23.2833°E], Meridion., 10-VIII-1974, A. Warchalowski, GSWRL [2003-34, 1♂ diss.], DEI; 1♂ diss., 4♂♂, 4♀♀, Keretschkoi [Kirechdzhi Khask'oy is Sladun; 41.85°N, 26.4667°E], Macedonia, A. Schatzmayer, *D. elongata* det. Fleischer, DEI [2003-18]; **CROATIA:** 1♂ diss., Metkovic [Metkovi; 43.054167°N, 17.648333°E], Dalmatien, E.A. Bottcher (Berlin), 168, MZHF [2005-03]; 1♂ diss., Metkovich [Metkovi], Dalmatia, NHMB [2003-25]; 1♀ diss., 1♀, Opuzen [43.00972°N, 17.56555°E], 26-V-1974, G.J. Slob, RBCN [2003-07], ZMAN; 1♂ diss., 5♂♂, 10♀♀, Ušće Neretve D. [43.01917°N, 17.44389°E; Neretva river mouth], 8-IX-1948, Novak [ZMHB], *D. elongata* det. Novak, HNHM [2003-04], ZMHB [2♂♂, 4♀♀]; **CYPRUS:** 1♂ diss., [specific locality not given], 1876, L. Shrader, Coll. Kunnemann, DEI [2003-13]; 2♂♂ diss., 1♀ diss., 6♂♂, 5♀♀, Larnaka [Larnaca; 34.916667°N, 33.6333°E], 25-VI to 1-VII-1939, Håkan Lindb., *D. elongata* det. Harald Lindb. [3♂♂, NMPC; 1♂, 1♀, NHRS], MZHF [2003-02, 2005-01, 02], NMPC, NHRS; 1♂, 1♀, Larnaca, Kamares Aqueduct, 19-X-1932, A. Ball, *D. elongata* det. V. Laboissière 1939, IRSNB; 2♂♂ diss., 1♀ diss., 3♀♀, Mt. Arménien [35.2875°N, 33.525°E], NMPC [2004-02, 2005-01, 02]; **EGYPT:** 3♂♂ diss., 2♀♀ diss., 1♀, Cairo [Al Qahirah; 30.05°N, 31.25°E], NHMB [2003-16, 52, 2004-01a, 2005-02, 03];

GREECE: 1♂ diss., Agia Marina, Star Beach [35.5193°N, 23.9275°E], Crete, 10-IX-2001, R. & N. Carruthers, on *Tamarix* sp. foliage, EIWRU-2001-1016, USNM [2003-18]; 1♀ diss., 3♀♀, Ammos [36.91270°N, 27.28170°E], Kos [Island], 27-VIII to 1-IX 1981, T. Palm, MZLU [2005-08]; 6♂♂ diss., 2♀♀ diss., Astro Beach [37.4433°N, 22.74861°E], north of, Pelopónnisos, 25-V-2003, J. Kashefi, on *T. hampeana*, GSWRL [2004-10, 2005-38, 39, 41–45]; 1♀ diss., Athens environs [37.96138°N, 23.63888°E], Dr. Krüper, NHMB [2004-03]; 1♂, 2♀♀, b. Athens, v. O., Collectie C. et O. Vogt Acq. 1960, ZMAN; 1♂ diss., 1♂, 2♀♀, Athos [40.166667°N, 24.333333°E], Macedonia, Schatzmayer, Coll. V. Heyden, *D. elongata* det. Fleischer, DEI [2003-19]; 2♂♂ diss., 3♂♂, Athos, Macedonien, 1908, Schatzm., NHMB [2003-26, 2006-02]; 1♀ diss., 1♂, 4♀♀, Attica [Attiki; 38.083333°N, 23.5°E], Stussiner, O. Leonard, DEI [2003-15]; 1♂, 3♀♀, Attica, Reitter, Coll[ection] Kambersky, *D. elongata*, NMPC; 2♂♂ diss., 1♂, 2♀♀, Attica, Reitter, 269 [MZLU ♀] *D. elongata* Brulle Emm. Reitter [ZMAN; 1♂, 1♀], Collectie P.v.d. Wiel Acq. 1962 [ZMAN], MZLU, ZMAN [2008-05, 17], ZMHB [1♂]; 1♂, Attica, Witte, coll[ection] V. Heyden, DEI; 1♀, Attica, Hymettos [Mts.], Emge., ZMAN; 1♀, Attica, v. Oertzen, ZMAN; 1♂, Attika, ZMHB; 1♀ diss., 1♂, 1♀, Crete [specific locality not given], *D. elongata* det. K. Lopatin, HNHM [2005-01]; 1♀ diss., 1♀, Diakophto [Diakofto; 38.1795°N, 22.2001°E], Pelop., IV-1936, Mař et Táb., Coll[ection] Bartoň, NMPC [2004-34]; 1♀ diss., Dimilia [36.2834°N, 28.0085°E], Rhodes [island], 16-VII-1933, A. Mochi, *D. elongata* det. Burlini 1967, MSNM [2003-14]; 1♂ diss., Euboea [Evvia Island; specific locality not given; approx. loc.: 38.5200°N, 23.72000°E], Coll. Kraatz, DEI [2003-14]; 1♂ diss., 1♀, Fileremo [Filerimos Hill; 36.3985°N, 28.1382°E], Rodi [Rhodes], 22-IV-1932, A. 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Burlini 1967, MSNM [2003-09]; **MONTENEGRO**: 1♂ diss., Sutomore [42.14277°N, 19.04666°E], 22-V-1978, G.J. Slob, RBCN [2003-03]; **PORTUGAL**: 2♂♂ diss., [specific locality not given], Coll. Letzner, DEI [2003-10, 2006-01]; **RUSSIA**: 1♂ diss., Daghestan [Respublika Dagestan; specific locality not given], Leder. Reitter, 4358, Coll[ection] Kouril P5/46/62, NMPC [2005-40]; **SPAIN**: 2♀♀ diss., 1♀, Estepona [36.4333°N, -5.1333°W], Malaga, 15-II-1982, H. Teunissen, RBCN [2003-13, 16]; **SYRIA**: 1♂ diss., [specific locality not given], *D. e. var. carinata*, MNMS [2004-04]; 1♀ diss., [specific locality not given], *D. elongata* det. Le Moults, IRSNB [2006-11]; **TURKEY**: 1♂ diss., 1♀ diss., Adana [37.001667°N, 35.328889°E], *D. elongata* [1♂ diss., NHMB], HNHM [2005-02], NHMB [2003-10]; 3♂♂ diss., 1♀ diss., 3♀♀, Adana, Asia Minor, Sterba, *D. v. carinata* det. TJS [1♀ undiss.], NMPC [2005-08-10, 12]; 1♀, Adana, Asia Minor, H. Rolle, ZMHB; 1♂ diss., Alanya, 10 km west [36.6°N, 31.89°E], 18-VII-1972, [on *T. smyrnensis* (Gerling and Kugler 1973)], T18, TAUI [2003-04]; 1♀ diss., Anamur, 30 km west [36.0845°N, 32.6082°E], 17-VIII-1972, [on *T. smyrnensis* (Gerling and Kugler 1973)], T17, TAUI [2003-09]; 1♀ diss., Ankara [39.927222°N, 32.864444°E], V-1937, Dr. Vasvari, *D. elongata* det. K. Lopatin 1961, HNHM [2004-08]; 1♂ diss., 2♀♀, Bergama, 5 km north [39.1553°N, 27.1629°E], 24-VIII-1972, [on *T. smyrnensis* (Gerling and Kugler 1973)], T38, TAUI [2003-06]; 3♂♂ diss., 1♀ diss., 1♂, 1♀, Bürücek [Burucek; 37.35°N, 34.83333°E], Toros [Mt.], Anat[olia], 29-31-VII-1947, Exp. N. Mus. CSR,

NMPC [2004-08, 2005-07, 14, 15]; 1♀ diss., 1♂, Cordélio [Karsiyaka; 38.4614°N, 27.1119°E], *D. elongata* det. V. Laboissière 1939, IRSNB [2006-10]; 1♂ diss., 2♀♀, Ephesos [Selcuk; 37.9517°N, 27.3747°E], 18-V-1992, V. Nemeč, EGRC [2005-03]; 1♂ diss., 2♂♂, Ereçkli [Ereçkli; 41.28944°N, 31.41805°E], Asia Minor, Bodemeyer, 824 [ZMHB], *D. elongata* [ZMHB], ZMHB [2003-08], NMPC; 1♂ diss., 2♀♀ diss., Eski-Chehir [Eskisehir; 39.77667°N, 30.52056°E], Asia Minor, Bodemeyer, NMPC [2004-29; 2005-29, 30]; 1♀ diss., Izmir, 10 km east [38.43°N, 27.19°E], 23-VIII-1972, [on *T. smyrnensis* (Gerling and Kugler 1973)], T41, TAUI [2003-08]; 1♂ diss., Kash [Kas], 30 km west [36.27°N, 29.333333°E], 20-VIII-1972, [on *T. smyrnensis* (Gerling and Kugler 1973)], T27, TAUI [2003-01]; 1♂ diss., Kassaba [Kasaba; 36.31111°N, 29.73472°E], Manisa Prov., Asia Minor, 1-VIII-1931, B.P. Uvarov, Brit. Mus. 1931-468, USNM [2004-01]; 1♂ diss., Malatya [38.353333°N, 38.311944°E], VI-1964, Seidenstücker, UH.G, DEI [2003-16]; 1♂ diss., 2♂♂, Ortakche [Ortakoy; 37.4167°N, 28.7167°E], east of Aydin on Menderes River, Asia Minor, 23-VII-1931, B.P. Uvarov, British Museum 1931-468 [ZIN], BMNH [2003-09], ZIN [1♂]; 2♀♀ diss., Selcuk, 10 km east [37.8871°N, 27.4106°E], 22-VIII-1972, [on *T. smyrnensis* (Gerling and Kugler 1973)], T37, TAUI [2003-05, 07]; 2♂♂ diss., Smyrna [Izmir; 38.407222°N, 27.150278°E], 1955, Erwerb, Coll. Brancsik, NHMB [2003-09, 11]; 1♂ diss., 5♀♀, Tarsus [36.91778°N, 34.89167°E], Asia Minor, Sterba, NMPC [2004-47]; 1♂ diss., 1♀ diss., 1♀, Turgutli [Turgutlu; 38.5008°N, 27.7058°E], 65 km east Izmir, 23-VIII-1972, [on *T. smyrnensis* (Gerling and Kugler 1973)], T40, TAUI [2003-02, 2004-01]; 1♂ diss., 1♀, Ushak, Abide [Usak; 38.68°N, 29.40805°E], 3-VI-1989, Kuff & Szailles, RBCN [2003-01]; 1♀ diss., Yeniköy [multiple possible geocoordinates], Toros [Mt.], Anat[olia], 30-VIII-1947, Exp. N. Mus. CSR, NMPC [2005-06]; **UNKNOWN COUNTRY**: 1♀ diss., Dobrujscha [Dobruja region; around border of Bulgaria and Romania by Black Sea; specific locality not given; app. location: 43.6843°N, 28.5364°E], *D. elongata*, 126, Coll. Schultheiss, DEI [2005-06]; 1♀ diss., Tichakir [geocoordinates not locatable], Tal Noda, Asia Minor [possibly an archaeological site near the Aegean Sea coast of Turkey], J. Weise collection, ZMHB [2003-07]; **UNITED STATES OF AMERICA** (introduced): **California: Yolo Co.**: 1♂ diss., Cache Creek near Rumsey [38.8895°N, -122.2333°W], 28-IX-2006, J. Herr, on *T. parviflora*, voucher [source: 3 km west Sfakaki (nr Stavramenos), Greece], GSWRL [2007-47]; **Texas: Howard Co.**: 1♂ diss., 4♂♂, 7♀♀, Higgins Ranch near Beals Creek, 32.251[069]°N, -101.386[506]°W, 8 km east of Big Spring, 18-VIII-2005, J.L. Tracy, on *T. chinensis/T. canariensis* [on regrowth following July defoliation by *Diorhabda*], voucher [source: 3 km west Sfakaki (nr Stavramenos), Greece], GSWRL [2006-11]; 5♂♂ diss., Higgins Ranch near Beals Creek, 32.24966°N, -101.38582°W, Big Spring, 1-IX-2006, J.L. Tracy, on *Tamarix chinensis/T. canariensis*, GSWRL [2008-01, 02, 03, 04, 05]; **Potter Co.**: 1♂ diss., 9♂♂, 5♀♀, Lake Meredith National Recreation Area, 35.52774°N, -101.76322°W, 11-IV-2006, V. Carney, on *T. ramosissima*, voucher [source: Posidi Beach, Greece], GSWRL [2006-18].

Distribution. General. *Diorhabda elongata* was most frequently collected from Italy to Bulgaria and central Turkey, but it occurs sporadically elsewhere around the Mediterranean in Lebanon, Egypt, Algeria, Portugal and Spain, and near the Caspian Sea in southern Russia (Dagestan Republic). Its native distribution is restricted to countries bordering on the Mediterranean Sea and the additional countries of Portugal, Bulgaria, Macedonia, and Russia (Map 2). Previous reports for the general distribution of *D. elongata* (Weise 1924, Heyden *et al.* 1891, Winkler 1924–1932, Ogloblin 1936, Wilcox 1971, Warchalowski 2003, Lopatin *et al.* 2004) are accurate only in their inclusion of the Mediterranean region to southern Russia. Further collections should provide specific localities of *D. elongata* along coastal areas of Portugal, France, Romania (Dobruja region), Syria, Algeria, and southern Russia (Dagestan Republic). Additional collections could also reveal *D. elongata* as common in Slovenia and uncommon in Serbia, Georgia and the coastal areas of Azerbaijan, Tunisia, Libya and Morocco. The *D. elongata* group is not reported from Israel (Lopatin *et al.* 2003).

Confirmed Records. We have dissected specimens of *D. elongata* from the following countries with previous literature records (Map 2): Portugal (Corréa de Barros 1924), Spain (Hopkins and Carruth 1954, Torres Sala 1962, Petitpierre 1988), Italy (Reiche and Saulcy 1858, Weise 1893, Porta 1934, Zocchi 1971, Lundberg *et al.* 1987b, Biondi *et al.* 1995), Greece (Brullé 1832, Reich and Saulcy 1858, Regalin 1997),

Bulgaria (Tomov 1969, 1979, 1984; Warchalowski 1974; Gruev and Tomov 1986, 1998), Turkey (Reiche and Saulcy 1858; Ogloblin 1936; Kerville 1939; Gerling and Kugler 1973 [list on p. 20 should indicate Turkey (T), not Israel (blank) beside *D. elongata*]; Aslan *et al.* 2000; Gök and Çilbıroğlu 2003, 2005; Gök and Duran 2004), Russia (Ogloblin 1936), Cyprus (Georghiou 1977), Syria (Reiche and Saulcy 1858, Ogloblin 1936), Lebanon (Reiche and Saulcy 1858 [as Syria], Ogloblin 1936 [as Palestine], Lopatin 1967 [as Lebanon]), Egypt (Reiche and Saulcy 1858, Weise 1925), Algeria (Reiche and Saulcy 1858, Peyerimhoff 1926), and the United States (Texas, California; introduced; Map 7, see *Potential in Tamarisk Biological Control* below for more details) (Riley *et al.* 2003, DeLoach *et al.* in prep., Hudgeons *et al.* 2007a). We dissected *D. elongata* from a series of Beirut, Lebanon, identified as *D. elongata* by Lopatin (1967). A male *D. elongata* we dissected was collected in 1982 by Thure Palm from Fiumi di Pollina, Sicily, Italy, and it probably is associated with studies Palm co-authored reporting collections by himself and others (Lundberg *et al.* 1987a) of *D. elongata* on *T. gallica* at Fiumi di Pollina (Lundberg *et al.* 1987b).

New Records. We have dissected *D. elongata* from the following countries for which we find no previous specific reports in the literature: Croatia, Bosnia and Herzegovina, Montenegro, Macedonia (The Former Yugoslav Republic), and Albania.

Unconfirmed Records. We cannot confirm reports of *D. elongata* from Georgia (Reiche and Saulcy 1858, Lozovoi 1961) and Azerbaijan (Samedov and Mirzoeva 1985; Mirzoeva 1988, 2001). Because of the predominance of *D. carinata* in these areas, we consider these reports to primarily involve *D. carinata* (see *D. carinata*—Distribution below), and the presence of *D. elongata* needs further confirmation. However, we have dissected *D. elongata* from the Dagestan region of Russia along the Caspian Sea (Fig. 19—Dagestan) and suspect that it is present in Georgia and Azerbaijan. Reports of *D. elongata* in areas east of the Caspian Sea in central Asia (east of 50°E) (e.g., Lopatin, 1977a, Medvedev and Voronova 1977b, Bieńkowski 2004) should refer instead to *D. carinata* and *D. carinulata*.

France lies between two countries with confirmed host records, Italy and Spain (Map 2). Therefore, although we have not examined *D. elongata* from France, we still consider the general locality record of France as accurate (Reiche and Saulcy 1858, Bedel 1892, Laboissière 1934, Chatenet 2002). All locations from which specimens were dissected in Bulgaria (9), Greece (49; with the exception of a single male specimen of *D. carinata* considered as mislabeled from Attica, Greece), and Italy (15) were *D. elongata* and we consider all literature records of *D. elongata* from these countries as accurate (Map 2). We examined a specimen of *D. elongata* from Italy (ZMUH) with an identification label of *D. e. ab. carinata* by Laboissière and we consider Porta's (1934) report of *D. e. ab. carinata* in Italy to be *D. elongata*. In Turkey, *D. carinata* is found as far west as 41.5°E and it is found near the south Turkish border in Halab, Syria at 37°E longitude (Map 3). Therefore, we are only confident in accepting literature records of *D. elongata* in Turkey that are in the area west of 35°E longitude, from which we dissected *D. elongata* from all 21 available locations (Map 2).

Below are 13 unconfirmed locality records of *D. elongata* that we consider as valid (Map 2):

BULGARIA: Blagoevgrad environs, near Struma River [42.01670°N, 23.08000°E], on *Tamarix* (Tomov 1979); 1 specimen, Melnik, 4-V-1971, Stück (Warchalowski 1974) [*D. elongata* dissected from same location]; **GREECE:** Kaiafas [37.5167°N, 21.6000°E], Peloponnes [Pelopónnisos Peninsula], west coast, 24-V-1995 (Serge Doguet, Fontenay-sous-Bois, France, pers. comm.); Plakias [35.200°N, 24.400°E], Crete, 13-16-VI-1995; Rethimnon nom. [Rethymnon; 35.3647°N, 24.4714°E], Crete, 13-16-VI-1995; Sèlia [Sellia; 35.4000°N, 24.2330°E], Crete, 13-16-VI-1995, (Regalin 1997; on *Tamarix smyrnensis*); **ITALY:** Fiume de Pollina [38.01667°N, 14.6667°E], 15 km east Cefalu, Sicily, on *Tamarix gallica* [*D. elongata* dissected from same location]; Fiume de Tusa [38.01667°N, 14.2667°E], 21 km east Cefalu, Sicily, on *Tamarix gallica* (Lundberg *et al.* 1987b); Trieste environs [45.6395°N, 13.7876°E] (Weise 1893); **TURKEY:** Asagigökdere village [37.59722°N, 30.82833°E], Isparta Province, 650 m [elev.], 12-V-2000 (2♂♂, 3♀♀), on *Tamarix smyrnensis*, 2-VII-2000 (3♂♂, 4♀♀), 10-X-2000 (1♂, 1♀), 4-V-2001 (3♂♂, 3♀♀) (Gök and Çilbıroğlu 2003, Gök and Duran 2004); 4 specimens, Edirne [41.67440°N, 26.56080°E], 15 m [elev.], 6-V-1960 (Tomov and Gruev 1975); 10 specimens, Yozgat dintorm [39.8200°N, 34.8044°E], Yozgat [Ili], 1,300 m [elev.], 26-VI-1975, G. Osella (Tomov 1984).

Because of the proximity to locations of *D. carinata*, the following two unconfirmed distribution records of *D. elongata* from east of 35°E in Turkey are uncertain (Map 2):

TURKEY: 1 specimen, Diyarbakir dintorm [37.9189°N, 40.2106°E], Diyarbakir [Ili], 5-VI-1971, G. Osella; 5 specimens, Bafra [41.56780°N, 35.9069°E], Samsun [Ili], 8-VII-1975, G. Osella (Tomov 1984).

Discussion. *Taxonomy.* *Diorhabda elongata* (Brullé) was described in the genus *Galeruca* by Brullé (1832) from Morée (= Pelopónnisos peninsula), Greece. We dissected a total of 16 male and 11 female topotypes from 12 locations of the type locality, Pelopónnisos, Greece (Map 2). These males and females shared unique genitalic characters among the *D. elongata* group, comprising a distinct genitalic morphotype pair along with all other specimens examined from Greece and the surrounding countries of Italy, Albania, Macedonia and Bulgaria as well as western Turkey (see discussion below; Figs. 14, 19, 24, 29, 34, 39, 44; Map 2). We are certain that this genitalic morphotype pair is a single species conspecific with *D. elongata*.

The endophallic sclerites of *D. elongata* bear several characters distinguishing them from those of the holotypes of *D. carinata*, *D. carinulata*, and *D. meridionalis* (as illustrated in Figs. 18–19 of Berti and Rapilly 1973) and other specimens of these species and *D. sublineata* examined in this revision (see **Male-Genitalia** above; Figs., 15–18, 20–23, 25–28, 30–33). Additional unique qualitative characters of the female genitalia distinguish *D. elongata* from other species in the *D. elongata* group (see **Female-Genitalia** above; Figs. 34–43). The distinctive genitalic characters of *D. elongata* are maintained in the same areas where *D. sublineata*, *D. carinata* and *D. carinulata* occur and near its abutting range boundary with *D. meridionalis*, and this is strong evidence for reproductive isolation between these species (see **Biogeography** below; Map 1, Table 8). Further evidence for reproductive isolation between *D. elongata* and several members of the *D. elongata* group is also found in previously discussed differences in component ratios of putative aggregation pheromones and reduced F2 hybrid egg viabilities.

Both the text and color habitus drawing accompanying Brullé's (1832, Plate 44, Fig. 10) original description lack any indication of striping or vittae on the elytra, but we find that *D. elongata* commonly has submarginal and substural vittae (Fig. 1). The elytral vittae in *D. elongata* are confined to the apical half of the elytra (Fig. 1), distinguishing them from some specimens of the other four species of the *D. elongata* group in which the elytral vittae, when present, may extend into the basal half of the elytra (Figs. 5, 9). We find that external characters previously used to distinguish *D. elongata* from the sibling species *D. carinata* and *D. sublineata* (Weise 1883, 1890; Laboissière 1934, Porta 1934, Bechyné 1961, Warchalowski 2003) are too variable for species diagnosis (for further details, see **Discussion—Taxonomy** under *D. carinata* and *D. sublineata*). We have dissected specimens of *D. elongata* that were misidentified by taxonomists using external diagnostic characters as *D. e. ab. carinata* in Italy, *D. e. var. sublineata* in Greece, and *D. e. ab. sublineata* in Italy (see **Material examined**). Gruev and Tomov (1986) provide a detailed description of external adult morphological characters for *D. elongata* but their given size range of 4.5–8 mm, is wider than the size range we find of 5.3–7.7 mm, and their range certainly includes that of sibling species that are smaller (*D. carinulata*) and larger (*D. carinata*) (Table 2). The size range of 5.5–8 mm given elsewhere in southern Europe (Porta 1934, Laboissière 1934) is closer to our observation regarding minimum size.

Mulsant (Mulsant and Wachanru 1852) described *G. costalis* Mulsant from Cilicia (along the coast of southwestern Turkey, towards Syria) from specimen(s) of unknown sex. The given body length is 5.6 mm, possibly making the type a male (see Table 2). The elytral vittae (as striae) are described beginning at a point 3/5th the length of the elytra from the base (starting in the apical half) and ending at a point 6/7th the length of the elytra from the base (ending near the apical tip). Confinement of the vittae to the apical half of the elytra agrees with our observations for *D. elongata*. We dissected *D. elongata* from all four locations available from the type locality of Cilicia (an area including Adana in southwest Turkey, Map 2). We dissected *D. carinata* and *D. meridionalis* from ca. 100 km southeast of Cilicia in Halab, Syria (Map 1). We follow Reiche and Saulcy (1858) in regarding *G. costalis* as a synonym of *D. elongata*. Other synonyms established by Reiche and Saulcy (1858) and Weise (1893) actually consist of the three valid species *D. carinata*, *D. sublineata*, and *D. carinulata*.

The number of spines on the endophallic sclerites and the shape of the elongate sclerite are fairly variable in *D. elongata* (Fig. 19) and males from certain series were often more similar to one another than those from other series. For example, a majority of males dissected from Promontorio de Gargano, Italy, and 60 km E. Thessaloniki, Greece had greater spination of both the elongate and palmate sclerites than males from Burucek, Turkey. However, the variability in spination is continuous (see Figs. 19 and 29, Methoni, Greece), and we detected no geographic pattern. We have seen only a few series of specimens collected from identified species of *Tamarix* hosts and further investigations should be made into potential patterns in morphological variability associated with host species. Lohse (1989) found sympatric and phenologically differing *Rumex* and *Polygonum* host ecotypes of *Galerucella aquatica* that could be distinguished by the coloration of the last abdominal sternite but not by endophallic sclerites. Studies of genetic relationships among *D. elongata* populations collected from various *Tamarix* spp. in southern Europe are in progress (R. Carruthers, USDA/ARS, Albany, CA, pers. comm.).

Common Name. The name “Mediterranean tamarisk beetle” refers to the great majority (ca. 80%; Fig. 52B) of collections of *D. elongata* being from the Mediterranean biome.

Biology. Host Plants. *Diorhabda elongata* has been collected from *Tamarix smyrnensis* Bunge, a close relative of *T. ramosissima* (Baum 1978), on Crete, Greece (Regalin 1997) and in Isparta Province of southwest Turkey (Gök and Çilbıroğlu 2003, 2005; Gök and Duran 2004) (Table 1). Table 5 of Gerling and Kugler (1973) lists *T. smyrnensis* as the host species for seven locations in western Turkey associated with dissected TAUJ specimens of *D. elongata* (see above **Material Examined**). *Tamarix gallica* is reported as a host in northern Sicily (Lundberg *et al.* 1987b), and we dissected a specimen from the Toscana province of Italy with a host label of *T. gallica*. *Diorhabda elongata* is reported from *Tamarix* sp. in Cyprus (Georghiou 1977). New host records from collections on Peloponnisos, Greece by Javid Kashefi (USDA-ARS) are *T. hampeana* Boissier and Heldreich and *T. parviflora*. *Tamarix parviflora* is also a reported host from Cache Creek, California (DeLoach *et al.* in prep.; R. Carruthers, pers. comm.). *Tamarix chinensis* × *T. canariensis*/*T. gallica* is a new host record for populations of *D. elongata* established at Big Spring, Texas (Table 1). Dalin *et al.* (in press) found that *D. elongata* from Crete preferred *T. parviflora* to a similar degree as *T. ramosissima* in multiple-choice field cage studies in California.

In Bulgaria, *D. elongata* severely defoliates *Tamarix* sp. trees (especially those in open areas) when it becomes numerous on the dry sandy terraces of the Struma River valley near Blagoevgrad (Tomov 1979). *Tamarix tetrandra* Pallas, a close relative of *T. parviflora* (Zieliński 1994), is common along the Struma River Valley and other parts of Bulgaria, Greece, and Turkey (Baum 1978, Zieliński 1994), where it may serve as a host for *D. elongata*. *Tamarix dalmatica* Baum, the prevalent *Tamarix* species along the eastern coastlands of the Aegean Sea (Baum 1978), may serve as a host in Croatia, Montenegro and Albania. Reports of *D. elongata* in Central Asia from the leguminous shrubs *Halimodendron* (Sinadsky 1960, Bieńkowski 2004), *Ammodendron* (Seitova 1974, Sinadsky 1968), and *Alhagi* (Sinadsky 1968) (Fabaceae) should refer to *Galerupipla* sp. (see DeLoach *et al.* 2003b).

No-choice larval host suitability studies by Milbrath and DeLoach (2006a) confirm that *D. elongata* larvae from Crete can survive to adulthood only on plants of the order Tamaricales, including *Tamarix* (Tamaricaceae) and, to a lesser degree, on three North American *Frankenia* spp. (Frankeniaceae): *F. salina*, *F. johnstonii*, and *F. jamesii*. Herr *et al.* (2006, in prep.) found larval survival on *F. salina* was not different than that on *T. ramosissima*. Multiple-choice adult oviposition studies in field cages revealed that the three North American *Frankenia* spp. provide little attraction for oviposition compared to *Tamarix* (Milbrath and DeLoach 2006a; Herr *et al.* 2006). *Diorhabda elongata* tended to oviposit less on *T. aphylla* compared to other invasive North American tamarisk, including *T. ramosissima*, *T. chinensis*, and *T. canariensis*/*T. gallica* in multiple choice field cage tests (Milbrath and DeLoach 2006a, Herr *et al.* 2006). However, in other multiple-choice field cage tests among *Tamarix* spp., oviposition by *D. elongata* on one accession of *T. aphylla* (Phoenix, Arizona) was not different than that on *T. ramosissima* × *T. canariensis*/*gallica*, *T. canariensis*/*T. gallica* and *T. parviflora* (Milbrath and DeLoach 2006b). In a no-choice laboratory cage experiment, *D. elongata* accepted *T. aphylla* for oviposition to a significantly lesser extent than *T.*

ramosissima but not *T. parviflora* (Herr *et al.* 2006). In this same no-choice experiment, the difference between oviposition by *D. elongata* on *F. salina* (inland variety) and *T. ramosissima*, *T. parviflora*, and *T. aphylla* was not significant (Herr *et al.* 2006). *Diorhabda elongata* accepted *T. aphylla* for oviposition to the same degree they accepted *T. ramosissima* × *T. chinensis* in no-choice field cage studies (Milbrath and DeLoach 2006b). In open field testing with transplanted potted plants at Big Spring, Texas, *D. elongata* oviposited little on *T. aphylla* compared to *T. ramosissima*/*T. chinensis* (Moran *et al.* in press), and almost no oviposition occurred on *F. salina* (Herr *et al.* 2006). *Tamarix aphylla* is at moderate risk of damage by *D. elongata* in the field and it is difficult to predict to what degree *D. elongata* would damage *T. aphylla*, especially in the absence of other *Tamarix* spp. (Milbrath and DeLoach 2006b). Based on open-field testing in south Texas, Moran *et al.* (in press) concluded that *D. elongata* will likely have limited establishment and impact on *T. aphylla*. *Frankenia* is at very low risk of damage from *D. elongata* (Milbrath and DeLoach 2006a). Risk of damage to both *T. aphylla* and *Frankenia* by *D. elongata* is probably much lower when these plants are not in the proximity of preferred *Tamarix* spp. (e.g., Blossey *et al.* 2001).

Ecology and Phenology. Tomov (1979) studied large populations of *D. elongata* from 1967–1971 along the Struma River near Blagoevgrad, Bulgaria. They report that the first eggs appear in early April and mating pairs are found from the middle of April until September. Larvae appear in early May until September, and the last adults are seen in October. Three population peaks of adults are seen near Blagoevgrad: late May and early June, late July and early August, and late September. Feeding by young larvae produces small holes in the lower epidermis and parenchyma of *Tamarix* leaves. Older larvae and adults eat entire leaves. Larvae pupate in loose cocoons in the soil. Late in the summer, many *Tamarix* shrubs, especially isolated ones, are completely defoliated along the Struma River by *D. elongata*.

Diorhabda elongata was noted in small numbers from May to October on *T. smyrnensis* in southwest Turkey (Gök and Çilbıroğlu 2003). Adult collection dates from our examined material are from May to September in Croatia, April to October in Greece, and April to October in Italy. Our only specimens from Spain were collected on 15 February at Estepona on the southern coast.

Milbrath *et al.* (2007) found that *D. elongata* from Crete overwintering at Temple, Texas had ca. 80–95% survival from early November through the middle of March when tamarisk leaves began budding. Overwintered adults emerged in mid to late March and commenced ovipositing at the beginning of April giving rise to four generations and a partial fifth generation. Fourth generation adults emerging in early September oviposited little in September and ceased oviposition by October when they appeared to enter diapause.

In Big Spring, TX, five generations were also observed with overwintering adults generally emerging from late March and early April and fifth generation adults appearing from October to early November (DeLoach 2008, DeLoach *et al.* in prep.). On the Rio Grande from Candelaria to near Presidio, TX, large numbers of adults were actively defoliating trees into mid-November (A. Berezin, Sul Ross State University, Alpine, TX, pers. comm.). From Big Spring during 2005–2008, data was collected on the population density of *D. elongata* and associated rate of tamarisk defoliation on trees along sample transects throughout the growing season to develop models of wave dispersal using both a mathematical deterministic model and a statistical spatial regression model (J. Sanabria, pers. comm., DeLoach 2008, and DeLoach *et al.* in prep.).

Development and Reproduction. Egg mass size in the field in Bulgaria ranged from 10 to 19 eggs (26 in the laboratory) (Tomov 1979). In laboratory studies at 28°C by Milbrath and DeLoach (2006b), *D. elongata* produced 16.0 ± 0.5 eggs per mass and fecundity averaged 219 ± 56.2 eggs with a population doubling time of 5.8 days on *T. ramosissima* × *T. chinensis*. On *T. aphylla*, fecundity was higher at 328.0 ± 60.4 but the population doubling time was longer at 6.6 days, which was partly due to both longer preoviposition and oviposition periods on *T. aphylla*. Milbrath *et al.* (2007) compared *D. elongata* from Crete with *D. carinulata*, *D. carinata* and *D. sublineata* at 28°C, and found *D. elongata* was similar to the other species with a development time of 21.0 days from egg to adult (with 78% survival), a fecundity of 281 eggs, and a population doubling time of 6.2 days.

Natural Enemies. Tomov (1974) reported the tachinid *Erynniopsis antennata* (Rondani) (= *E. rondanii* Townsend) emerging from third instar larvae of *D. elongata* collected on 10 July in Bulgaria. *E. antennata* is also reported from southern France and Italy, and it also attacks the elm leaf beetle, *Xanthogaleruca luteola* (Müller) (Tschorsnig and Herting 1994). Adult *E. antennata* oviposit on beetle larvae and tachinid adults emerge from late stage third instar larvae (prepupae) during the growing season and from overwintering beetles in the early spring (Dreistadt and Dahlsten 1990). In 1939, *E. antennata* was introduced from Europe and established in California for control of the exotic elm leaf beetle (Flanders 1940). The parasitic fly has now spread throughout California (Dahlsten *et al.* 1998), and is also reported from Oregon (USNM collection data). In California, parasitism rates of overwintering elm leaf beetle adults can reach 65%, but the fly is limited by a eulophid hyperparasite *Baryscapus erynniae* (Domenichini) (Dreistadt and Dahlsten 1990). A protozoan microsporidian, *Nosema* sp., was found in adult *D. elongata* originating from near Sfakaki, Crete, Greece (shipment EIWRU-2002-1002) (identified by J. Siegel) and Posidi Beach, Greece (shipment EIWRU-2002-1009) (D. Bean, pers. comm.).

Biogeography. *Comparative.* *Diorhabda elongata* differs from other tamarisk beetles by the following combination of biogeographic characteristics: (1) strongly maritime and generally found within ca. 250 km from a sea coast, under 1,400 m elevation; (2) usually found in warm temperate Mediterranean woodlands or Temperate Broadleaf and Mixed forest biomes; and (3) latitudinal range of 30–45°N and most common from 35–43°N (Table 7, Figs. 51–52). *Diorhabda sublineata* is marginally sympatric with *D. elongata* in Portugal, Spain and Egypt and both occur in the Mediterranean Forests, Woodlands and Scrub biome around the Mediterranean Sea (Map 1, Tables 8 and 9, Fig. 52B). However, *D. elongata* predominates in the northeastern Mediterranean in Europe and Asia while *D. sublineata* predominates in the western Mediterranean and all of North Africa, including more xeric biomes such as desert and flooded grasslands in which *D. elongata* is rare or absent. *Diorhabda sublineata* additionally differs from *D. elongata* in being common further south at 31–35°N and ranging much further south to 16°N (Figs. 51–52). *Diorhabda* are unreported along two ca. 600–700 km stretches of land around the Mediterranean where the main distributions of *D. elongata* and *D. sublineata* should interface in western Italy and Israel and Palestine, and no *D. sublineata* are reported from the main area of distribution of *D. elongata* (Map 1). If these *D. elongata*/*D. sublineata* interface zones actually lack *Diorhabda* populations, it may be worth investigating the potential existence of some form of localized competitive mutual exclusion between these species.

Diorhabda elongata is probably marginally sympatric with *D. carinata* in eastern Turkey, western Syria, and, possibly, southern Russia, Georgia and Azerbaijan. *Diorhabda elongata* is marginally sympatric with *D. carinulata* in southern Russia (Dagestan) (Map 1; Table 8). Both *D. carinata* and *D. carinulata* are strongly continental and are mostly found in desert and grassland biomes from which *D. elongata* is not known. *Diorhabda meridionalis* is apparently parapatric with *D. elongata* in Syria and differs from *D. elongata* in being common both in deserts and further south at 26–31°N (Tables 7 and 8; Map 1; Figs. 51–52).

Descriptive. *Diorhabda elongata* is found in the west-central Palearctic realm (Maps 1). It is primarily collected from 35–43°N in the northeastern Mediterranean from Italy to Bulgaria and western Turkey in two biomes: the Mediterranean Forests, Woodlands and Scrub and the Temperate Broadleaf and Mixed Forests (Map 2). Ecoregions (Olson and Dinerstein 2002) inhabited by *D. elongata* from 35–43°N in the Mediterranean Forests, Woodlands and Scrub biome, based on frequency of collection, are the Ilyrian Deciduous Forests from Croatia to western Greece, the Crete Mediterranean Forests, and the Aegean and Western Turkey Sclerophyllous and Mixed Forests from coastal Greece to Turkey (Map 2). The latter ecoregion is the center of distribution for *T. hampeana* (Boratyński *et al.* 1992, Zieliński 1994), a host plant of *D. elongata*. *Tamarix hampeana* occurs only rarely in the western Mediterranean area (De Martis *et al.* 1986), similar to *D. elongata* (Map 2). The primary range of another host of *D. elongata*, *T. parviflora*, is also in the eastern Mediterranean (Map 2). In the Temperate Broadleaf and Mixed Forests biome, *D. elongata* inhabits the Balkan Mixed Forests from Macedonia to northwest Turkey. This area is a possible source for a putative northern interior lowland *D. elongata* climatype occurring from 41–42°N and 200–500 m elev.

Potential in Tamarisk Biological Control. Summary. The Mediterranean tamarisk beetle is providing effective biological control of *T. parviflora* at Cache Creek, California and *Tamarix ramosissima*/*T. chinensis* near Big Spring and Pecos, Texas (Map 7). Based on its biogeographic characteristics, *D. elongata* is most suitable for Mediterranean biome of northern California (Figs. 51–52; Map 13). *D. elongata* from Crete readily accepts the novel host *T. chinensis* × *T. canariensis*/*T. gallica* at Big Spring, Texas, and its absence in the deserts and grasslands of central Asia is probably due to poorer adaptation to the bioclimatic conditions of deserts and grasslands compared to other *Diorhabda* species rather than the lack of suitable *Tamarix* hosts. *Diorhabda elongata* will establish in west Texas grasslands and deserts around 31–32°N, but our HSI model predicts other *Diorhabda* species are better biogeographically suited to deserts and grasslands of the southwestern U.S., including *Diorhabda carinulata*, *D. carinata*, and *D. sublineata*. More adapted *Diorhabda* species may eventually replace *D. elongata* where it establishes in desert and grassland habitats (Map 13).

Discussion. The Mediterranean tamarisk beetle attacks and defoliates *Tamarix* (Tomov 1979) in Temperate Broadleaf and Mixed Forest biome at ca. 42°N in Bulgaria. *Tamarix smyrnensis* is a close relative of the invasive *T. ramosissima* in North America (Baum 1978, Zieliński 1994), and it is attacked by *D. elongata* in Greece and Turkey. *Diorhabda elongata* attacks and damages both invasive *T. parviflora* and *T. ramosissima*/*T. chinensis* in North America. It has a moderate risk of damaging *T. aphylla* (Milbrath and DeLoach 2006b) and very low risk of damaging *Frankenia* (Milbrath and DeLoach 2006a), and both these risks are probably much reduced at less proximity to preferred *Tamarix* spp. (e.g., Blossey *et al.* 2001).

The Mediterranean tamarisk beetle may be best adapted for areas from 35–43°N in the maritime temperate warm Mediterranean Forests, Woodlands and Scrub biome and the Temperate Broadleaf and Mixed Forests biome (see **Biogeography**). Of these two biomes, only the Mediterranean Forests, Woodlands and Scrub biome is found in the western U.S. From 35–43°N, the Mediterranean biome is represented by the California Interior Chaparral and Woodlands and the California Montane Chaparral and Woodlands ecoregions (Map 13). The Mediterranean species *T. parviflora* is the dominant invasive tamarisk in these ecoregions (Map 7). *Diorhabda elongata* from Crete has established well on *T. parviflora* near Cache Creek, California (39°N, Map 7), where it entirely defoliated over 200 hectares of tamarisk along an ca. 40 km reach in 2007, and over ca. 250 ha. (600 acres) along 50 km (including parts of nearby Bear Creek) in 2008 (DeLoach *et al.* in prep.; R. Carruthers, pers. comm.). This estimate of defoliated area is based upon an analysis of aerial photography which revealed ca. 396 ha of *T. parviflora* along a similar 40 km reach (ca. 10 ha of tamarisk per creek km) of Cache Creek in 2001 (Ge *et al.* 2006). Tamarisk is estimated to occur at about half this density (ca. 5 ha. per km) over most of Cache and nearby Bear creeks where *Diorhabda* is well established (R. Carruthers, pers. comm.). Initial establishment at Cache Creek was slow, with very low populations persisting from 2004–2005, and only ca. 1.4 ha defoliated in 2006, and *D. elongata* has only weakly established and not established at some other northern California sites (John Herr, USDA/ARS, Albany, CA, pers. comm.). The possibility that establishment of *D. elongata* was slowed by predators or the need to adapt to a colder climate and to colder weather starting at longer daylengths earlier in the season should be investigated. At the Cache Creek site, potential parasitism of *D. elongata* by the previously discussed exotic parasitoid tachinid fly *Erynniopsis antennata* is being monitored (J. Herr, pers. comm.).

Diorhabda elongata from Crete is also well established on *T. chinensis* × *T. canariensis*/*T. gallica* (identified by J. Gaskin) in the Temperate Grasslands, Savannas and Shrublands biome (Western Short Grasslands ecoregion) near Big Spring, Texas (32°N, Map 7) (Hudgeons *et al.* 2007a). During the first year of establishment at Big Spring in 2004, about four small trees were defoliated throughout the season, the first two trees being defoliated in July. In 2005, field populations increased and, by late September, over 200 tamarisk trees were totally defoliated, representing 0.17 ha of tamarisk canopy covered over a 0.66 ha area. By late October 2006, tamarisk over an ca. 7 ha area was defoliated (Everitt *et al.* [2007] classified defoliation from remote sensing by color aerial photography), ca. 13 ha was defoliated in 2007, and over 40 ha was defoliated in 2008, including defoliation of an ca. 7 km stretch of Beals Creek with satellite populations defoliating scattered trees over a 19 km wide area around Big Spring. At each of two sites in the Trans-Pecos Chihuahuan Desert on the Pecos River near Pecos and Imperial, Texas (Map 7), ca. 1 ha of tamarisk trees

were defoliated in 2007 during the second year post release (Mark Muegge, The Texas AgriLIFE Extension Service, Fort Stockton, TX, pers. comm.). By November 2008, defoliation by *D. elongata* along the Pecos River north of Pecos progressed to ca. 3.2 river km, but no defoliation was found near Imperial. Establishment was initially marginal or unsuccessful at other Texas AgriLIFE release sites in west Texas, but the use of ant baits in 2008 appears to be improving establishment at several of about 16 additional sites (A. Knutson, pers. comm.; see Map 7). Releases of populations of *D. elongata* from Crete were first made along the Rio Grande in Texas at several sites from Candelaria towards Presidio (Tyrus Fain, Rio Grande Institute, La Junta Project, Marathon, TX, pers. comm.) in the summer of 2007. Releases were made again in these areas in 2008 and in Big Bend National Park (Joe Sirotnak, Big Bend NP, TX, pers. comm.) and nearby Adams Ranch (M. Muegge, pers. comm.). Partial defoliation by *D. elongata* of several trees surrounding the release cages were noted at three sites between Presidio and Candelaria in the late summer and fall of 2008 (Mark Donet, USDA-NRCS, Alpine, TX, and Andrew Berezin, pers. comm.). In 2008, further releases were also made at various sites in west Texas, such as Iraan and Twin Buttes Reservoir near San Angelo (A. Knutson, pers. comm.), and at Holloman AFB, New Mexico (D. Thompson, pers. comm.).

In the Western Short Grasslands at Lake Meredith in north Texas (35°N, Map 7), *D. elongata* from Posidi Beach, Greece (40°N), overwintered in the open field after its release in 2005 and produced spotty damage to tamarisk, dispersing about 1 km, but it was present in only small numbers in 2008 (Erin Jones, Texas AgriLIFE Research, Amarillo, TX, pers. comm.). *D. elongata* from Crete failed to establish at Seymour, Texas in the Central and Southern Mixed Grasslands in 2004, but *D. carinata* from Qarshi, Uzbekistan was released there in 2008 and appeared to be establishing, defoliating over 0.2 ha during the first year of release (C. Randal, pers. comm.). In 2003, populations of *D. elongata* from Crete were released in the Chihuahuan Desert near Artesia, New Mexico (33°N, Map 7) and initially increased in 2004, but severely declined in early 2005 and could not be found through 2008.

Although the Mediterranean tamarisk beetle appears to be very promising for tamarisk biocontrol across the southern U.S. (Milbrath *et al.* 2007), it has never been recorded in its native habitat from two biomes: Deserts and Xeric Shrublands and Temperate Grasslands, Savannas and Shrublands (Table 9; Fig. 52B). We are not aware of a desert or grassland ecotype of *D. elongata*. During 2004–2007, *D. elongata* defoliated ca. 13.8 ha in the grassland biome at Big Spring compared to ca. 200 ha in the Mediterranean biome on Cache Creek. If the trend continues for more rapid defoliation in California, this could further support our biogeographic models showing that the Crete beetle is best suited to Mediterranean biomes. Other species of tamarisk beetles are common in desert and grassland biomes (Map 1, Table 9), and they may be better suited to much of the large area of these biomes invaded by tamarisk in North America as estimated by our relative Habitat Suitability Index Models (Map 13). Species distribution models incorporating climatic data are planned to better evaluate the potential suitability of *D. elongata* for climates across the western U.S. Making accurate predictions regarding potential North American ranges of any *Diorhabda* could be complicated if their field host preferences for *Tamarix* spp. vary significantly across their distributions.

***Diorhabda carinata* (Faldermann, 1837)**

larger tamarisk beetle

(Figs. 3, 4, 15, 20, 25, 30, 35, 40)

Galeruca carinata Faldermann, 1837:329 (Type locality: Transcaucasus region [Georgia, Armenia and Azerbaijan]; as *Galleruca*).

Galeruca elongata: Reiche and Saulcy, 1858:42 (part, l'Immerétie [western Georgia], Syria, Turkey, as *Galleruca*); Joannis, 1866:83 (part, monograph; Syria, as *Galleruca*).

Diorhabda elongata: Weise, 1883:316 (part, established genus; Transcaucasus); Holdhaus, 1920:45 (Assur [Ash Sharqat], Iraq); Ogloblin, 1936:79 (part, Iran, Syria, Turkey, Transcaucasus, central Asia); Rusanov, 1949:118 (part, Central Asia; as *Diorhabda*); Kyrzhanovskiy, 1952:198 (part, Turkmenistan), 1965:392 (part, middle Asia); Pavlovskii and Shtakelberg, 1955:566 (part, southwest Europe, as *Diorhabda*); Yakhontov and Davletshina, 1955:58 (part,

biology; Amu Darya Delta, northern Uzbekistan); Sinadsky, 1957:950, 1963:84, 1968:64 (part, biology; Amu Darya Valley, Uzbekistan; as *Diorrhabda*); Medvedev, 1959:118 (part, Turkmenistan); Yakhontov, 1959:338 (part, biology; Uzbekistan); Lozovoi, 1961:86 (part, eastern Georgia); Kulinich, 1962:73 (part, biology; Tajikistan); Pripisnova, 1965:83 (part, biology, Tajikistan); Kulenova, 1968:171 (part, southeastern Kazakhstan); Lopatin and Tadzhibaev, 1972:591 (part, Tajikistan); Lopatin, 1977a:282 (part, Asia), 1981:375 (Robate–Ghozlog [Robat–e Qozlog], Iran); Davletshina *et al.*, 1979:79 (part, southwest Kyzyl–Kum Desert, central Uzbekistan); Habib and Hasan, 1982:19 (host range; northern Pakistan); Tomov, 1984:377 (part, Artvin, Turkey); Samedov and Mirzoeva, 1985:712 (part, Azerbaijan); Mirzoeva, 1988:?, 2001:48 (part, Azerbaijan); Lopatin and Kulenova, 1986:129 (part, Kazakhstan); Myartseva, 1995:4, 1999:1, 2001:1 (part, biology; Turkmenistan); Kovalev, 1995:78 (part, south-central Palearctic); Richter and Myartseva, 1996:316 (parasitoid, Turkmenistan); Gruev and Tomov, 1998:70 (part, Transcaucasus, mid-Asia); Aslan, 1998:287 (Ezorum Ili, province of northeast Turkey); Aslan *et al.*, 2000:30 (part, eastern Turkey); Anonymous, 2001:52N (part, Turkmenistan); DeLoach *et al.*, 2003a:230 (part, Uzbekistan [Qarshi]), 2003b:126 (part, host range; Pakistan, Uzbekistan, Turkmenistan, Georgia, Azerbaijan), (2008, in prep.) (part, Qarshi, Uzbekistan); Khamraev, 2003:11 (part, Uzbekistan); Milbrath *et al.*, 2003:225 (part, Qarshi, Uzbekistan); Riley *et al.*, 2003:69,189 (part, catalog of North America [introduced]); Warchalowski, 2003:328 (part, taxonomic keys; Caucasus and Central Asia); Bienkowski, 2004:76 (part, keys; eastern Europe, Caucasus, Iran, Iraq, Central Asia, Kazakhstan); DeLoach and Carruthers, 2004a:13, 2004b:311 (part, Uzbekistan [Qarshi]); Gök and Duran, 2004:17 (part, Turkey); Lopatin *et al.*, 2004:127 (part, central Asia); Gates *et al.* 2005:28 (parasitoid; Ashgabat, Turkmenistan); Dudley, 2005a:13, 2005b:42N (part, biological control; ex: Uzbekistan); Milbrath and DeLoach, 2006a:32, 2006b:1379 (part, host specificity; Qarshi, Uzbekistan); Dudley *et al.*, 2006:137 (part, host range; Qarshi, Uzbekistan); Milbrath *et al.* (2007) (part, biology; Qarshi, Uzbekistan); DeLoach (2008); Bean and Keller (in prep.) (part, diapause induction; Qarshi, Uzbekistan); Thompson *et al.* (in prep.) (part, laboratory hybridization; Qarshi, Uzbekistan).

Diorhabda elongata var. *carinata*: Heyden *et al.*, 1891:375 (part, catalog for Europe and Caucasus); Weise, 1893:635, 1132 (part, Transcaucasus); Jacobson, 1901:137 (part, Amu Darya (river), Turkmenistan, as *Dirrhabda*).

Diorhabda elongata ab. *carinata*: Weise, 1924:78 (part; world catalog; Transcaucasus; Turkmenistan, Amu Darya); Winkler, 1924–1932:1307 (part, Palearctic catalog, Transcaucasian region); Warchalowski, 2003:328 (part, taxonomic keys, Caucasus and Central Asia).

Diorhabda rybakovi: Mityaev, 1958:86 (part, biology, Kazakhstan, as *rybakovi*).

Diorhabda elongata carinata: Bechyné, 1961:256 (Pol–e khomri [Polichromi], Afghanistan; central Asia); Lopatin, 1963:355 (Afghanistan); Wilcox, 1971:63 (world catalog, Afghanistan); Medvedev, 1983:123 (zoogeography, Afghanistan); 1985:44 (Afghanistan); Lopatin *et al.*, 2004:127 (east Kazakhstan, northwest China); Dalin *et al.* (in press) (host range; Qarshi, Uzbekistan).

Diorhabda elongata sublineata: Gressitt and Kimoto, 1963a:407 (part, Asia Minor, W. Asia); Wilcox, 1971:63 (part, world catalog, Asia Minor, W. Asia).

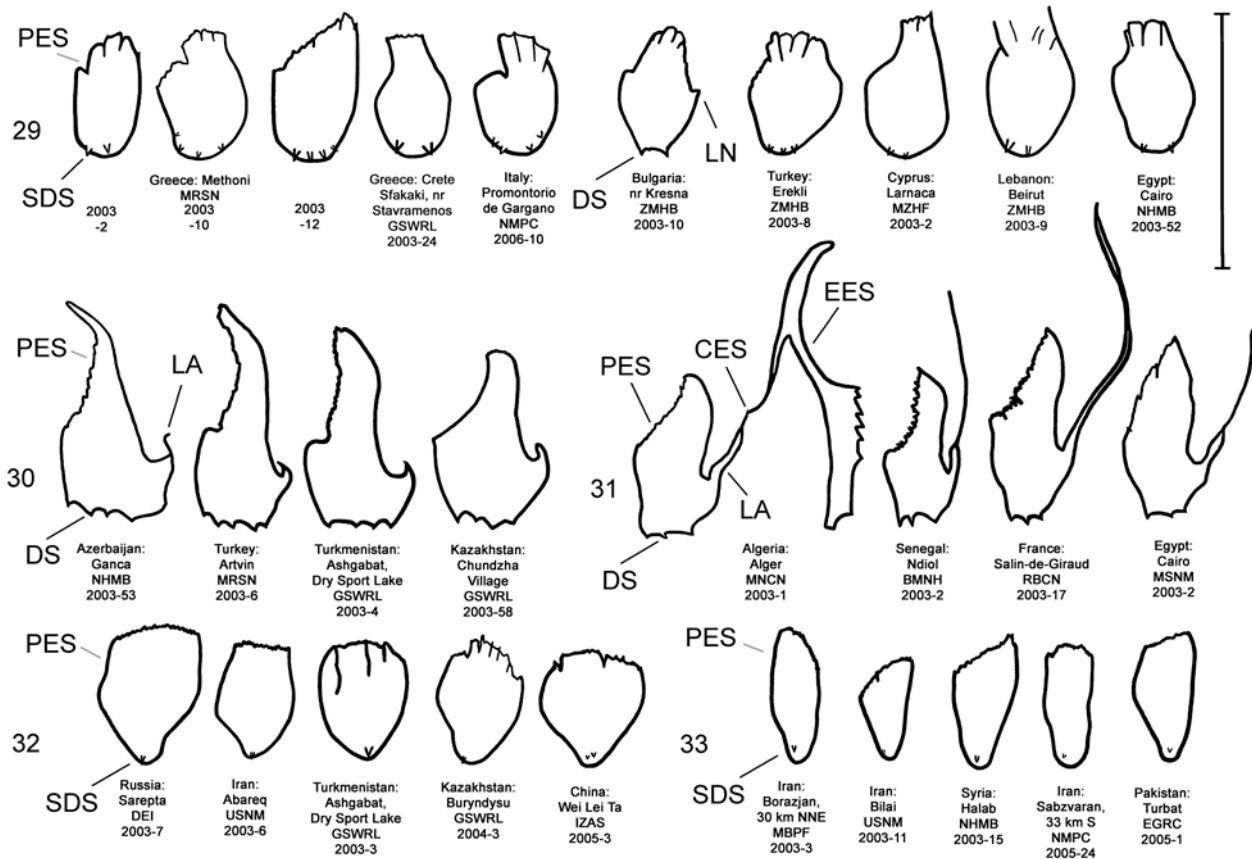
Diorhabda carinata: Berti and Rapilly, 1973:881 (restored species, Transcaucasus), DeLoach *et al.*, 2003b:126.

Male. Genitalia. *Diorhabda carinata* can be distinguished from all other members of the *D. elongata* group by a combination of characters of the palmate endophallic sclerite (PES) and the lack of a connecting endophallic sclerite (CES). The palmate endophallic sclerite (PES) in *D. carinata* always bears a strong lateral appendage (LA) and the distal margin is truncate-serrate with two to six (commonly four to five) usually distal spines, a maximum of one spine being subdistal (Figs. 15, 30). In contrast, the PES of *D. carinulata* (Figs. 17, 32) and *D. meridionalis* (Figs. 18, 33) lacks a lateral appendage (but may bear a lateral notch) and the distal margins of the PES are narrowly rounded and generally smooth with one or two small subdistal spines that sometimes project beyond the distal margin. The PES of *D. elongata* also lacks a lateral appendage and is usually rounded with mostly subdistal spines and a maximum of two distal spines (Figs. 14, 29). *Diorhabda sublineata* bears a CES connecting the PES to the elongate endophallic sclerite (EES) (Figs. 16, 21, 31), but the CES is lacking in *D. carinata* (Figs. 15, 20, 30) (in some darkly sclerotized specimens of *D. carinata*, a faint lateral line is seen where a CES would be found). In *D. carinata*, the spined area of the EES extends greater than or equal to 0.34 times the length of the EES (Figs. 15, 20). In contrast, the spined area of the EES is confined to less than or equal to 0.16 times the length of the sclerite in *D. elongata* (Table 3; Figs. 14, 19, 24, 48). In *D. carinata*, spines of the EES are often irregularly spaced along the blade with conspicuous gaps (Fig. 20). In *D. carinulata* and *D. meridionalis*, spines along the EES are usually evenly and closely spaced along the blade (Figs. 22–23). The EES of *D. meridionalis* additionally bears a hooked apex that is absent in *D. carinata*.

Measurements. See Tables 2 and 3.

Female. Genitalia. Female *D. carinata* may be distinguished from all other members of the *D. elongata* group except *D. sublineata* by their triangulate vaginal palpi (VP) that are wider than long with a width to length ratio (LP/WP) of 0.50–0.89 ($n = 21$) (Fig. 35, Table 4). In contrast, the vaginal palpi are broadly rounded with length to width ratio of 0.94–1.36 in the sympatric *D. carinulata* (Fig. 37) and *D. meridionalis* (Fig. 38; Table 4). The vaginal palpi are also broadly rounded in *D. elongata* (Fig. 34). In addition, the width of the widest lobe of the stalk (WLS) of internal sternite VIII (IS VIII) is usually larger in *D. carinata* (range 0.11–0.17 mm; Fig. 35) compared to *D. elongata* (range 0.06–0.11 mm; Fig. 34). Some female *D. carinata* can be distinguished from *D. sublineata* by having the tips of both lobes (TL) of the stalk of IS VIII strongly curved inward with the tips either pointed or rounded (Fig. 40—Baghdad, Ashgabat, and Pul-e Charki), a combinations of characters never found in *D. sublineata* (Figs. 36, 41). Some female *D. sublineata* can be distinguished from *D. carinata* by having the tips of the lobes of the stalk of IS VIII either not curved or curved outward toward the apical lobe with the tips either rounded or quadrate (Fig. 41—Ndiol, Perpignan, Kom Ombo). Female *D. carinata* and *D. sublineata* with at least one lobe of the stalk of IS VIII curved only slightly inward (Figs. 35–36, 40—Lagodekhi and Ardanuc, 41—Biskra and Tamri) are indeterminable to species, except on the basis of geographic distribution outside of the area of known sympatry in Iraq.

Measurements. See Tables 2 and 4.

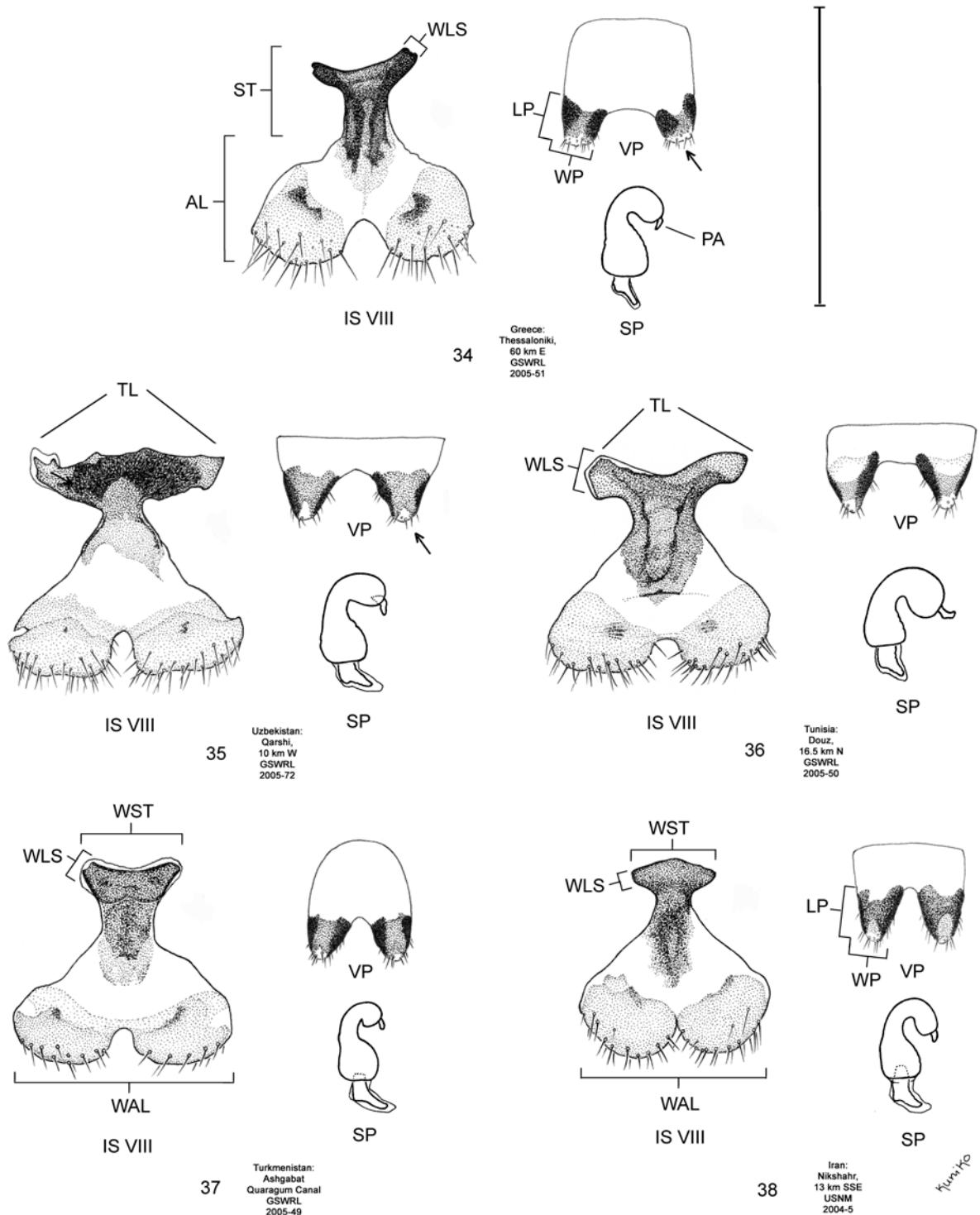


FIGURES 29–33. Palmate (dorsal) endophallic sclerite (dorsal view). 29—*Diorhabda elongata*, 30—*D. carinata*, 31—*D. sublineata*, 32—*D. carinulata*, 33—*D. meridionalis*. CES—connecting endophallic sclerite, DS—distal spines, EES—elongate endophallic sclerite, LA—lateral appendage, LN—lateral notch, PES—palmate endophallic sclerite, SDS—subdistal spines. Scale bar 1.0 mm.

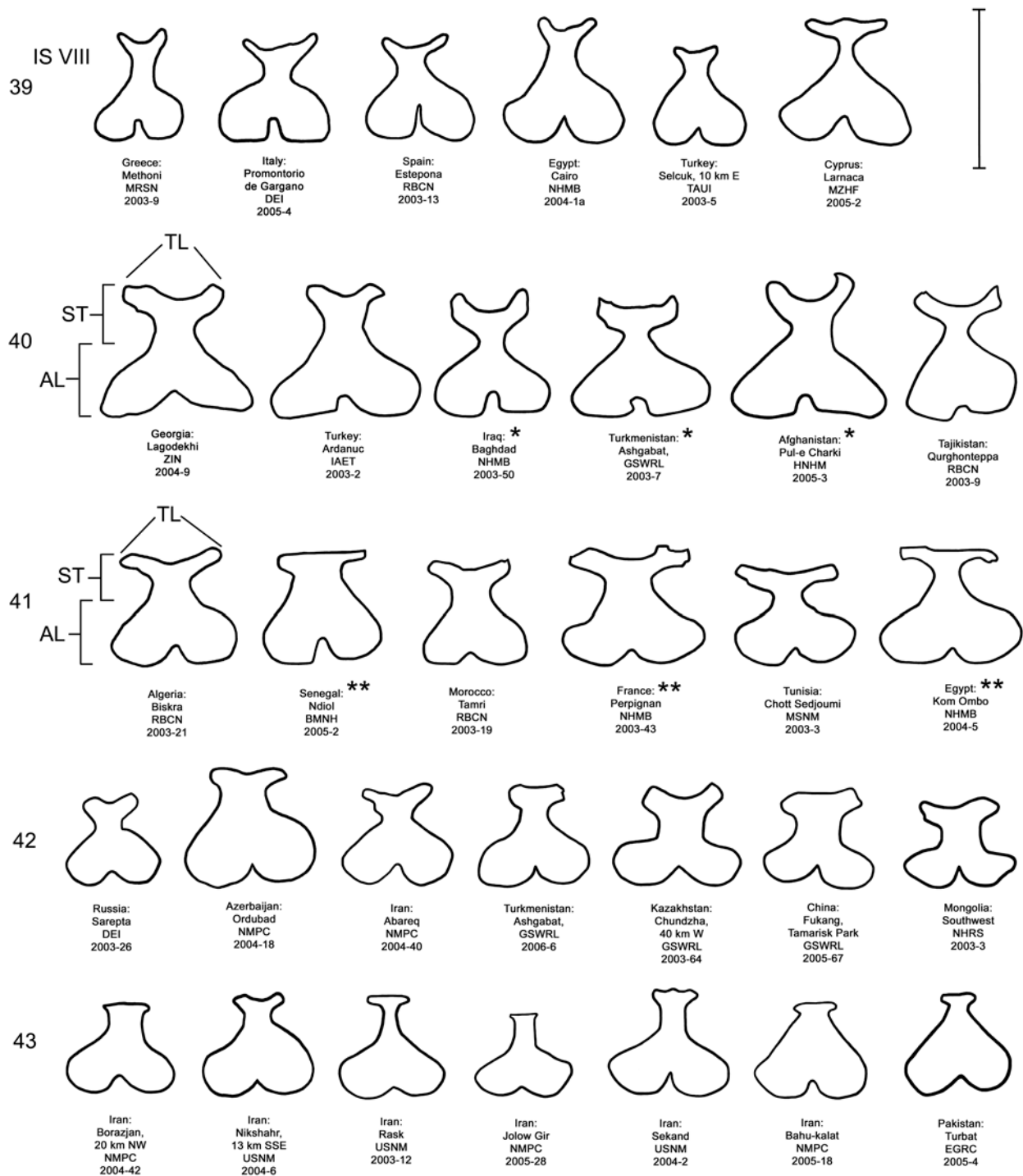
Coloration. Subsutural and submarginal elytral vittae are often present in *D. carinata* (Fig. 9), and the vittae may extend well into the basal half of the elytra, such as in *D. sublineata* (Fig. 5). In contrast, the elytral vittae, if present, are confined to the apical half of the elytra in *D. elongata* (Fig. 1). The elytral vittae are less often present in *D. carinata* (Fig. 3) compared to *D. sublineata*. Live specimens of *D. carinata* tend to have

less greenish-yellow tinting in veins of the elytra (Fig. 4) than do *D. elongata* (Fig. 2). In contrast, *D. sublineata* (Fig. 6) and *D. carinulata* (Fig. 8) both lack greenish-yellow tinting.

Type material. According to Berti and Rapilly (1973), the Faldermann type material of *D. carinata*, consisting of a male holotype, is deposited in the Mniszech Collection at MNHN. We studied the original description by Faldermann (1837), based on an unspecified number of specimens, the illustration of the endophallus of the male holotype by Berti and Rapilly (1973), and topotypes from the Transcaucasus.



FIGURES 34–38. Female genitalia: internal sternite VIII (IS VIII), vaginal palpi (VP), and spermatheca (SP). 34—*Diorhabda elongata*, 35—*D. carinata*, 36—*D. sublineata*, 37—*D. carinulata*, 38—*D. meridionalis*. AL—apical lobe of IS VIII, LP—length vaginal palpus, PA—pointed appendage of SP, ST—stalk of IS VIII, TL—tips of lobes of IS VIII, WAL—width apical lobe of IS VIII, WLS—width lobe of stalk of IS VIII, WST—width stalk of IS VIII. Scale bar 1.0 mm.



FIGURES 39–43. Female internal sternite VIII (IS VIII). 39—*Diorhabda elongata*, 40—*D. carinata*, 41—*D. sublineata*, 42—*D. carinulata*, 43—*D. meridionalis*. AL—apical lobe, ST—stalk, TL—tips of lobes of stalk, *—IS VIII distinctly identifiable as *D. carinata*, **—IS VIII distinctly identifiable as *D. sublineata*. Scale bar 1.0 mm.

Material examined. 122♂♂ dissected (diss.), 67♀♀ diss., 87♂♂, 125♀♀. **AFGHANISTAN:** 1♂ diss., 3♂♂, Gerab [Sare Gearbid Mt.; 33.89667°N, 66.64583°E], Orurgan [Velayat–e Oruzgan], 1,300 m, 12-VI-1970, O. Kabakov, ZIN [2004-02] [from series listed as *Diorhabda elongata carinata* from Uruzgan, Herab by Medvedev (1985)]; 1♂ diss., Polichromi [Pol-e khromi; 35.948889°N, 68.714167°E], 28-V-1956, H.G. Amsel, [from series listed as *D. e. carinata* by Bechyné (1961)], NHMB [2003-23]; 1♀ diss., Polichromi [Pol-e khromi], 700 m, 5-VI-1956, H.G. Amsel, NHMB [2005-05]; 2♂♂ diss., 1♀ diss., 4♂♂, 6♀♀, Pul-e-Charkhi [Pul-e Charki; 34.541944°N, 69.348889°E], 22–24 km east northeast Kabul, 1,780 m [elev.],

19-VI-1974, L. Papp, No. 163, *D. elongata* det. V. Tomov, HNHM [2004-09, 2005-03, 04]; 1♂ diss., Tangi–Gharuh a. Kabul–Fluss [Tangi Gharu Pass, Kabul River; 34.62°N, 69.62°E], 1,600 m [elev.], 8-VII-1952, J. Klapperich, *D. elongata* det. K. Lopatin, HNHM [2004-05] [from series listed as *D. e. carinata* by Lopatin (1963)]; **ARMENIA**: 1♂ diss., 1♀, Eriwan [Yerevan; 40.181111°N, 44.513611°E], Caucasus, NHMB [2003-39]; 1♂, Eriwan, Caucasus, 1893, Horváth, *D. elongata* det. K. Lopatin [HNHM]; **AZERBAIJAN**: 1♂ diss., 2♂♂, 16♀♀, Aresch [a district of the 19th century Russian Caucasus located in present-day northern Azerbaijan according to Frisch (2007)], Caucasus, Schekownikow, *D. e. ab. carinata* det. Le Moul, IRSNB [2006-08]; 1♀ diss., Dzhafarkhan [39.9431°N, 48.4917°E], 23-V-1939, AMA [2004-01]; 2♂♂ diss., 2♂♂, 2♀♀, Elisabetpol [Ganca; 40.682778°N, 46.360556°E], Caucase, Babadjanides, *D. elongata* [1♂]; O. Leonhard [collection; 1♂], DEI [2003-08, 2005-09]; 2♂♂ diss., 2♂♂, 2♀♀, Elisabetpol, Caucasus, *D. elongata* det. K. Lopatin [HNHM], NHMB [2003-53], ZMAN [2008-20], DEI [1♂], HNHM [1♂, 1♀]; 1♂ diss., Geoktapa [Geok–Tapa stream; 39.188056°N, 48.679444°E], 18-VII-1901, P. Schmidt, rice fields, ZIN [2004-22]; 1♀ diss., Geok–Tapa [stream], Transcaucasus, G. C. Champion, BMNH [2003-10]; 1♂ diss., Karadonly [Qaradonlu; 39.7914°N, 48.0428°E], on banks of Araks [Aras] River, 29-V-1911, P. Schmidt, ZIN [2004-04]; 1♂ diss., Khankendy [Xankandi; 39.8153°N, 46.7519°E], Erivansk.g [Erivanskaya gubernia; Xankandi was formerly of Armenia, and now it is in the contested Nagorno-Karabakh zone], Maljushenco, NHMB [2003-42]; 1♂ diss., Mingeçaur [Mingacevir; 40.77°N, 47.0489°E], 19-IV-1959, AMA [2004-03]; 1♂ diss., Ordubad [38.9081°N, 46.0278°E], Araxesthal [Aras River], Caucasus, Col[lection] Matcha, NMPC [2004-53]; 1♀, Ordubad, Caucasus, Col[lection] Matcha, NMPC; 4♂♂ diss., 2♂♂, 2♀♀, Ordubat [Ordubad], [19]14, Dr. Veselý, NMPC [2004-10, 55, 2005-38, 39]; 1♂ diss., Ordubat [Ordubad], VI-1910, Javůrek, Coll[ection] Dr. J. Veselý, *D. elongata*, NMPC [2004-07]; 2♂♂ diss., Qobustan [40.08416°N, 49.41583°E], 18-IV-1984, N. Mirzoeva, AMA [2004-04, 05]; 1♂ diss., Sabirabad [40.0128°N, 48.4789°E], 6-VI-1929, AMA [2004-02]; **CHINA: Xinjiang Uygur Zizhiqu**: 1♂ diss., 1♂, 1♀, Kuldja [Yining; 43.9000°N, 81.35000°E], Tien-Shan, Sven Hedins Exp. Ctr. Asien, *D. elongata*, NHRS [2008-01]; 1♀ diss., 1♀, Ili [Ili Kazakh Autonomous Prefecture, includes Yining], V-[19]06, Collectie C. & O. Vogt Acq. 1960, ZMAN [2008-18]; **GEORGIA**: 1♂ diss., 1♀ diss., 1♂, Eldari [41.28833°N, 46.46305°E], 18-IV-1910, G. Vinogradov–Nikítin, ZIN [2004-06, 23]; 1♀ diss., Eldari, 3-VIII-1984, G. Jacobsen, ZIN [2004-03]; 1♂ diss., 1♀ diss., Lagodekhi [41.8228°N, 46.2756°E], 15-V-1910, L. Miokosiewicz, ZIN [2004-09, 24]; 2♂♂ diss., 2♀♀ diss., 2♂♂, Owtshaly [Avchala; 41.79028°N, 44.8261°E], 24-VI-1879, G. Sievers, ZIN [2004-08, 11, 25, 26]; 1♂ diss., 1♂, 1♀, Mtzchet [Mts'khet'a; 41.8439°N, 44.7164°E], Caucasus, [18]79, Leder (Reitter), ZIN [1♂ diss., 2004-19], NMPC; 1♂ diss., 1♀, Tflis [T'blisi; 41.725°N, 44.79083°E], Caucasus, Leder (Reitter), *D. elongata*, Coll. Reitter, HNHM [2004-01], NMPC; **IRAN**: 2♂♂ diss., 2♀♀ diss., Borazjan, 30 km north northeast [29.53333°N, 51.40000°E]; 10 km N Dalaki, Hableh Rud River; *Tamarix* sp. present (Hoberlandt 1983), 18-19-IV-1977, Exped. Nat. Mus. Praha Loc. No. 298, NMPC [2004-41, 48, 2005-36], MPBF [2003-04]; 2♂♂ diss., Jeugir (33° 27' N, 49° 01' E) [sic; Jolow Gir; 32.96667°N, 47.81611°E; coordinates corrected from relation to Sarab–e Jahangir], 20 km southeast Sarab–e Jahangir [32.326994°N, 48.51111°E], Lorestán, 8-10-X-1998, Chvojka, *D. elongata* det. A. Warchalowski, NMPC [2004-11, 2006-02]; 2♂♂ diss., 4♀♀, Omidiyeh, 34 km south southeast [30.55°N, 49.91667°E]; Rud-e Zohreh river, *Tamarix* sp. present (Hoberlandt 1983), 16-17-IV-1977, Exped. Nat. Mus. Praha Loc. No. 292, NMPC [2004-33, 2005-34]; 1♂ diss., 1♂, Golhak [Qolhak; 35.7803°N, 51.4919°E], 1400m [elev.], near Teheran [Teheran], VI-VIII, 1961, J. Klapperich, *D. elongata* det. I.K. Lopatin, HNHM [2003-02]; 1♀ diss., Robat–e Qozlog [Robat–Ghozlog; 36.7°N, 54.61667°E; valley of small river; *Tamarix* not recorded (Hoberlandt 1974)], [10 km] south of Gorgan, 500 m [elev.], 26-VII-1970, Exped. Nat. Mus. Praha Loc. No. 74, *D. elongata* det. I.K. Lopatin 1964, NMPC [2004-04] [from series listed as *D. elongata* by Lopatin (1981)]; 1♂ diss., 1♀, Semnan to Dameqan [Damghan] road, 35° 46' 13" N, 53°, 44' 47" E [35.77028°N, 53.74639°E], 1,975 m elev., 13-V-2000, J. Gaskin, on *Tamarix*, No. 870, GSWRL [2003-38]; 1♂ diss., 1♂, 3♀♀, Shushtar [32.05°N, 48.85°E; river Karun; *Tamarix* sp. present (Hoberlandt 1983)], 13-IV-1977, Exped. Nat. Mus. Praha Loc. No. 287, NMPC [2004-35a]; 2♀♀ diss., Wildlife Park, vicinity of Dasht, 650 m [elev.] [37.38°N, 55.89°E; Mohammad Reza Shah Wildlife Park (= Golestan Biosphere Reserve), east tributary of the river

Rud-i Gorgan; *Tamarix* not recorded; coordinates adjusted based on elevation and forest description (Hoberlandt 1974)], 27-30-VII-1970, Exped. Nat. Mus. Praha Loc. No. 77, NMPC [2004-17, 20]; **IRAQ**: 4♂♂ diss., 5♀♀ diss., 4♀♀, Assur [Ash Sharqat; 35.45861°N, 43.25722°E], Mesopotamia, 1910, Pietschmann, *D. elongata* [1♀ diss.], Mesopot. Exp. Nat. O.V. 1910, NHMB [2003-06, 21, 33, 34, 35, 36, 47, 51, 2004-04] [from series listed as *D. elongata* by Holdhaus (1920)]; 1♂ diss., Assur [Ash Sharqat] Mesopotamia, Coll. F. Hauser, NHMB [2006-01]; 1♂ diss., Baghdad [33.33861°N, 44.37722°E], summer 1923, B.W. G. Hingston, B.M. 1923-486, BMNH [2005-03]; 2♂♂ diss., 2♀♀ diss., 3♀♀, Baghdad, IV-1936, Frey, NHMB [2003-07, 22, 32, 50]; 4♂♂ diss., 1♀ diss., 5♀♀, 4♂♂, Baghdad, Káalová, NMPC [2004-06, 09, 13, 54, 56]; 1♀ diss., Khanikin [Khaniqin; 34.34694°N, 45.40056°E], 9-IV-1936, Frey, *D. persica* Faldermann det. H. Bollow 1938, NHMB [2003-37]; **KAZAKHSTAN**: 1♀ diss., Aulie-Ata [Taraz; 42.9°N, 71.3667°E], Turkestan, K. Arris, *D. sulphureus* Reitter det. H. Bollow 1939, *D. e.* subsp. *carinata* Fald. det. J. Bechyné 1955, NHMB [2003-30]; 2♀♀, Aulie Ata, Syr Darja, NMPC; 1♂ diss., Chilik [Shelek] near, Chilik River Valley [43.6003°N, 78.2963°E], 6-VI-1999, I.D. Mityaev and R. Jashenko, on *Tamarix ramosissima*, voucher shipment GSWRL-1999-8, GSWRL [2004-01] [28 specimens from Lot GSWRL-1999-1 identified as *D. elongata* by A. Konstantinov on 20-VII-1999 at USDA Systematic Entomology Laboratory (SEL), SEL Lot # 9904498]; 2♂♂ diss., Chundzha Village, Charin [Charyn] River [43.5161°N, 79.2437°E], Gorodinski, V-1994, *D. elongata* det. D. Sassi 2000, GSWRL [2003-58, 59]; 1♂ diss., Sargotay [Sarytogay] Locality [43.43240°N, 79.15040°E], Charyn River, 700 m [elev.], 2-VII-1907, A.G. Jacobson, ZIN [2005-01]; 1♀ diss., Shelek, near, 1-VIII-1999, I.D. Mityaev and R. Jashenko, on *Tamarix ramosissima*, voucher shipment GSWRL-1999-15, GSWRL [2005-94]; **KYRGYZSTAN**: 1♂ diss., 2♂♂, Kugart-su River [Kugart stream], Ferghana Valley [40.8667°N, 72.8833°E], 8-V-1925, F. Dobrzanski, ZIN [2004-10]; **PAKISTAN**: 1♀ diss., Kund [33.9306°N, 72.2289°E], 4-VI-1976, CIBC [Commonwealth Institute of Biological Control], larvae feeding on *T. aphylla*, *D. elongata*, Tam-6/76-147-II, 2364, C.I.E. coll. A 9076, CABP [2003-01] [from series listed as *D. elongata* by Habib and Hasan (1982)]; 1♀ diss., Nomal [36.07305°N, 74.25444°E], 25-VI-1962, CIBC, adult feeding on *T. cf. indica* [as *T. cf. troupii*], *D. elongata*, CIBC Wol-6/62-465-III, 947, CIE. Coll. No. 18503, CABP [2003-02]; 1♂ diss., 1♀ diss., Shorkot [31.90972°N, 70.87722°E], west Pakistan, 17-IV-1967, M. Nararullah, on *Tamarix* sp., *D. elongata* N.A. Aslam det. 1970, *D. elongata* det. M.L. Cox 1982, CIE Coll. No. 3509, Comm. Inst. Ent. B.M. 1981-315, BMNH [2003-06, 07]; **SYRIA**: 2♀♀ diss., 1♀, Alep[po] [Halab; 36.20278°N, 37.15861°E], Syrie, NHMB [2003-14, 44]; **TAJIKISTAN**: 1♀ diss., 1♀, Dushanbe [38.5600°N, 68.7739°E], May-June 1966, Král, NMPC [2005-32]; 1♂ diss., 2♂♂, 1♀, Khodzhen [Qayraqqum; 40.2647°N, 69.7894°E], Samarkand Ob[last], 23-IV-1903, Val'nev, ZIN [2004-13]; 1♂ diss., 3♂♂, 1♀, Ghissar and Karateghin Mt. Ranges [approximate location; 39.06°N, 69.82°E], ZIN [2004-27]; 1♂ diss., Hissar [Hisor; 38.48194°N, 68.59694°E], Buchara, [*D.*] *sulphurea*, MSNM [2003-16]; 1♂ diss., 1♂, Karatack [Karatag; 38.617°N, 68.333°E], Buchara, Stauding, [*D.*] *sulphurea* m.n.sp., *D. sulphurea* Reitt., DEI [2003-11]; 2♂♂ diss., 4♂♂, 4♀♀, Karatag, west Buchara, 916 m [elev.], 1898, F. Hauser, *D. [e.] a. carinata* [2♂♂ diss., 1♂, 1♀ of DEI], DEI [2005-12], NHMB [2005-07; 3♂♂, 2♀♀ not diss.], BMNH [1♀]; 1♀ diss., Karatag, west Buchara, *D. [e.] v. carinata*, NMPC [2005-33]; 1♀ diss., Kurgan-Tsu BG [Qurghonteppea or Kurgan-Tyube; 37.83639°N, 68.78028°E], Rußland, 28-IV-1989, *D. elongata* R. Beenen det. 2002, RBCN [2003-09]; 2♂♂ diss., 1♀, Nurek [Norak; 38.38833°N, 69.325°E], Dušanbe [Dushanbe] environs, 25-VI-1976, Josef Král, NMPC [2004-38, 39]; 2♂♂, 2♀♀, diss., Sary-pul [38.4167°N, 70.1333°E], Mts. Karategin, 1,482 m [elev.], 1898, F. Hauser, *D. e. v. carinata* R. det [1♂ of BMNH], NHMB [2003-29], BMNH [2005-04 and 1♀]; 1♂ diss., Vachsch [Vakhsh] River [approximate location: 37.5629°N, 68.5275°E], 23-IV-1992, RBCN [2003-15]; **TURKEY**: 1♀ diss., 3♂♂, 7♀♀, Ağri [Agri], 9 km west on road to Horasan [39.7393°N, 42.9235°E], 1,600 m [elev.], Ağri Prov., 1-VIII-2000, C. Morkel, on Asteraceae, *D. elongata* det. D. Erber 2001, ZMHB [2006-01]; 1♂ diss., Aralich [Aralik; 39.872778°N, 44.519167°E], Caucasus, 1893, Horváth, [*D.*] *e. var. sublineata* det. K. Lopatin 1958, [HNHM 2003-09]; 1♂ diss., 1♀ diss., Ardanuç [Ardanuc; 41.12861°N, 42.05916°E], 600m, Artvin [Prov.], 9-VII-1998, I. Aslan, *D. elongata* det. I. Aslan, IAET [2003-01, 02] [from series listed as *D. elongata* by Aslan *et al.* 2000]; 1♂ diss., 2♀♀, Artvin [41.18222°N, 41.81944°E], 2-VII-1975, 700 m [elev.], Osella, MRSN [2003-06]; 1♂ diss., 1♂, 1♀, Artvin, 13-15-VIII-

1976, Bohao, ex coll. Josef Kral, Prag, 1987–1989, coll. U. Arnold, Berlin, *D. elongata carinata* R. Beenen det 1993, RBCN [2008-01]; 1 ♀ diss., Artvin, 12 km east [41.1329°N, 41.8978°E], 26-V-1990, P. Kanaar, *D. elongata* ssp. *carinata* R. Beenen det. 1992, RBCN [2003-06]; 1 ♀ diss., 6 ♀♀, Siirt, southwest, on riverbank [37.8192°N, 41.8679°E], ca. 550 m [elev.], southeast Anatolia, 28-VII-1985, Heinz, *D. e. carinata* det. Beenen 1996 [2 ♀♀], *D. elongata* det. Beenen 1998 [1 ♀ diss., 4 ♀♀], ZMHB [2006-04]; **TURKMENISTAN:** 2 ♂♂ diss., 1 ♀ diss., Ashgabat, 2-IX-2002, S.N. Myartseva, on *T. ramosissima*, GSWRL [2003-02, 04, 07]; 2 ♂♂ diss., Ashgabat [37.95°N, 58.36667°E], Dry Sport Lake, 26-IX-1996, S. N. Myartseva, on *Tamarix* sp. [prob. *T. aralensis* J. Gaskin], [parasitoid] wasp found in abdomen [1 ♂], GSWRL [2005-36, 102] [7 specimens from Lot GSWRL(CJD)-1996-4 identified as *D. elongata* by S.M. Clark on 28-X-1996 at West Virginia Dept of Agric.] [8 specimens (no. 9204) from Lot GSWRL(CJD)-1997-1 identified as *Diorhabda* n. sp. by A. Konstantinov on 21-V-1997 at USDA SEL, SEL Lot # 9704023] [parasite *Baryscapus diorhabdivorus* Gates & Myartseva (Hymenoptera: Eulophidae) found in 1 adult in lot GSWRL-2005-01 identified by M. Gates on 28-VII-2005 at USDA SEL]; 1 ♀ diss., 4 ♂♂, 7 ♀♀, Ashgabat, Dry Sport Lake, 11-V-1997, S. N. Myartseva, on *T. ramosissima* [prob. *T. aralensis* J. Gaskin], voucher shipment GSWRL(CJD)-1997-11, 9005–9012, 9020–9022, *D. elongata* det. I. Lopatin 1999 [4 ♂♂, 7 ♀♀], GSWRL [2005-66] [8 specimens (nos. 9200, 9201) from Lot GSWRL(CJD)-1997-1 identified as *Diorhabda* n. sp. by A. Konstantinov on 21-V-1997 at USDA SEL, SEL Lot # 9704023]; 4 ♂♂ diss., 2 ♀♀ diss., Ashgabat, Dry Sport Lake, 11-VI-1997, S. N. Myartseva and P. Boldt, on *T. ramosissima* [prob. *T. aralensis* J. Gaskin], USDA lab colony at Temple, Texas, voucher (1997, J.L. Tracy), voucher shipment GSWRL(CJD)-1997-12, *D. elongata* det. I. Lopatin 1999 [1 ♂ diss.], 9004, GSWRL [2003-11, 2005-09, 59, 60, 61, 62]; 7 ♂♂ diss., 7 ♂♂, 5 ♀♀, Ashgabat, Dry Sport Lake, 17-18-VIII-1998, A Knutson, Andrey Averin and Allen Knutson [7 ♂♂], on *T. ramosissima* [prob. *T. aralensis* J. Gaskin], defoliating shrubs, voucher shipment GSWRL-1998-15, *D. elongata* det. I. Lopatin 1999 [1 ♂ diss., 5 ♂♂, 3 ♀♀], 8993–8996, 8998–9003, GSWRL [2005-25; 2008-12, 13, 14, 15, 16, 17] [photo of damage to tamarisk in DeLoach *et al.* (2003b), Fig. 3]; 1 ♀ diss., 6 ♂♂, 2 ♀♀, Ashgabat, Dry Sport Lake, 26-IX-2002, S.N. Myartseva, on *Tamarix* spp., GSWRL [2006-10]; 1 ♂ diss., 3 ♀♀ diss., Ashgabat, Karakum [Quaragum] Canal, 12-IX-2002, S.N. Myartseva, on *T. ramosissima*, GSWRL [2003-A1, A2, A3, A4]; 2 ♀♀ diss., Cardruj [Turkmenabat; 39.10139°N, 63.575°E], Buchara, [*D.*] *e. var. sublineata* det. K. Lopatin 1958, HNHM [2003-13, 2004-02]; 1 ♂ diss., 2 ♂♂, Chardzhuy [Turkmenabat], 21-VI-[19]04, Z. Fisher, ZIN [2005-03]; 2 ♂♂ diss., Cemenibit [35.4489°N, 62.3958°E], 22 km north Kujka, 1-IV-1992, Snilek, EGRC [2005-02, 07]; 1 ♀ diss., Chule [Chuli] Canyon, 53 km west Ashgabat (10, 852 km odom.) [38.08°N, 57.77°E], 25-V-1995, on *Tamarix ramosissima*, C.J. DeLoach, GSWRL [2004-13]; 1 ♂ diss., Danata Village [39.08389°N, 55.1617°E], 157 m [elev.], 31-V-2000, J. Gaskin, on *T. aucheriana* [det. J. Gaskin], Coll. No. 1044, GSWRL [2003-55]; 3 ♂♂ diss., 3 ♀♀ diss., Svintsovyi Rudnik Village [Svintsovy Rudnik; 37.88472°N, 66.45138°E], Kughitangolarja [Kugitang] River, Kughitang Mts., 3-V-1989, Osipov Coll., GSWRL [2003-66, 67, 68, 69, 2004-06, 07]; 1 ♂ diss., 1 ♀ diss., 1 ♂, 1 ♀, Tedzhen [Tejen; 37.37861°N, 60.49611°E], *D. elongata*, Coll. Reitter, HNHM [2004-03, 04]; 1 ♀ diss., 1 ♀, Tschardsui [Turkmenabat; see Cardruj], Turkestan, *D. sulfurea* Rt. det. Dr. Fleischer, NMPC [2005-03], 1 ♀, Tschardsui [Turkmenabat], Trans-Caspia, 4358b, coll[ection] Kõuril P5/46/62, NMPC; **UKRAINE:** 1 ♂ diss., 1 ♀ diss., Izium v[illage] [geocoordinates not locatable], Odessa Reg. [mapped approximate location in Odessa region as Izmayil: 45.3500°N, 28.8330°E], southwest Ukraine, 15-VII-1974, Osipov Coll., GSWRL [2003-71, 2004-09]; **UNITED STATES OF AMERICA** (introduced): **Texas: Hutchinson Co.:** 4 ♂♂ diss., 1 ♀, Johnson Ranch (cage 7) on Canadian River near Borger [approx., 35.7294°N, -101.4126°W], 26-VI-2007, E. Jones, on *T. ramosissima*/*T. chinensis*, voucher [source: 7 km W of Qarshi, Uzbekistan], GSWRL [2007-54, 55, 56, 57]; **Baylor Co.:** 1 ♂ diss., 2 ♂♂, 1 ♀, Lake Kemp, west side, Waggoner Ranch site B, 33.709267°N, -99.276395°E, 7–9-X-2008, Charles Randal, on *T. ramosissima*/*T. chinensis*, voucher [source: 7 km W of Qarshi, Uzbekistan], GSWRL [2008-25]; **UNKNOWN COUNTRY:** 1 ♂ diss., Attica [location of Attiki, Greece; considered as mislabeled], Reitter, ZMAN [2008-05]; 1 ♂ diss., 1 ♀, Araxes [Aras River of Armenia, Azerbaijan and Iran], VI-[19]10, J. Vesely, Coll[ection] Dr. J. Vesely, NMPC [2004-23]; 2 ♂♂, 2 ♀♀, Araxes, coll. Purkyně, ZMAN; 1 ♀ diss., Araxesthal [Aras River], Reitter, HNHM [2003-12]; 1 ♂ diss., Dulicata

[geocoordinates not locatable, possibly Dul'ta, Uzbekistan], Turkestan, NHMB [2003-03]; 1♂ diss., Ferolash [geocoordinates not locatable], Caucasus, *D. elongata*, DEI [2005-10]; **UZBEKISTAN**: 2♂♂ diss., 3♀♀ diss., Buxoro, 5 km northwest [39.8228°N, 64.39134°E], along the road to Gazli, 27-IX-2002, R. Sobhian, on *Tamarix*, USDA [Buchara] lab colony at Albany, California, voucher (2002-2003, D. Bean), shipment EIWRU-2002-1010, GSWRL [2003-39, 2005-52, 55, 57, 58]; 1♂ diss., 1♀ Ferghana [Farg`ona; 40.3933°N, 71.7794°E], V-1961, L. Medvedev, *D. elongata* det. L. Medvedev, GSWRL [2004-12]; 3♂♂ diss., 3♀♀ diss., 6♂♂, 4♀♀, Karshi [Qarshi], 10 km west [38.92278°N, 65.73307°E], 7-IV-1999, A. Kirk & R. Sobhian, on *Tamarix*, *D. elongata* det. I.K. Lopatin 1999 [3♂♂ diss., 3♀♀ diss., 4♂♂, 3♀♀], 9052–9064, GSWRL [2003-44, 2005-71, 72, 2007-02, 2008-18, 2008-19]; 4♂♂ diss., 5♀♀ diss., Qarshi, 7 km west [38.90721°N, 65.76314°E], 26-IX-2002, R. Sobhian, on *Tamarix*, USDA lab colony at Temple, Texas, voucher (2003, L. Milbrath [nos. 1298-1300]), USDA lab colony at Albany, California, voucher (1♂, 3♀♀, 26-VI-2002 and 20-I-2003, D. Bean), shipment EIWRU-2002-1010, GSWRL [2003-16, 18, 72, 73, 2005-69, 70, 85, 88, 89] [released in north Texas in 2006] [used in biological studies of Milbrath and DeLoach (2006a, 2006b), Milbrath *et al.* (2007), Herr *et al.* (in prep.), Bean and Keller (in prep.), and Thompson *et al.* (in prep.)]; 1♂ diss., 2♂♂, Namangan City [40.99527°N, 71.6725°E], Ferghana Valley, 30-III to 15-IV-1903, Yankovskii, ZIN [2004-07]; 1♀ diss., 4♀♀, Samarkand [Samarqand; 39.6542°N, 66.9597°E], Turkestan or[iental], daroval Král, NMPC [2006-03]; 1♂ diss., Sansar [Kirk; 39.7167°N, 68.0167°E], Turkestan, 1892, Glasnov, NHMB [2004-02]; 2♂♂ diss., 4♀♀, 2♂♂, Saratoff. [Saratovskiy; 40.7667°N, 68.6667°E], Turkestan, NHMB [2003-24, 2005-06]; 2♂♂ diss., 1♀ diss., 6♂♂, 5♀♀, Tashkent [Toshkent], 140 km south [approximate location: 40.29057°N, 68.91332°E], 10-IV-1999, Kirk & Sobhian, on *Tamarix* spp., *D. elongata* det. I. Lopatin 1999 [1♂ diss., 1♀ diss., 6♂♂, 3♀♀], 9067–9077, GSWRL [2003-51, 52, 2004-16]; 1♂ diss., 7♂♂, 9♀♀, Tashkent [Toshkent], 50 km east [41.3206°N, 69.8273°E], 11-IV-1999, Kirk & Sobhian, on *Tamarix* spp., *D. elongata* det. I. Lopatin 1999 [6♂♂, 6♀♀], 9078, 9080–9090, GSWRL [2003-81].

Distribution. General. The native distribution of *D. carinata* ranges from Ukraine, eastern Turkey and Syria east to northwest China, Kyrgyzstan and Pakistan, extending as far south as southern Iran (Maps 3, 6). Further collections could give an exact location for *D. carinata* within the Odes'ka Oblast' of Ukraine and possibly expand its range to include the coast of the Black Sea in eastern Romania and southern Russia, and the semi-arid regions of northwestern India.

Confirmed Records. We have dissected specimens listed above (see **Materials Examined**) and confirmed the presence of *D. carinata* in the following countries with previous literature records (Map 3): Armenia (as Transcaucasus, Faldermann 1837), Azerbaijan (as Transcaucasus, Faldermann 1837), Georgia (as Transcaucasus, Faldermann 1937), Turkmenistan (as *D. e.* var. *carinata*) (Jacobson 1901), Afghanistan (as *D. e. carinata*) (Bechyné 1961; Lopatin 1963; Wilcox 1971; Medvedev 1983, 1985), Kazakhstan, and China (as *D. e. carinata*) (Lopatin *et al.* 2004). Specimens were dissected from three of four regions of Afghanistan listed with *D. e. carinata* by Medvedev (1983) (central, Badakshan, and Kabul-Jalalabad) and close to the fourth region (western) at Cemenibit, Turkmenistan. *Diorhabda carinata* were dissected from three series identified in publications as *D. e. carinata* in Afghanistan: Polichromi [Pol-e khromi] (Bechyné 1961), Tangi-Gharuh [Tangi Gharu Pass] at Kabul River (Lopatin 1963), and Gerab Orugan [Sare Gearbid Mt, Velayat-e Oruzgan] (Medvedev 1985).

New Records. We have dissected *D. carinata* from the following countries for which we find no previous specific reports of *D. carinata* in the literature: Turkey, Iran, Iraq, Syria, Uzbekistan, Kyrgyzstan, Tajikistan, Pakistan, Ukraine, and the United States of America (Texas; introduced; Map 7, see **Potential in Tamarisk Biological Control** below for additional details). With the exception of Ukraine and Kyrgyzstan, past reports of *D. elongata* occur from all these countries that should refer, at least in part, to *D. carinata* (see synonymy above). Yakhontov and Davletshina (1955) site a potential report of *D. elongata* in Ukraine by Degtarev (1928), but we were unable to obtain this reference for verification. We dissected *D. carinata* from four series with published identifications of *D. elongata*: Assur [Ash Sharqat], Iraq (Holdhaus 1920); Robat-e Qozlog [Robate-Ghozlog], Iran (Lopatin 1981); Kund, Pakistan (Habib and Hasan 1982); and Artvin, Turkey (Aslan *et al.* 2000).

Unconfirmed Records. We cannot confirm a listing of *D. carinata* (as *D. e. var. carinata*) from Russia (Heyden 1891), but suspect it may be present along the Caspian Sea in the Dagestan region of southern Russia (Map 8b). We consider records of *D. e. var. carinata* from France (Laboissière 1934) and *D. e. ab. carinata* from Italy (Porta 1934) as erroneous (see lists of material examined with these identifications by Laboissière for specimens from France and Italy under *D. sublineata* and *D. elongata*, respectively). We consider as mislabeled a single male specimen bearing the label of “Attica, Reitter” (Greece) from ZMAN (2008-05).

We dissected only *D. carinata* from all seven available locations in Afghanistan (four) and Pakistan (three) (Map 3). Therefore we consider as *D. carinata* five unconfirmed records of *D. elongata* from northern Pakistan (Habib and Hasan 1982; three records) and *D. e. carinata* from Afghanistan (Medvedev 1985; two records), but *D. carinulata* may also be present at some locations. Specimens of *D. carinata* were dissected from all nine available localities in Azerbaijan and *D. carinulata* was also dissected from two of these same localities. Consequently, we accept all nine unconfirmed collection records of *D. elongata* in Azerbaijan (Samedov and Mirzoeva 1985) as *D. carinata*, but *D. carinulata* may also be present at some of these localities. Mirzoeva (2001) reported that *D. carinata* (as *D. elongata*) was found in all four major regions of Azerbaijan and was most common in the Great Caucasus and Small Caucasus. Specimens dissected from all five available locations in eastern Georgia were *D. carinata*, and we consider Lozovoi’s (1961) report of *D. elongata* from eastern Georgia to be *D. carinata*. We dissected *D. carinata* from all five available locations in Turkey east of 41°E, including three locations in Arvin Ili. The closest occurrence of *D. elongata* to *D. carinata* in Turkey is in Malatya, which is 316 km north northwest of *D. carinata* in Siirt. Therefore, we regard two unconfirmed records of *D. elongata* in Artvin Ili and neighboring Ezurum Ili to also be *D. carinata*. We dissected *D. carinata* from nine and *D. carinulata* from one of the ten available locations in Tajikistan. Therefore we consider nine unconfirmed records in Tajikistan to be *D. carinata*, but *D. carinulata* may also be present at some sites. We regard a report of *D. elongata* at Mikhaylovka [Sarykemer], Kazakhstan (Kulenova 1968) to be *D. carinata* because of its proximity to a collection of *D. carinata* from Auliye–Ata [Taraz], Kazakhstan.

Below are 28 unconfirmed locality records that we consider as *D. carinata*, but are listed as *D. e. carinata* in Afghanistan (2) and *D. elongata* in Azerbaijan (9), Kazakhstan (1), Pakistan (3), Tajikistan (9), and western Turkey (4) (Map 3):

AFGHANISTAN: 2 spms., Banu [Banow], southwest [35.63420°N, 69.25260°N], Baglan [Velyat–e Baghlan], 2,000 m [elev.], 14–VIII-1972; 1 spm., Samti [west; 37.5854°N, 69.9592°N], Pan’ [Panj] River, Badakhshan [Velyat–e Badakhshan], 1,100 m [elev.], IV-1971 (Medvedev 1985); **AZERBAIJAN:** Akstafa [Agstafa; 41.1189°N, 45.4539°E], 25-V-1958; Belokany [Balakan; 41.7258°N, 46.4083°E], 3-V-1972; Dzhul’fa [Culfa; 38.9500°N, 45.6319°E], 13-V-1933; Matsekh [Matsex; 41.6553°N, 46.5811°E], 3-V-1972; Mingachaur [Mingacevir; 40.7700°N, 47.0489°E], 23-V-1946 [*D. carinata* dissected from same location]; Neftechala [Neftcala; 39.3586°N, 49.2469°E], 28-V-1980; Saatly [two possible geocoordinates], 26-VI-1969; Sumgait [Sumqayit; 40.5897°N, 49.6689°E], 12-VII-1935; Yevlakh [Yevlax; 40.6172°N, 47.1500°E], 12-VI-1903 (Samedov and Mirzoeva 1985); **KAZAKHSTAN:** Mikhaylovka [Sarykemer; 43.0000°N, 71.5000°E] (Kulenova 1968); **PAKISTAN:** Chitral [35.8419°N, 71.7819°E], *Tamarix* spp.; Gilgit [35.9167°N, 74.3000°E], *Tamarix* spp.; Islamabad [33.7000°N, 73.1667°E], *Tamarix* spp. (Habib and Hasan 1982); **TAJIKISTAN:** Baljuan [Baljuvon; 38.3108°N, 69.6669°E], 11-V-1951, E.P. Luppova; Dushanbe [38.5600°N, 68.7739°E] [*D. carinata* dissected from same location], P.N. Kulinich; Kal’ aiKhumb, behind and on right side, on Pyanj River [Darya–ye Panj] [38.4489°N, 70.81529°E], 6-VII-1960, L.V. Soboleva; Khoja Obigarm [38.9003°N, 68.8008°E], P.N. Kulinich; Kondara [38.1190°N, 68.8283°E] canyon, VI-VII-1956, P.N. Kulinich (Kulinich 1962); Kurgan–Tyube [Qurghonteppa; 37.8364°N, 68.7803°E] environs [*D. carinata* dissected from same location] (Lopatin 1959); Pyanj [Panj; 37.2383°N, 69.0969°E] environs, P.N. Kulinich (Kulinich 1962); Shaartuz [Shahrtuz; 37.2594°N, 68.1347°E] (Lopatin 1959); Vaidar village [Vaydara; 38.9667°N, 70.1833°E], 20-V-1961, L.V. Soboleva (Kulinich 1962); **TURKEY:** Artvin [41.1822°N, 41.8194°E], 5-VII-1994, I. Aslan [*D. carinata* dissected from same location]; Sarigol [40.9553°N, 41.4989°E],

5-VII-1994, I. Aslan; Yusufeli [40.8167°N, 41.5500°E], 5-VII-1994, I. Aslan (Aslan *et al.* 2000); 2♂♂, 3♀♀, Uzundere [40.5314°N, 41.5531°E], Ezurum Ili, 1,100 m [elev.], 7-VI-1995 (Aslan 1998).

Discussion. *Taxonomy.* *Galeruca carinata* Faldermann (1837) (as *Galleruca carinata*) was described from the Transcaucasus and synonymized under *G. elongata* by Reiche and Saulcy (1858). Weise (1893) proposed the variety *D. elongata* var. *carinata* under which he incorrectly synonymized *G. carinulata* (Desbrochers 1870) of southern Russia. Weise (1924) later proposed the aberration *D. elongata* ab. *carinata* and this has been followed by several taxonomists (Winkler 1924–1932, Laboissière 1934, Warchalowski 2003). Bechyné (1961) proposed the subspecies *D. e. carinata* with an implied range from the Transcaucasus to central Asia and Afghanistan. Several other taxonomists followed Bechyné in reporting *D. e. carinata* from Afghanistan (Lopatin 1963, Wilcox 1971, Medvedev 1983), Kazakhstan, and China (Lopatin *et al.* 2004). Berti and Rapilly (1973) studied the endophalli of type specimens of *D. carinata* and *D. carinulata* and restored their species status, removing them from synonymy with one another and, by implication, with *D. elongata*. However, Berti and Rapilly (1973) omit *D. elongata* in their discussion and provide no distributional data for *D. carinata*. We find that the external characters they provide regarding elytral carinae and the shape of the pronotum are variable and insufficient for species diagnosis (further discussed below). In addition, they provide no information on variability of the endophallus. This lack of data has apparently contributed to the lack of recognition of *D. carinata* as a species in recent taxonomic treatments (Riley *et al.* 2003, Warchalowski 2003, Bieńkowski 2004, Lopatin *et al.* 2004).

We dissected 25 males from 16 locations of the type locality of *D. carinata* in the Transcaucasus (Georgia, Armenia and Azerbaijan) with endophalli matching that of the type specimen of *D. carinata* as illustrated by Berti and Rapilly (1973) (Map 3). One male and two female *D. carinulata* were dissected from two of the same locations with *D. carinata* in Azerbaijan. Three key characters of the endophallus of *D. carinata* that distinguish it from other members of the *D. elongata* group can be seen in the illustration of the holotype (Fig. 18 of Berti and Rapilly 1973) and our illustration (Fig. 15): (1) the presence of spines irregularly spaced along the distal blade of the elongate endophallic sclerite; (2) a lateral appendage on the palmate endophallic sclerite; and (3) the lack of a connecting endophallic sclerite between the palmate and elongate sclerites. We are certain that specimens we studied with endophalli matching that of *D. carinata* (Figs. 15, 20, 25, 30) form a single species conspecific with *D. carinata*. We find additional characters in the endophallic sclerites and female genitalia (vaginal palpi and internal sternite VIII) of *D. carinata* throughout its range from west to central Asia that distinguish it from *D. elongata*, *D. carinulata* and other members of the *D. elongata* group (Figs. 15, 20, 25, 30, 35, 40; Map 3). The distinctive genitalic characters of *D. carinata* are maintained in the same areas where *D. elongata*, *D. carinulata*, *D. meridionalis*, and *D. sublineata* occur, and this is strong evidence for reproductive isolation between these species (see **Biogeography** below; Map 1, Table 8). Therefore, we firmly support Berti and Rapilly in restoring *D. carinata* to species status, removing it from synonymy with both *D. elongata* and *D. carinulata*.

If *D. carinata* were an interbreeding subspecies of *D. elongata*, we should see intermediate morphologies of the distinguishing characters found in the two endophallic sclerites and the vaginal palpi. Such intermediate forms should increase along a geographic gradient approaching range contact of these species in Turkey, Georgia and Syria. For example, we should see intermediate forms of the palmate sclerite in a progression from broadly rounded (in *D. elongata*; Fig. 29) to truncate serrate (in *D. carinata*; Fig. 30). However, no intermediate forms of palmate sclerites were seen in field collections of 157 male *D. elongata* and 122 male *D. carinata*, including 21 male *D. elongata* in Turkey and Syria and 11 male *D. carinata* in Turkey and Georgia. Similarly, intermediate forms in vaginal palpi ranging from broadly rounded (as in *D. elongata*; Fig. 34) to triangulate (as in *D. carinata*; Fig. 35) were not seen in 85 female *D. elongata* or 67 female *D. carinata*, including 14 female *D. elongata* from Turkey and 9 female *D. carinata* from Turkey, Georgia, and Syria (Map 1). The lack of intermediate forms is evidence of reproductive isolation between *D. elongata* and *D. carinata*. Further evidence for reproductive isolation between *D. carinata* and several members of the *D. elongata* group is also found in previously discussed differences in component ratios of putative aggregation pheromones and reduced hybrid egg viability.

Faldermann (1837) gave a length of 7 mm for the male type of *D. carinata* which is too large to have included the sympatric *D. carinulata* in which males only reach 6.09 mm (Table 2). Male *D. carinata* commonly exceed 7 mm in length (range 5.12–7.34 mm). The application of the name “*D. elongata*” to both *D. carinata* and *D. carinulata* where these species are sympatric can be seen in the given range in length of 4.5–8 mm for males and females of “*D. elongata*” in taxonomic keys of Russia (Ogloblin 1936) and central Asia (Medvedev 1959, Lopatin 1977b, Lopatin and Kulenova 1986). Overall ranges in length for both sexes are 4.63–6.99 mm for *D. carinulata* and 5.05–8.44 mm for *D. carinata* (Table 2).

We find that external characters used in separating *D. carinata* from sibling species are inadequate and that genitalic characters must be used. Weise (1893) noted black markings on the pronotum and abdominal sternites as characters distinguishing *D. carinata* (as *D. e. var. carinata*) from *D. elongata*, but this character is highly variable in both taxa. Black spots on the pronotum were also noted as a distinguishing character for *D. carinata* (as *D. e. ab. carinata*) by Laboissière (1934) and Porta (1934), who also noted black spots on the femora of the leg. Warchalowski (2003) notes black spots on both the pronotum and head as distinguishing characters for *D. carinata* (as *D. e. ab. carinata*). However, we find that black spots on the head, pronotum, and femora variably occur in both *D. elongata* and *D. carinata*, making these characters unsuitable for species diagnosis. Bechyné (1961) noted two differences between *D. e. carinata* and the Mediterranean form, *D. e. elongata*: (1) *D. carinata* reaches a greater length, ca. 7 mm and (2) the sublateral carina approaches the lateral margins of the elytra more closely towards the apex than in *D. e. elongata*. However, both of these external characters are variable and overlap between *D. carinata* and *D. elongata* (although it is uncommon for *D. elongata* to exceed 7 mm in length). We have dissected specimens of *D. carinata* that were misidentified by taxonomists using external diagnostic characters as *D. elongata* in eleven countries and *D. e. var. sublineata* in Turkey and Turkmenistan (see **Material examined**).

Berti and Rapilly (1973) proposed that the following five external characters of *D. carinata* can be used to distinguish it from *D. carinulata*: (1) length of ca. 6.7 mm, (2) posterior angles on the pronotum are more pronounced and farther from the base, (3) pronotum is broader, (4) only a lateral carina is clearly present on the elytra, and (5) punctuation on the elytra is simple. They give the following contrasting characters for *D. carinulata*: (1) length of ca. 4.9 mm, (2) posterior angles on pronotum are less pronounced and closer to the base, (3) pronotum is narrower, (4) in addition to a lateral carina on the elytra, a median carina (along a clear humeral furrow) and a sutural carina are seen, and (5) punctuation on the elytra is almost confluent in places. In keys for separating *D. carinulata* from *D. elongata* (considered as including *D. carinata*), Warchalowski (2003) used three of the above characters: body length, the posterior angle of the pronotum, and number of elytral carinae. However, we find all these external characters as too interspecifically variable for species diagnosis, and the only taxonomically reliable characters provided by Berti and Rapilly (1973) are their well illustrated differences in the morphology of the endophalli of *D. carinata*, *D. carinulata*, and *D. meridionalis*.

We consider *D. e. carinata* as regarded by Bechyné to be synonymous with *D. carinata*. Because of the incorrect synonymization of *D. carinulata* (as *G. carinulata*) under *D. elongata* var. *carinata* by Weise (1893), Wilcox (1971) included *D. carinulata* under the name *D. e. carinata*. But Bechyné (1961) did not mention *D. carinulata* in his description of *D. e. carinata* and the larger stated size of ca. 7 mm would exclude almost all *D. carinulata* (Table 2). We examined a specimen of *D. carinata* from the series that Bechyné referred to *D. e. carinata* from Pol-e khomri (as Polichromi), Afghanistan. Also, a specimen of *D. carinata* was dissected from Taraz (= Auliye-Ata), Kazakhstan with a determination label of *D. e. carinata* by Bechyné in 1955.

We dissected genitalia from four possibly 50–100 year old specimens of *D. carinata* from central Asia with the following four identification labels: “*Diorhabda sulphurea* Reitt” (Karatack [Karatag], Tajikistan; DEI), “*D. sulfurea* Rt” (Tshcardsui [Turkmenabat], Turkmenistan; NMPC), “*sulphurea*” (Hissar [Hisor], Tajikistan; MSNM), and “*Diorhabda sulphureus* Reitter det. H. Bollow 1939” (Aulie-Ata [Taraz], Kazakhstan; also with label “*D. e. carinata* Fald. det. J. Bechyné 1955”; NHMB). The specimen from Karatag, Tajikistan also bore the label “m.n.sp. [manuscript nova species] *sulphurea*” indicating that “*D. sulphurea*” was an unpublished manuscript name, probably of the German coleopterist Edmund Reitter who

actively published ca. 1870–1915. We find no publication of the manuscript name “*D. sulphurea*”. In any case, Faldermann’s (1837) description of *D. carinata* precedes Reitter’s works.

In the field in central and southwest Asia, it would be useful to distinguish live adults of *D. carinata* from the sympatric and partially syntopic species *D. carinulata* and *D. meridionalis*. Differences in minimum and maximum sizes reached by males and females of *D. carinata* compared to *D. carinulata* and *D. meridionalis* can aid in identification of some specimens (see Table 2). In some living females, the internal sternite VIII appears as a dark Y-shaped area visible through the translucent last visible abdominal sternite (see Lewis *et al.* 2003b, Fig. 1G). Female *D. carinata* often have the lobes of internal sternite VIII both pointed and curved inward (Fig. 40—Baghdad, Ashgabat), a condition not seen in *D. carinulata* and *D. meridionalis* (Figs. 42–43). As discussed below, a high incidence of *Diorhabda* egg masses on *Tamarix* bark (Milbrath *et al.* 2007) also can indicate the presence of *D. carinata*.

Common Name. The vernacular name “larger tamarisk beetle” refers to the statistically significant larger mean size of *D. carinata* compared to all other species in the *D. elongata* group. Among the *D. elongata* group, only *D. carinata* exceeds 7 mm in length in males and 8 mm in length in females (Table 2). *Diorhabda carinata* is especially larger than the two species with which it is moderately to partially sympatric and syntopic, *D. carinulata* and *D. meridionalis*.

Biology. Host Plants. Because of the misapplication of the name *D. elongata* to both *D. carinata* and *D. carinulata* over a wide area of west and central Asia, we cannot conclusively distinguish biological literature that refers to *D. carinata* alone. *Diorhabda carinata* is more commonly collected than *D. carinulata* in the following areas where we consider field observations to primarily involve *D. carinata* (see *Unconfirmed Records* above): eastern Georgia (Lozovoi 1961), Azerbaijan (Samedov and Mirzoeva 1985), southern Turkmenistan (Myartseva 1995, 1999, 2001), and Tajikistan (Kulinich 1962).

All previous reports of hosts for *D. carinata* were made under the name *D. elongata*. *D. carinata* (as *D. elongata*) feeds upon *Tamarix ramosissima* and *T. smyrnensis* (as *T. hohenackeri* Bunge) in eastern Georgia (Lozovoi 1961), *T. meyeri* Boissier and *T. smyrnensis* in Azerbaijan (Samedov and Mirzoeva 1985), and *T. ramosissima*, *T. hispida* Willdenow and *T. arceuthoides* Bunge in Tajikistan (Kulinich 1962) (see *Unconfirmed Records* above) (Table 1). We also examined specimens of *D. carinata* collected from *T. ramosissima* near Shelek (Chilik), Kazakhstan by I.D. Mityaev and R. Jashenko, and in Chuli Canyon, Turkmenistan by C.J. DeLoach. *Tamarix* sp. is recorded as a host for material we examined of *D. carinata* collected from Shorkot, Pakistan. We report the following four new host records from our dissected material: *T. aralensis* Bunge from Dry Sport Lake, Ashgabat, Turkmenistan collected by S. Myartseva; *T. aucheriana* (Decaisne) Baum from Village Danata, Turkmenistan collected by C.J. DeLoach; *T. aphylla* from Kund, Pakistan (as *D. elongata* in Habib and Hasan [1982]); and *T. ramosissima*/*T. chinensis* from near Borger and Seymour, Texas. We also examined an adult collected on *T. cf. indica* Willdenow (as *T. cf. troupii* Hole) from Nomal, Pakistan. Dalin *et al.* (in press) found that *D. carinata* (as *D. e. carinata*) from Uzbekistan preferred *T. parviflora* to a similar degree as *T. ramosissima* in multiple-choice field cage studies in southern California, making *T. parviflora* a potential new host. *Diorhabda carinata* shares four of its eight known *Tamarix* spp. hosts with *D. carinulata*: *T. ramosissima*, *T. arceuthoides*, *T. hispida*, and *T. aralensis* (Table 1). *Diorhabda carinata* was collected syntopically from the same trees with *D. carinulata* on *T. aralensis* at Dry Sport Lake (nr Ashgabat), Turkmenistan, and *T. ramosissima* near Shelek, Kazakhstan and Quaragum Canal (nr Ashgabat), Turkmenistan.

In no-choice larval host suitability studies, *D. carinata* larvae from Uzbekistan can only survive to adulthood on plants of the order Tamaricales, including *Tamarix* (Tamaricaceae) and, to a generally lesser degree, on three North American *Frankenia* spp. (Frankeniaceae): *F. salina*, *F. johnstonii*, and *F. jamesii* (Milbrath and DeLoach 2006a, Herr *et al.* in prep.). Multiple-choice adult oviposition studies in field cages (Milbrath and DeLoach 2006a) reveal that the three North American *Frankenia* spp. provide little attraction for oviposition by *D. carinata* compared to *Tamarix*. In field cage no-choice studies, oviposition by *D. carinata* on *F. jamesii* and *F. johnstonii* was not different from non-host coyote willow (*Salix exigua*) and adults experienced increased mortality compared to *T. ramosissima* × *T. chinensis* treatments (Milbrath and

DeLoach 2006a). Among invasive North American *Tamarix* spp. in large field cages, adult *D. carinata* oviposited as much on *T. aphylla* as on *T. ramosissima*, *T. parviflora* or *T. chinensis* × *T. canariensis*/*T. gallica*, and oviposited significantly more on *T. aphylla* than on *T. canariensis*/*T. gallica*. However, in a later similar multiple-choice field cage test among *Tamarix* spp., Milbrath and DeLoach (2006b) found that *D. carinata* oviposited significantly less on *T. aphylla* than on all other *Tamarix*, including *T. ramosissima* × *T. chinensis*, *T. ramosissima* × *T. canariensis*/*T. gallica*, *T. canariensis*/*T. gallica* and *T. parviflora*. In less discriminating no-choice field cage studies, *D. carinata* accepted *T. aphylla* for oviposition to the same degree they accepted *T. ramosissima* × *T. chinensis* (Milbrath and DeLoach 2006b). *Tamarix aphylla* is at moderate risk of damage by *D. carinata* in the field and it is difficult to predict to what degree *D. carinata* would damage *T. aphylla*, especially in the absence of other *Tamarix* spp. (Milbrath and DeLoach 2006b). *Frankenia* is at low risk to damage from *D. carinata* (Milbrath and DeLoach 2006a). Risk of damage to both *T. aphylla* and *Frankenia* by *D. carinata* is probably much lower when these plants are not in the proximity of preferred *Tamarix* spp. (e.g., Blossey *et al.* 2001).

Ecology and Phenology. Kulinich (1962) found *D. carinata* (as *D. elongata*) damaging leaves and young shoots of tamarisk in Tajikistan, where it occurs from May to September. According to our data from examined material, *D. carinata* was collected as early as 23 April in Tajikistan. In southern Tajikistan, *D. carinata* (as *D. elongata*) can have four generations (Pripisnova 1965). Samedov and Mirzoeva (1985) report *D. carinata* (as *D. elongata*) as “frequently badly damaging” bushes of both *T. meyeri* and *T. smyrnensis* in Azerbaijan, where it has three generations from April to October. Lozovoi (1961) commonly found *D. carinata* (as *D. elongata*) on tamarisk throughout eastern Georgia from 1959–1960, but never in sufficient quantity to damage the plants. We have seen collection records from 18 April to 3 August in Georgia.

Diorhabda carinata severely defoliated tamarisk at Dry Sport Lake, near Ashgabat, Turkmenistan in August of 1998, and this was photographed by A. Knutson (for photo, see DeLoach *et al.* 2003b, Fig. 3) (see **Material examined**, specimen no. GSWRL 2005-25). We also found *D. carinulata* at this site in 1997 and 1998, but it was in much lower numbers than *D. carinata*. Our collaborator, Myartseva (1999) made season long observations of *D. carinata* (as *D. elongata*) at Dry Sport Lake in 1999. Five generations were observed, with the overwintered adults emerging and copulating in mid-March, the first eggs appearing in April, and the fifth generation adults emerging in late August and going into diapause. In July and August, temperatures often reached ca. 40°C during many days in which adults and larvae were absent, and this absence may be associated with a period of possible aestivation in the pupal or adult stage. Collection dates from our examined material range from 1 April to 12 September in Turkmenistan, 7 April to 26 September in Uzbekistan, and 9 April to 10 October in Iraq and Iran.

Milbrath *et al.* (2007) found that adult *D. carinata* (as *D. elongata* from Qarshi, Uzbekistan) overwintering at Temple, Texas had ca. 60–80% survival from early November through the beginning of March but survival dropped precipitously to ca. 10% by mid-March when the tamarisk leaves were just budding. Overwintered adults began ovipositing in late March giving rise to five generations and a partial sixth generation. Fifth generation adults emerging in early September oviposited for several weeks before ceasing oviposition in November when they appeared to enter diapause.

Five generations were also found in the field at Lake Kemp near Seymour, Texas in 2008 where adults were released in late April and the fifth generation adults emerged in the field by late September. Hundreds of adults could be easily found feeding in this area through 9 October. In late July, a group of ca. 2,000 adults emerged and congregated on a group of large tamarisks and over the course of 12 days appeared to migrate en masse east northeast for 46 meters, congregating on certain tamarisk trees, first at 18 meters and depositing eggs and then moving another 46 meters. (C. Randal, pers. comm.).

Milbrath *et al.* (2007) observed that *D. carinata* may deposit as much as one-third of its egg masses on the bark of trunks and branches of tamarisk. In contrast, *D. carinulata*, *D. sublineata*, and *D. elongata*, all deposit their eggs on tamarisk leaves, with the exception of *D. sublineata* rarely ovipositing on tamarisk stems (Milbrath *et al.* 2007). A high incidence of *Diorhabda* eggs found on the bark of trunks and branches of tamarisk can indicate the presence of *D. carinata* in areas of sympatry with other tamarisk beetles.

Development and Reproduction. Milbrath *et al.* (2007) found that, at 28°C, *D. carinata* (as *D. elongata* from Qarshi, Uzbekistan) had a development time of 18.6 days from egg to adult (with 73% survival), a fecundity of 233 eggs, and a population doubling time of 5.7 days. These values were all very similar to those found for *D. carinulata* (Turpan and Fukang), *D. elongata* (Crete), and *D. sublineata* (Tunisia) (all as *D. elongata*) in the same study.

Natural Enemies. The tachinid *Erynniopsis antennata* (Rondani) is reported as a parasite of larvae and pupae of *D. elongata* in Ashgabat, Turkmenistan (Richter and Myartseva 1996). *Diorhabda elongata* does not occur in Turkmenistan and this record probably should refer to *D. carinata* which is generally much more abundant than *D. carinulata* in Ashgabat. An adult parasitoid wasp, *Baryscapus diorhabdivorus* Gates & Myartseva (Hymenoptera: Eulophidae), was found inside an adult *D. carinata* collected from Ashgabat, Turkmenistan in late September. Previous reports of adult *B. diorhabdivorus* from both larvae and adults of *D. elongata* in Ashgabat (Gates *et al.* 2005) should also refer to *D. carinata*. The ground beetle, *Lebia holomera* Chaudior (Coleoptera: Carabidae), preys especially upon leaf beetles of the genus *Diorhabda* in south-central Asia and in the eastern Caucasus (Kyrzhanovskiy 1965), areas where *D. carinata* is common. The protozoan microsporidian parasite, *Nosema* sp., was found in adult *D. carinata* originating from two collections at Ashgabat, Turkmenistan (shipments GSWRL(CJD)1996-28 [identified by T. Poprawski] and GSWRL(CJD)-1997-12 [identified by G.M. Thomas]). The fungal pathogen *B. bassiana* was also found in adult *D. carinata* from Ashgabat, Turkmenistan (shipment GSWRL(CJD)1996-28) (identified by T. Poprawski).

Biogeography. Comparative. *Diorhabda carinata* differs from other tamarisk beetles by the following combination of biogeographic characteristics: (1) primarily continental with distribution usually greater than 500 km from the oceans and ranging to 2,900 m elevation; (2) usually found in warm temperate desert and grassland biomes; and (3) latitudinal range of 30–44°N and most common from 36–41°N (Table 7, Figs. 51–52). *Diorhabda carinata* is moderately sympatric with *D. carinulata*, their ranges overlapping in a large area that includes Azerbaijan and central Asia (northern Iran, Turkmenistan, Uzbekistan, Kazakhstan, Tajikistan, Kyrgyzstan, and western China), where both species have been referred to as *D. elongata* (see synonymy above; e.g., Ogloblin 1936, Yakhontov and Davletshina 1955, Kulinich 1962, Sinadsky 1968, Lopatin 1977a, Samedov and Mirzoeva 1985, Lopatin *et al.* 2004) (Map 1; Table 8). *Diorhabda carinulata* differs from *D. carinata* in ranging further north to 49°N and in being more common from 42–44°N. Conversely, *D. carinata* is more commonly collected than *D. carinulata* in some more southern areas from 35–42°N, especially in the deserts of the Transcaucasus and grasslands of Tajikistan. However, *D. carinulata* appears to be more common than *D. carinata* from 31–34°N in deserts of eastern Iran (Map 6). Further studies are needed to better understand the differing climatic preferences of these species. *Diorhabda carinata* and *D. carinulata* are also syntopic in some areas, having been collected together in the same series from the same tamarisk trees at three localities: Dry Sport Lake and Quaragum Canal, near Ashgabat, Turkmenistan, and Shelek, Kazakhstan. *Diorhabda carinata* and *D. carinulata* were also collected together in the same series (and probably also the same tamarisk trees) at Ordubad, Azerbaijan, and three locations in Uzbekistan: Buxoro (5 km northwest), Qarshi (10 km west), and 140 km south of Toshkent. These species were collected in the same locations but differing series at Qobustan, Azerbaijan; Golestan Biosphere Reserve, Iran; Sarytogay Forest, Kazakhstan; and Yining, China. Care must be taken to separate *D. carinata* and *D. carinulata* in laboratory colonies begun from areas of sympatry and syntopy in Central Asia.

Diorhabda carinata is partially sympatric with *D. meridionalis* in western Iran and Syria (Maps 1, 6; Table 8). These species are probably also syntopic over some areas, having been collected together in the same series at Halab, Syria and at four locations in western Iran: Jolow Gir, 34 km SE of Omidiyeh, Shushtar, and 30 km NNE of Borazjan. *Diorhabda meridionalis* differs from *D. carinata* in being maritime and common further south at 26–31°N (Figs. 51–52). In the small sample sizes in which *D. carinata* and *D. meridionalis* were collected together from 29.5–36°N, *D. carinata* was a little more abundant than *D. meridionalis* north of 30°N while *D. meridionalis* was a little more abundant south of 30°N (at 30 km NNE Borazjan). *Diorhabda carinata* is most similar to *D. meridionalis* and *D. carinulata* in terms of inhabited biomes (Fig. 53).

Diorhabda carinata is marginally sympatric with *D. sublineata*, their distributions meeting in Baghdad, Iraq. *Diorhabda sublineata* differs from *D. carinata* in being primarily maritime with a strong presence in the Mediterranean biome, and in ranging further south to 16°N where it is most common from 31–35°N. *Diorhabda carinata* is most biologically different from *D. sublineata*, the species with which it is most morphologically similar (Tables 9 and 10; Fig. 53). *Diorhabda carinata* is probably marginally sympatric with *D. elongata* in eastern Turkey, western Syria, and, possibly, southern Russia, Georgia and Azerbaijan (Map 1). *Diorhabda elongata* differs from *D. carinata* in being maritime with a strong presence in the Mediterranean biome (Figs. 51–52).

Descriptive. *Diorhabda carinata* is primarily found in the south central Palearctic realm, but two collection locations in northern Pakistan (Shorkot and Islamabad) fall within the borders of the Indo-Malayan realm (Maps 1, 3, 6). Most collections originate between 37° and 41°N in two biomes of Central Asia: the Deserts and Xeric Shrublands (ca. 0–800 m elevation) and Temperate Grasslands, Savannas and Shrublands (ca. 250–1,600 m) (Map 3, Table 9). Reports of *D. carinata* damaging tamarisk (Kulinich 1962, Samedov and Mirzoeva 1985, Myartseva 1999) originate from these two biomes in this region. Primary ecoregions for *D. carinata* in the Temperate Grasslands, Savannas and Shrublands biome from 37–41°N include the Gissaro–Alai Open Woodlands (ca. 250–450 m) and the Alai–West Tian Shian Steppe (ca. 400–1,600 m) in south central Kazakhstan and western Uzbekistan, Tajikistan and Kyrgyzstan (Map 3). Primary ecoregions with *D. carinata* in the Deserts and Xeric Shrublands biome from 37–41°N include the Azerbaijan Shrub Desert and Steppe (ca. 0–400 m) and the Central Asian Southern Desert in south central Kazakhstan, southern Uzbekistan and Turkmenistan (ca. 200–350 m). *Diorhabda carinata* occurs more frequently in the Temperate Conifer Forests biome than any other *Diorhabda* species, where it may be found from 33–41°N in northwestern Iran, eastern Turkey and northern Pakistan (ca. 550–1,600 m; Maps 3 and 6; Table 9). Other biomes with *D. carinata* from 37–41°N include the Temperate Broadleaf and Mixed Forests of northern Iran and northeast Turkey (ca. 350–550 m) and Montane Grasslands and Shrublands (Kopet Dag Woodlands and Forest Steppe ecoregion) along the border of Iran and Turkmenistan (ca. 200–850 m).

The westward distribution limit of *D. carinata* in Turkey and Ukraine corresponds well with the westward distribution limit of one of its host plants, *T. ramosissima* (Map 3). The distribution of the host *T. meyeri*, which ranges across deserts from Azerbaijan eastwards to Uzbekistan and Afghanistan (Rusanov 1949, Baum 1978; not shown), corresponds to the center of distribution of *D. carinata* in central Asia. The distribution of the host plant *T. aralensis* approximately coincides with the distribution of *D. carinata* in deserts of its southern range in Iran and Iraq as well as over its north-central range in Turkmenistan, Uzbekistan and Tajikistan (Map 3). The northern distribution of the host *T. aucheriana* also coincides with the range of *D. carinata* in Iraq and Iran (Map 3). The north central distribution of the host *T. arceuthoides* (Rusanov 1949, Baum 1978, Browicz 1991; not shown) coincides with the heavy areas of occurrence of *D. carinata* in its northeastern range in Tajikistan and southern Uzbekistan. *Tamarix arceuthoides* is a very common *Tamarix* from eastern Iraq to Tajikistan (100–3,000 m elevation) that occurs more commonly in mountainous rocky or pebbly substrates than does *T. ramosissima* (Rusanov 1949, Liu 1987, Browicz 1991) and prefers lower salinity habitats compared to *T. aucheriana* (Leonard 1992).

We find no reports of damage by *D. carinata* from the southern portion of its range, at 29–37°N (Map 6). Habib and Hasan (1982) studied *Tamarix* insect herbivores in northern Pakistan, but did not report any damage by *D. carinata* (as *D. elongata*) from 33–36°N. South of 37°N, *D. carinata* is primarily found in the Deserts and Xeric Shrublands biome of Iraq, Afghanistan, and Pakistan (ca. 50–1,500 m), but it also occurs in the Temperate Broadleaf and Mixed Forests and Temperate Conifer Forests biomes of western and northern Iran (ca. 1,150–1,900 m) (Maps 3 and 6; Table 9).

Potential in Tamarisk Biological Control. **Summary.** The larger tamarisk beetle is apparently establishing near Seymour, Texas (Map 7). *Diorhabda carinata* may be the most effective tamarisk beetle for control of *T. ramosissima*/*T. chinensis* in the temperate grasslands biome, including the Western Short Grasslands and Central and Southern Mixed Grasslands, and temperate conifer forest biome which includes the Arizona Mountains Forests of New Mexico and Arizona (Map 13). *Diorhabda carinata* may co-dominate with *D.*

carinulata in some temperate warm desert areas such as the Trans-Pecos Chihuahuan and Mojave deserts and southern portions of the Great Basin Shrub Steppe and Colorado Plateau shrublands (Map 13).

Discussion. The larger tamarisk beetle damages *Tamarix* in west to central Asia from latitude ca. 38–41°N and ca. -10–1,000 m elevation in Azerbaijan (Samedov and Mirzoeva 1985), Turkmenistan (Myartseva 1999), and Tajikistan (Kulinich 1962). *Diorhabda carinata* attacks *T. ramosissima* throughout the northern portion of its range in Georgia (Lozovoi 1961), Turkmenistan (present study), Tajikistan (Kulinich 1962) and Kazakhstan (present study), and damages *T. smyrnensis*, a close relative of *T. ramosissima*, in Azerbaijan (Samedov and Mirzoeva 1985). We expect *D. carinata* would attack and probably damage and control *T. ramosissima*/*T. chinensis* in North America. It has a moderate risk of damaging *T. aphylla* (Milbrath and DeLoach 2006b) and very low risk of damaging *Frankenia* (Milbrath and DeLoach 2006a), and both these risks are probably much reduced at less proximity to preferred *Tamarix* spp. (e.g., Blossey *et al.* 2001).

Diorhabda carinata appears to be establishing on Lake Kemp, near Seymour, Texas where it was released in April, 2008 and defoliated more than 0.2 ha by August and was common over a 0.8 ha area (C. Randal, pers. comm.; Maps 7 and 13). *Diorhabda carinata* defoliated portions of a few saltcedar trees in the summer of 2008 following its spring release at Matador Wildlife Management Area (WMA) near Paducah, Texas (Mike Janis, Texas Parks and Wildlife Department, Matador WMA, pers. comm.). It appeared to be weakly established on the Canadian River near Borger, Texas where it was first released (under permit as *D. elongata*) in July 2006, but populations could not be found in 2008 (J. Michels and E. Jones, pers. comm.). *D. carinata* was also released in west Texas at Roaring Springs, Rotan, and Guthrie in the summer of 2008, but it has not yet established at these sites (A. Knutson, pers. comm.). *D. carinata* was caged in the Mojave Desert at Camp Cady, California in 2008 and permissions are being sought for release at this site in 2009 (T. Dudley, University of California, Santa Barbara, CA, pers. com.).

Northern climatypes of larger tamarisk beetles originating from the Desert and Xeric Shrublands and Temperate Grasslands and Shrublands biomes between 37–41°N probably have the greatest potential to damage tamarisk in corresponding latitudes and biomes within 0–1,000 m elevation in North America (Map 13). Areas of primary ecoregions matching these criteria are the Western Short Grasslands in western Kansas, portions of the Great Basin Shrub Steppe and Colorado Plateau shrublands, and some of the extreme northern Mojave Desert (Map 13). Elevations above 1,100 m from 37–41°N should be suitable, but in some cases suboptimal, for *D. carinata*. Milbrath *et al.* (2007) found that a northern climatype of *D. carinata* from 38°N in Uzbekistan suffered higher overwintering mortality in early March at 31°N in Temple, Texas than did *D. sublineata* and *D. elongata*. Higher mortality in the northern *D. carinata* climatype may have been related to asynchronization in the breaking of adult quiescence (not diapause, which probably ends in early winter in all the tamarisk beetles) with bud break in tamarisk as signaled by late winter/early spring temperatures. At 31°N in Temple, higher temperatures in late winter/early spring may occur several weeks before tamarisk bud break (temperatures begin to gradually warm before bud break), but at 38°N these same higher temperatures may occur later in the season and be more closely associated with tamarisk bud break (temperatures may more sharply warm up before bud break). A more southern climatype of *D. carinata* (see below) may be better synchronized in responding to higher temperatures as a signal to ending of winter quiescence at 31°N.

Several North American ecoregions correspond to the most northern areas inhabited by *D. carinata* in its native distribution from 41–45°N (Map 13). These regions include northern portions of the Western Short Grasslands and southern portions of the Wyoming Basin Shrub Steppe (Map 13). Much of these northern areas may be more suitable for *D. carinulata*.

Southern climatypes of *D. carinata* (Map 6) may be best suited to ecoregions in the Temperate Grasslands, Savannas and Shrublands biome between 31–37°N (Map 13). These include the southern portions of the Western Short Grasslands in eastern New Mexico and northwest Texas and southwest portions of the Central and Southern Mixed Grasslands in north central and western Texas (Map 13). Several temperate warm desert regions in North America correspond to native habitats for southern *D. carinata* climatypes in the Desert and Xeric Shrublands biome between 31–37°N. These desert ecoregions include southern portions of the Colorado Plateau Shrublands, portions of the Mojave Desert in southern California and Nevada, and the

Trans-Pecos Chihuahuan Desert in Texas, New Mexico and northern Chihuahua, Mexico (Map 13). Larger tamarisk beetles might damage tamarisk in some of these southern grassland and desert ecoregions. *Diorhabda carinata* appears to be the best suited species to the Temperate Conifer Forests among the *D. elongata* group (Tables 9 and 13). This would make *D. carinata* the best suited species to tamarisk invaded riparian areas of the Arizona Mountains Forests ecoregion of Arizona and New Mexico, such as along the Rio Hondo within the pinyon-juniper woodlands near Hondo, New Mexico (Map 13). Southern maritime subtropical desert areas of 31–29°N, such as the Sonoran Desert, may not be as suitable for *D. carinata* as for other more southern sibling species (Map 13, Table 7).

***Diorhabda sublineata* (Lucas, 1849) REVISED STATUS**

subtropical tamarisk beetle

(Figs. 5, 6, 16, 21, 26, 31, 36, 41, 45)

Galeruca sublineata Lucas, 1849:542 (Type locality: Hippône [Annaba], Algeria; as *Galleruca*).

Galeruca elongata: Reiche and Saulcy, 1858:42 (part; France, Egypt, Algeria; as *Galleruca*); Joannis, 1866:83 (part, monograph, France, as *Galleruca*).

Diorhabda elongata: Heyden *et al.*, 1891:375 (part, catalog for Europe and Caucasus, southern Europe), Bedel, 1892:158 (part, France, as *Dirrhabda*); Weise, 1893:635 (part, Algeria), 1925:225 (Egypt); Corr a de Barros, 1924:9 (part, Portugal); Peyerimhoff, 1926:359 (part, Algeria, Senegal, hosts); Laboissiere, 1934:54 (part, France, Senegal, host); Ogloblin, 1936:79 (part; European and African coast of Mediterranean Sea, south to Senegal); Normand, 1937:126 (Tunisia); Kocher, 1958:109 (Morocco, to 2,000 m); Hopkins and Carruth, 1954:1129 (part, Spain, host); Jolivet, 1967:331 (part, Morocco, Mediterranean, hosts); Torres Sala, 1962:327 (part, Comunidad Valenciana, Spain); Petitpierre, 1988:93 (part, Spain); Gruev and Tomov, 1998:70 (part, Mediterranean); Kovalev, 1995:78 (part, southwest Palaearctic); Campobasso *et al.*, 1999:145 (part, host, Europe and Middle East); Anonymous, 2001:52N (part, Africa); Chatenet, 2002:223 (part, France, Spain, Morocco, Algeria, Tunisia); DeLoach *et al.*, 2003a:230 (part, Tunisia [Sfax]), 2003b:126 (part, host range, North Africa, France), (2008, in prep.) (part, Sfax, Tunisia); Milbrath *et al.*, 2003:225 (part, Sfax, Tunisia); Riley *et al.*, 2003:69,189 (part, catalog of North America [introduced]); Warchalowski, 2003:328 (part, taxonomic keys, Mediterranean Region); DeLoach and Carruthers, 2004a:13, 2004b:311 (part, Tunisia [Sfax]); Lopatin *et al.*, 2004:127 (part, Mediterranean); Dudley, 2005a:13, 2005b:42N (part, biological control, ex: Tunisia); Milbrath and DeLoach, 2006a:32, 2006b:1379 (part, host specificity, Sfax, Tunisia); Dudley *et al.*, 2006:137 (part, host range, Sfax, Tunisia); Milbrath *et al.* (2007). (part, biology, Sfax, Tunisia); Bean and Keller (in prep.) (part, diapause induction, Sfax, Tunisia); DeLoach (2008); Moran *et al.* in press (host range of *D. sublineata* [ex: Sfax, Tunisia] × *D. elongata* [ex: Crete] hybrid); Thompson *et al.* (in prep.) (part, laboratory hybridization, Sfax, Tunisia).

Diorhabda elongata var. *sublineata*: Weise, 1893:1132 (part, Algeria).

Diorhabda sublineata: Boehm, 1908:68 (Egypt, as *Dirrhabda*).

Diorhabda elongata ab. *sublineata*: Weise, 1924:78 (part, world catalog, Algeria); Winkler, 1924–1932:1307 (part, Palearctic catalog, Algeria); Laboissiere, 1934:53 (part, France, Algeria); Normand, 1937:126 (part, Tunisia); Alfieri, 1976:233 (Egypt, on *Tamarix* spp.); Warchalowski, 2003:328 (part, taxonomic keys, Mediterranean Region).

Diorhabda elongata ab. *carinata*: Laboissiere, 1934:54 (part; Narbonne, France).

Diorhabda elongata ab. *bipustulata* Normand, 1937:126 (Type locality: Kairouan, Tunisia) (NEW SYNONYM); Wilcox, 1971:63 (world catalog).

Diorhabda elongata sublineata: Gressitt and Kimoto, 1963a:407 (part; North Africa, West Asia; not Asia Minor, China, and Mongolia); Wilcox, 1971:63 (part, world catalog, North Africa, West Asia); DeLoach *et al.*, 2003b:126 (part, host range, North Africa).

Male. Genitalia. Male *D. sublineata* may be distinguished from all other species in the *D. elongata* group by the unique presence of a connecting endophallic sclerite (CES) from the palmate endophallic sclerite (PES) to the elongate endophallic sclerites (EES) (Figs. 16, 21, 26, 31). In weakly sclerotized teneral adult *D. sublineata*, the CES can appear to evanesce and be faint. *Diorhabda elongata*, *D. carinata*, *D. carinulata* and *D. meridionalis* all lack the CES (Figs. 14–15, 17–20, 22–25, 27–30, 32–33), but darkly sclerotized *D. carinata* may uncommonly bear a faint lateral line in place of a CES. Additional characters of the EES and PES, similar to those found in *D. carinata*, can be used to separate *D. sublineata* from *D. elongata*, *D.*

carinulata, and *D. meridionalis*. The PES of *D. sublineata* (Figs. 16, 31) always bears a strong lateral appendage and the distal margin is truncate-serrate with two to six (commonly three to four) usually distal spines, a maximum of one spine being subdistal. In contrast, the PES of *D. carinulata* (Figs. 17, 32) and *D. meridionalis* (Figs. 18, 33) lacks a lateral appendage (but it may bear a lateral notch) and the distal margins of the PES are narrowly rounded and generally smooth with one or two small subdistal spines that sometimes project beyond the distal margin. The PES of *D. elongata* also lacks a lateral appendage and is usually rounded with one to five usually subdistal spines with a maximum of two of these spines being distal (Figs. 14, 29). The elongate endophallic sclerite in *D. sublineata* always bears a basally pointed lateral appendage (LA) or lateral notch (LN) serving as a point of attachment for the CES (Figs. 16, 21), but these are always lacking in *D. elongata*, *D. carinulata*, and *D. meridionalis* (Figs. 14, 17–19, 22–23). The EES of *D. carinata* only occasionally bears a lateral appendage (Figs. 20—Artvin) or a lateral notch (Fig. 20—Ashgabat). In *D. sublineata*, the spined area of the EES extends greater than or equal to 0.31 times (or greater than about one third) the length of the EES (Figs. 16, 21, 48; SL). In contrast, the spined area of the EES is confined to less than or equal to 0.16 times (or less than about one fifth) the length of the sclerite in *D. elongata* (Table 3; Figs. 14, 19, 24, 48). In *D. sublineata*, spines of the EES are often irregularly spaced along the blade with conspicuous gaps (Fig. 21). In *D. carinulata* and *D. meridionalis*, spines along the EES are usually evenly and closely spaced along the blade (Figs. 22–23). The EES of *D. meridionalis* additionally bears a hooked apex that is absent in *D. sublineata*.

Measurements. See Tables 2 and 3.

Female. Genitalia. Female *D. sublineata* may be distinguished from all other members of the *D. elongata* group except *D. carinata* by their triangulate vaginal palpi (VP) that are wider than long with a width to length ratio (LP/WP) of 0.46–0.85 ($n = 19$) (Fig. 36; Table 4). In contrast, the vaginal palpi are broadly rounded with a length to width ratio of 0.94–1.36 in the allopatric *D. carinulata* (Fig. 37) and *D. meridionalis* (Fig. 38; Table 4). The vaginal palpi are also broadly rounded in *D. elongata* (Fig. 34). In addition, the width of the widest lobe of the stalk (WLS) of internal sternite VIII (IS VIII) is often larger in *D. sublineata* (range 0.08–0.18 mm; Fig. 36) compared to *D. elongata* (range 0.06–0.11 mm; Fig. 34). Some female *D. sublineata* can be distinguished from *D. carinata* by having the tips of the lobes (TL) of the stalk of IS VIII either not curved or curved outward toward the apical lobe and the tips either rounded or quadrate (Fig. 41 – Ndiol, Perpignan, Kom Ombo), a state never found in *D. carinata*. Some *D. carinata* can be distinguished from *D. sublineata* by having the tips of both lobes of the stalk of IS VIII strongly curved inward at the tip and the tips either pointed or rounded (Fig. 40 – Baghdad, Ashgabat, and Pul-e Charki). Female *D. sublineata* and *D. carinata* with at least one lobe of the stalk of IS VIII curved only slightly inward (Figs. 35–36, 40—Lagodekhi and Ardanuc, 41—Biskra and Tamri) are indeterminable to species, except on the basis of geographic distribution outside of the area of known sympatry in Iraq.

Measurements. See Tables 2 and 4.

Coloration. In *D. sublineata*, subsutural and submarginal elytral vittae are often present, extending well into the basal half of the elytra (Fig. 5) and live specimens are tannish-yellow in hue, lacking any greenish-yellow tinting (Fig. 6). This is in contrast to *D. elongata* in which the elytral vittae, if present, are confined to the apical half of the elytra (Fig. 1) and in which live specimens possess an olivaceous hue from greenish-yellow tinting (Fig. 2). *Diorhabda carinata* differs from *D. sublineata* in more often lacking elytral vittae (Fig. 3) and in having some degree of greenish-yellow tinting in veins of the elytra (Fig. 4). Living *D. sublineata* (Fig. 6) and *D. carinulata* (Fig. 8) are very similar in coloration, and Chen (1961) notes the similar appearance of dead *D. carinulata* (as *D. e. deserticola*) and *D. sublineata* (as *D. e. ab. sublineata*).

Type material. Specimens from Lucas's collections, which should include the type specimen(s) for *D. sublineata*, should be found at MNHN (Groll 2006). The curator at MNHN communicated intent to inform us of the status of the type material and perhaps lend it for examination, but after four years, we have not heard of the status of the Lucas type material. Once it can be ascertained that the type material is lost, a neotype should be designated using a dissected male specimen from near the type locality of Annaba, Algeria. We studied the original description by Lucas (1849), possibly based on several individuals he stated were collected at

Annaba, with his accompanying color habitus illustration. We also studied specimens from the broad vicinity of the type locality in Algeria and Tunisia. The location of type specimens for *D. e. ab. bipustulata* Normand (1937) is unknown and we studied the original description and specimens from the vicinity of the type locality of Kairouan, Tunisia.

Material examined. 89♂♂ dissected (diss.), 51♀♀ diss., 170♂♂, 191♀♀, 9 unsexed specimens. **ALGERIA:** 2♀♀ diss., [specific location not given], Reitter, NMPC [2004-21, 25]; 1♂, [specific location not given], Uyttenboogaart, Coll. Dr. D.L. Uyttenboogaart, ZMAN; 1♂ diss., 2♂♂, 3♀♀, Abadla [31.0167°N, -2.7333°W], Kouril, P5/46/62, 4358a, NMPC [2004-03]; 1♂ diss., 6♀♀, Abadla, V. Zoufal, Kouril, P5/46/62, 4358a, *D. elongata* a. *sublineata* [ZMHB], NMPC [2004-14], ZMHB [1♀]; 1♀, Abadla, ZMHB; 1♂ diss., 7♂♂, 8♀♀, Alger [36.76305°N, 3.05055°E], environs, Ch. Lalleman, *Diorhabda elongata* var. *carinata* det V. Laboissière 1939 [8♂♂, 8♀♀], *D. e. var. sublineata* det V. Laboissière 1939 [1♀], IRSNB [2006-02]; 1♂, Algir [Alger], coll[ection] Reitter, *D. elongata*, HNHM; 1♂ diss., Argel [Alger], St. Perez Arcas, *Galeruca elongata*, MNMS [2003-01]; 1♂ diss., Biscra [Biskra; 34.85°N, 5.73333°E], *Diorhabda elongata* det I.K. Lopatin, Coll. Lichtnekert, HNHM [2003-03]; 1♂ diss., 1♂, 2♀♀, Biskra, environs, Obenb., NMPC [2004-22]; 1♂ diss., 1♀ diss., 2♂♂, 6♀♀, Biskra, C.J. Dixon, Museum Lieden, RBCN [2003-08, 21]; 1♂ diss., 2♀♀ diss., 2♂♂, 1♀, Biskra, G.C. Champion, G.C. Champion Coll. B.M. 1927–409, BMNH [2003-03, 2003-11, 2005-01]; 1♀ diss., 1♀, Biskra, 1-III-1931, Dr. R. Meyer, NHMB [2005-08]; 2♀♀ diss., 3♀♀, Biskra, 30-III-1985, M. Bergeal, MBPF [2003-01, 02]; 1♂, 3♀♀, Biskra, P. Jolivet, IRSNB; 1♀, Biskra, J. Sahlb., MZHF; 1♂ diss., Blidah [Blida; 36.41667°N, 2.828889°E], V-1867, H. Clark, 65-56, BMNH [2003-08]; 1♀ diss., Boghari [Boghni; 36.5422°N, 3.9531°E], V-1897, Dr. A. Chobaut, NMPC [2004-01]; 1♀ diss., Qued Hamman [Oued Hammam (Mascara State)], 10 km south Perregaux [Mohammadia] [35.50806°N, 0.040833°E], 9-V-1964, Eckerlein, Coll[ection] K.H. Mohr, DEI [2005-05]; 1♂ diss., 8♂♂, 13♀♀, Teniet el Had [Theniet el Had] to Affreville [Khemis Miliana] [app. location; 36.13950°N, 2.20749°E], Dr. Vauloger, *D. elongata* det. Le Moul, IRSNB [2006-07]; **EGYPT:** 5♂♂, 1♀, [specific locality not given], Reitter, *D. sublineata* det. V. Laboissière 1913 [HNHM], NMPC [4♂♂, 1♀], HNHM [1♂]; 1♂, [specific locality not given], coll[ection] Mus Murray, Fry coll[ection] 1905.100, *Galleruca costipennis* Dej cat [Dejean catalogue; *nomen nudum*; Dejean 1837, p. 377], BMNH; 2♂♂, [specific locality not given], ZIN; 1♂ diss., Cairo [Al Qahirah; 29.98333°N, 31.13333°E], Dachor, 29-I-1933, Schatzm. Koch., [*D. e. ab. sublineata* det. Burlini 1966, MSNM [2003-17]; 1♂ diss., 1♂, 1♀, Cairo [Al Qahirah], Pyramidi, 3-X-1933, W. Wittmer, *D. e. ab. sublineata* det. Burlini 1966 MSNM [2003-02]; 10♂♂ diss., 3♀♀ diss., 43♂♂, 50♀♀, Com Ombo [Kom Ombo; 24.45°N, 32.93333°E], XI-1954, *D. e. ab. sublineata* det. J. Bechyne 1951, H. Hofbrauer, NHMB [2003-01, 04, 08, 2004-05, 06, 07, 08, 09; 2008-01, 02, 03, 04, 05]; 1♂ diss., 9 specimens, Dakhla Oasis [25.50722°N, 28.94722°E] MUT, 10-XII-1977, R.T. Simon Thomas, ZMAN [2008-11]; 1♂ diss., 1♂, 1♀, Dakhla Oasis, 4-III-1995, G. Strauss, RBCN [2003-02]; 1♂ diss., 3♂♂, 1♀, Ezbet El Nakl [Izbat an Nakhl; 30.15°N, 31.31666°E], 22-VIII-1933, W. Wittmer, [*D. e. ab. sublineata* det. Burlini 1967, MSNM [2003-10]; 1♀ diss., 2♀♀, Fajum [Al Fayyum; 29.30778°N, 30.84°E], U. Sahlb., [no.] 610, MZHF [2003-01]; 1♀ diss., Hawara [pyramid; 29.27389°N, 30.90139°E], 2-V-1904, *D. elongata* det. L. Burgeon, *D. e. var. sublineata* det. V. Laboissière 1939, L. Burgeon Collection, IRSNB [2006-06]; 1♂ diss., 1♀, Heluan [Helwan des Bains; 29.85°N, 31.3333°E], 18-IX-1957, dr. Gozmány, in desert on *Tamarix*, Exc. Egypt Mus. Nat. Hung., *D. e. var. sublineata* det K. Lopatin, HNHM [2003-07]; 1♀ diss., Ismailia [30.5833°N, 32.2667°E], II, F. Lotte, USNM [2003-17]; 1♂, 2♀♀, Ismailia, F. Lotte, Février, ZIN; 4♂♂, 5♀♀, Ismailia, NMPC; 1♂ diss., 1♂, 5♀♀, Le Caire [Al Qahirah], NMPC [2004-45]; 1♂ diss., 1♂, Port Said [31.2667°N, 32.3°E], VI (June), F. Lotte, USNM [2003-19]; 1♀ diss., 1♀, Sakkarah, [ruins; 29.8457°N, 31.2104°E], Cairo (Gizeh), 19-II-1933, C. Koch, *D. elongata* det. Burlini 1966, MSNM [2008-03]; 1♂ diss., Siala [Silah; 29.3561°N, 30.9689°E], 21-VIII-1910, collection L. Burgeon, *D. e. var. sublineata* det. V. Laboissière 1939, IRSNB [2006-01]; 1♀ diss., Wadi Hoff [Ain Elwan Station; 29.86667°N, 31.31667°E], 20-V-1922, Alfieri, [no.] 1972, NHMB [2004-01]; **FRANCE:** 1♂ diss., 1♂, 3♀♀, Almanane [beach near Hyères; 43.0790°N, 6.1258°E], *D. elongata* det. V. Laboissière 1939, IRSNB [2006-03]; 1♂ diss., 11♂♂, 22♀♀, Camargue [region], Gallia, L. Puel, coll[ection] Leonhard [DEI], coll. H.K. Mohr [DEI], *D. elongata* [DEI], DEI [2005-08; 4♂♂, 2♀♀], IRSNB [collection P.

Jolivet; 7♂♂, 20♀♀; 10 specimens, Iliis [37.8833°N, 21.3833°E], Olympia, Ellas, 2–3-X-1962, Ent. Exe. Zoöl. Mus., ZMAN; 2♂♂ diss., 2♂♂, 2♀♀, Le Lavandou [43.1322°N, 6.3645°E], Exped. Obenb., NMPC [2004-19, 2008-01]; 2♀♀, Le Lavandou, IV-1910, H. Desbordes, *D. elongata* det. Le Moul, IRSNB; 1♂ diss., 1♂, Le Barcares [42.78333°N, 3.03333°E], 19-V-1973, G.J. Slob, RBCN [2003-05]; 1♂ diss., Stes. Mairies [Les Saintes Maires, 43.45°N, 4.4333°E], Camargue, 11-13-IX-1951, H.H. Weber, NHMB [2003-19]; 1♀ diss., Les Stes.–Maries [Les Saintes Maires], 14-VII, W. Liebmann, DEI [2005-07]; 1♂ diss., 5♂♂, Marseille [43.3°N, 5.4°E], 16-VIII-1952, Hakan Lindb., MZHF [2004-01]; 1♂ diss., Montpellier [43.6°N, 3.833°E], Jentsson, tamarisci, Janis, DEI [2003-17]; 1♂ diss., 1♂, 1♀, Palavas [Palavas–les–Flots; 43.53333°N, 3.93333°E], [no.] 25-11, MBPF [2003-06]; 1♀ diss., Perpignan [42.68333°N, 2.88333°E], Pyr[ennes Mts.], Or[iental], IV-1953, J.V. Bechyné, NHMB [2003-43]; 1♂ diss., 3♂♂, 10♀♀, Salin–de–Giraud [43.4167°N, 4.7333°E], B du Rhône, Camargue, 12-IX-1970 [RBCN 2003-17; 2♀♀ ZMAN], 14-IX-1970 [ZMAN], C. van Nidek, *D. elongata* [ZMAN], ZMAN, RBCN [2003-17]; 1♂ diss., Séveillé [geocoordinates not locatable], southern France, coll[ection] Bourgoin, *D. elongata* det. Le Moul, IRSNB [2006-05]; **IRAQ**: 1♂ diss., Baghdad [33.33861°N, 44.37722°E], IV-1936, Frey, NHMB [2003-31]; **MOROCCO**: 1♀ diss., Asni [31.25°N, -7.98333°W], 1,000 m [elev.], High Atlas [Mts.], 9-VII-1993, Stn. Sammlung Dieter Siede, *D. elongata* det. R. Beenen 1995, RBCN [2003-10]; 2♂♂ diss., Driouch [34.9833°N, -3.3833°W], near Midar, Nador [Prov.], 24-VI-1992, J.M. Vela, *D. elongata* det. Vela 1992 [1♂ diss.], GSWRL [2003-36, 2005-78]; 1♂ diss., Essaouira environs [31.51305°N, -9.76972°W], Ounara, 3-V-1983, S. Doguet, MBPF [2003-08]; 1♂ diss., Goundafa [Talaat n' Yakoub; 30.9833°N, -8.15°W], 1,200 m [elev.], Haut Atlas [Grand Atlas Mts.], 15-30-IV-1933, Schwingenschus, NHMB [2003-18]; 1♂ diss., 2♀♀, Marrakesch [Marrakech; 31.6333°N, -8.000°W], 15-V-1992, Liebegott, *D. elongata* det. Eber 1995 [1♂ diss., ab. *bipustulata*], ZMHB [2006-03]; 1♂ diss., 1♀, Marrekech, 21–23-V-1926, Lindberg, MZHF [2008-02]; 1♂ diss., 6♀♀, 2♂♂, Tachedirt [31.1667°N, -7.85°W] Schwingenschus, NHMB [2003-02]; 1♀ diss., Tamri [30.6978°N, -9.8253°W], Kuste [coast], 31-VII-1993, Stuben, *D. elongata* det. R. Beenen 1995, RBCN [2003-19]; 2♂♂ diss., 3♀♀, 1♂, Tanger [Tangier; 35.78472°N, -5.812778°W], Rolph, *Galeruca elongata*, tag 1444, DEI [2003-06, 23]; 1♀ diss., Tanger [Tangier], 25–29-IV-1926, Lindberg, 889, MZHF [2008-01]; 1♂ diss., Tanger [Tangier], 1897, MNMS; 2♂♂ diss., 1♀ diss., 5♂♂, 3♀♀, Tarondant [Taroudannt], 12 km east [30.52268°N, -8.759°W], 11-V-1958, C.J. Davis, on *Tamarix* sp., #83, 58-9590, 58-9591, 58-9592, USNM [2003-01, 02, 03]; 1♂ diss., 1♂, Taroudant [Taroudannt; 30.4833°N, -8.8667°W], 28-V-1985, G. Sama, MRSN [2003-04]; 1♂ diss., Taroudannt, Sous Valley, 18-IV-1990, Z. Kejval, *D. elongata*, EGRC [2005-06]; 1♂ diss., 3♀♀, Tiz-n-Test Pass [30.83333°N, -8.33333°W], High Atlas [Mts.] 20-VI-1994, Szailles, RBCN [2003-11]; **PORTUGAL**: 1♂ diss., Lusitania [Portugal, specific locality not given], Reitter, ZMAN [2008-16]; **SENEGAL**: 1♂ diss., specific locality not given, Mion, ZMHB [2006-06]; 2♂♂ diss., 1♀ diss., 8♂♂, 2♀♀, Ndiol [Ndiol Nar; 16.14778°N, -16.31306°W], 25 km northeast St. Louis, 15-VIII-1979, P. Jolivet, on *T. senegalensis*, *D. sp. nr. elongata* det. S.L. Shute 1979, BMNH [2003-01, 02, 2005-02]; **SPAIN**: 1♀ diss., [specific locality not given], Lolobregato, NHMB [2003-05]; 2♂♂, 3♀♀, m[eridionalis; southern; specific locality not given], Minsmer, [18]99, ZMAN; 1♂, 1♀, [specific locality not given], L. Miller, coll. Ed. Everts, ZMAN; 1♂ diss., Almeria [36.8833°N, -2.45°W], Tabernas Desert, 21-VII-1965, La Greca, MRSN [2003-03]; 2♂♂, Andalucia [Comunidad Autonoma de Andalucia; specific locality not given]; coll[ection] Reitter, *D. elongata*, HNMB; 1♂, 1♀, Andalusia [Andalucia], Baly coll[ection], *Galeruca sublineata*, BMNH; 1♂ diss., Barcelona [41.3833°N, 2.1833°E], X-1940, F. Monros, USNM [2003-07]; 3♀♀ diss., Barcelona, Farola de Llobregat, 15-VII-1940, F. Monros Coll., USNM [2005-02, 05, 06]; 1♂ diss., Cabo de Gata [El Cabo de Gata; 36.7833°N, -2.2333°W], 4-VI-1977, Hinterseher, *D. elongata* det. Erber 1985, *D. elongata* det. R. Beenen 1996, ZMHB [2008-03]; 1♂ diss., 5♂♂, Cordoba [37.83333°N, -4.7667°W], Col del Sur Perez Arcas, *G. elongata*, MNMS [2004-03]; 1♀ diss., Galicia [Autonomous Community; specific locality not given; estimate approx. locality in Pontevedra Province, the only province of Galicia where *Tamarix* is noted (Cirujano 1993): 42.0186°N, -8.87510°E], [*D.*] *elongata*, NMPC [2005-31]; 2♀♀ diss., Halizia [Galicia Autonomous Community; specific locality not given], [*D.*] *elongata*, NMPC [2004-16, 2005-27]; 1♂ diss., Rambla del Grao, Quadix [37.3°N, -3.1333°W], Granada, F.S. Pinero, JOSV68935, GSWRL [2005-77]; 1♂

diss., 3♂♂, Lorca [37.6667°N, -1.7°W], Murcia, VIII-1943, G. Menor, MNMS [2004-02]; 1♂ diss., Madrid [40.4°N, -3.6833°W], Montarco, Peris Torres, MNMS [2004-01]; 1♀ diss., 14♂♂, 14♀♀, Palamos [41.85°N, 3.1333°E], Catalonien, ZHMB [2003-06]; 1♂ diss., 4♂♂, 3♀♀, Playa de Aro [41.8167°N, 3.0667°E], 2-17-VII-1963, *D. elongata* det. L. Borowiec, MZLU [2005-04]; 1♀ diss., Sierra de Javalambre [Mt.; 40.1°N, -1.0°W], Teruel, 1,600m [elev.], 25-VII-1965, La Greca, *D. e.* subsp. *sublineata* det. Daccordi 1971, MSNM [2003-04]; 1♂ diss., 2♂♂, 4♀♀, Tossa de Mar [Tossa; 41.7167°N, 2.9333°E], 29-VI to 19-VII-1968, Th. Palm, *D. elongata* det. L. Borowiec, MZLU [2005-03]; 1♂ diss., Totana [37.7667°N, -1.5°W], Murcia, V-1938, Balaguer, *D. elongata* det. Petitpierre, GSWRL [2003-05]; 1♂ diss., 1♂, Valencia [39.4667°N, -0.3667°W], Maru'der, MNMS [2003-02]; 1♂ diss., 2♀♀, Vera [37.2500°N, -1.8667°W], with Almira [Almeria], 4-VI-1977, brookside, *D. elongata* det. Steinhausen [1♂ diss.], *D. elongata* det. Eber 1985 [2♀♀], ZMHB [2006-02]; **TUNISIA**: 1♂ diss., Belvedere [36.82472°N, 10.18638°E], 25-IX-1929, A. Schatzmayer, [*D. e.* ab.] *sublineata* det. Burlini 1967, MSNM [2003-07]; 1♀ diss., Boughrara [33.5378°N, 10.6761°E], 9-IV-1977, S. Mahunka, *D. elongata* det. V. Tomov, No. 99, HNHM [2003-08]; 1♂ diss., 1♀ diss., 1♂, 1♀, Douz, 16.5 km north [33.6075°N, 9.005°E], 19-V-2000, A. Kirk, on *Tamarix* spp., GSWRL [2003-42, 2005-50]; 1♂ diss., 1♀ diss., Chott el Guetar [34.39°N, 8.84°E], [9.3 km southeast] Gafza [Gafsa], 200m [elev.], Lortess, 18-IV-1993, R. Regalin, *D. elongata* det. D. Regalin 1995 [♀], Coll[ection] D. Sassi [♀], GSWRL [2003-61], MRSN [2003-08]; 1♂ diss., 1♀ diss., 2♀♀, Chott Sedjoumi [36.765°N, 10.15055°E], 27-IX-1929, A. Schatzmayer, *D. e.* ab. *sublineata* det. Burlini 1967, MSNM [2003-01, 03]; 1♂ diss., Djedeida [Jedeida; 36.83111°N, 9.92416°E], 14-X-1929, A. Schatzmayer, [*D. e.* ab.] *sublineata* det. Burlini 1967, MSNM [2003-05]; 2♂♂ diss., 1♂, 7♀♀, Marith, 18.7 km southeast on road C116, 33.5760°N, 10.4553°E, 20-V-2008, Javid Kashefi, on *Tamarix* sp. in desert wadi, shipment EBCLGR-JK-2008-004, New Mexico, Las Cruces, NMSU lab colony F4 generation, 8-27-X-2008, D. Guenther, voucher shipment GSWRL-2008-03, GSWRL [2008-23, 24]; 1♀ diss., 2♀♀, Gabes [33.7425°N, 10.20567°E], Medenine road, 15-V-2000, A. Kirk, on *Tamarix* spp., GSWRL [2003-49]; 2♂♂ diss., Gabes, beach at Hotel Chems [33.20530°N, 11.20970°E], 6-V-2007, J. Kashefi, *Tamarix* sp. (not *T. aphylla*) (1♂), *T. aphylla* (1♂), shipment GSWRL-2007-01, GSWRL [2007-48, 49]; 1♂ diss., 3♂♂, 4♀♀, Kebili [33.70483°N, 8.942333°E], Tozeur side, 18-V-2000, A. Kirk, on *Tamarix* spp., GSWRL [2003-43]; 2♂♂ diss., 4♀♀ diss., 1♂, 1♀, Sfax [34.7406°N, 10.7603°E], Gargour, Nahkia, 14-V-2000, A. Kirk, on *Tamarix* sp., GSWRL [2003-09, 12, 50, 65, 76, 79]; 4♂♂ diss., 4♀♀ diss., Sfax, 15 km south [34.66°N, 10.67°E; not Tunis as in some shipping records], 30-IX-2002, A. Kirk, on *Tamarix* spp., voucher USDA lab colony at Albany, California (22-I-2003, 2003, D. Bean), voucher USDA lab colony at Temple, Texas (1♂, 1♀, 26-VIII-2003, 5-IX-2003, L. Milbrath [nos. 1286, 1283]), shipment EIWRU-2002-1008, GSWRL [2003-14, 15, 22, 23, 74, 75, 86, 87] [released in south Texas in 2005] [used in biological studies of Milbrath and DeLoach (2006a, 2006b), Milbrath *et al.* (2007), Herr *et al.* (in prep.), Bean and Keller (in prep.), and Thompson *et al.* (in prep.)]; 1♂ diss., Sfax, 15 km South [34.63980°N, 10.65280°E], 6-V-2007, J. Kashefi, *Tamarix* sp. (not *T. aphylla*), shipment GSWRL-2007-01, GSWRL [2007-50]; 1♀ diss., Sfax, 17 km South [34.65°N, 10.66°E], 6-III-1995, Kirk & Sobhian, on *Tamarix* spp., 9137, *D. elongata* det. I. Lopatin 1999, GSWRL [2004-15]; 1♂ diss., 2♂♂, Tozeur [33.92055°N, 8.13333°E], 14-XII-1928, Torre e Tasso, [*D. e.* ab.] *sublineata* det. Burlini 1967, MSNM [2003-06]; **UNKNOWN COUNTRY**: 1♂ diss., Pyrennean [not locatable, probably Pyrennes Mts., possibly France], Porrir, Scheider der Kelch, DEI [2003-12]; **YEMEN**: 2♀♀ diss., Yemen [specific locality not given], Arabia, Millingen [approx. location near Haraz Mts. (Millingen 1874): 14.87820°N, 43.65640°E], Fry Coll. 1908.100, BMNH [2003-04, 05].

Distribution. *General.* *Diorhabda sublineata* ranges from Portugal, Spain and France to Morocco, Senegal, Algeria, Tunisia, Egypt, Yemen, and Iraq (Map 4). Chatenet (2002) reported *Diorhabda* was little common in France and Petitpierre (1988) reported it as infrequent along the northeastern Mediterranean coast of Spain. It is apparently of sporadic occurrence in southern Spain, where surveys of *Tamarix* in July 2005 revealed no *Diorhabda* (J. Sanabria and J. Vela, pers. comm.). But Hopkins and Carruth (1954) report *Diorhabda* as common in Huelva Province of southwest Spain. Boehm (1908) found *D. sublineata* to be the most common galerucine in Egypt and Pierre Jolivet (Paris, France, pers. comm.) collected specimens which we have dissected from a dense population in the thousands at Ndiol Nar, Senegal. Reports of *D. e.* var.

sublineata (Weise 1890), *D. e. ab. sublineata* (Medvedev and Voronova 1977b, Medvedev 1982), and *D. e. sublineata* (Gressitt and Kimoto 1963a; Lopatin 1968, 1975, 1977b) from Mongolia or China should refer to *D. carinulata*. Further collections should reveal that the range of *D. sublineata* includes Western Sahara, Mauritania, Libya, Sudan, Saudi Arabia, and Kuwait and yield specific locations in Portugal, north Yemen, and the Pontevedra (Galicia) and Huelva provinces of Spain. *Tamarix aphylla* and the probable host, *T. nilotica*, are found in east Africa in Ethiopia and Somalia (Baum 1978), where *D. sublineata* may also occur. Two *Tamarix* spp. are endemic to southern Africa (in Angola, Namibia and South Africa; Baum 1978), where surveys for *D. sublineata* should be made.

Confirmed Records. We have dissected specimens from (see **Material Examined**) and confirmed the presence of *D. sublineata* (as *D. e. var. sublineata*, *D. e. ab. sublineata*, and *D. sublineata*) in the following countries with previous literature records (Map 4): Algeria (Lucas 1849, Peyerimhoff 1926), Egypt (Boehm 1908, Alfieri 1976), Tunisia (Normand 1937), and France (Laboissière 1934).

New Records. We dissected specimens of *D. sublineata* from the following countries for which we find no previous specific reports of this species in the literature: Portugal, Spain, Morocco, Senegal, Iraq, and Yemen. With the exception of Yemen, we find past reports of *D. elongata* from these countries that should refer, at least in part, to *D. sublineata* (see above synonymy).

Specimens at BMNH from Yemen with a label of “Millingen” were probably collected circa 1873 on a journey by Dr. Charles Millingen to north Yemen where he noted tamarisk in lowlands surrounding the Haraz Mountains (Millingen 1874).

Unconfirmed Records. No country records of *D. sublineata* remain unconfirmed. On the basis of evidence discussed below, we accept as *D. sublineata* several locality records of *Diorhabda* from France, Spain, and North Africa. *Diorhabda sublineata* has been released in the United States (Texas), but establishment is not yet confirmed (Map 7, see **Potential in Tamarisk Biological Control** below for additional details).

Specimens of *D. sublineata* were dissected from all 11 available locations from France. We examined a specimen of *D. sublineata* from France (IRSNB) with an identification label of *D. e. var. carinata* made by Laboissière in 1939. Therefore, we consider Laboissière’s (1934) report of *D. e. var. carinata* in France as *D. sublineata*, although *D. elongata* may also be present. Of 14 locations in Spain, *D. sublineata* was dissected from 13 of these while *D. elongata* was dissected from only one. Therefore, we believe Hopkins and Carruth (1954) found *D. sublineata*, rather than *D. elongata*, to be common in the Huelva Province of southwest Spain. Torres Sala (1962) reported *D. sublineata* (as *D. elongata*) from Comunidad Valenciana, Spain. Petitpierre (1988) found *D. sublineata* (as *D. elongata*) was infrequent along the northeastern coast of Spain.

Specimens of *D. sublineata* were dissected from all 40 specific localities available from North Africa. *D. elongata* was also present at only one specific locality, Al Qahirah (Cairo), Egypt, and one general locality, Algeria, from a series predominated by *D. sublineata*. Consequently, we accept as *D. sublineata* all of the 23 unconfirmed North African collection records of *D. sublineata* (Lucas 1849; see also below **Discussion-Taxonomy**), *D. e. ab. sublineata* (Normand 1937, Alfieri 1976), *D. e. ab. bipustulata* (Normand 1937), and *D. elongata* (Peyerimhoff 1926; Normand 1937; Jolivet 1967; A. Kirk; USDA/ARS, Montferrier-sur-Lez, France, retired, pers. comm.; S. Doguet, pers. comm.). Weise (1925) reported that an expedition to Anglo-Egyptian Sudan collected *D. sublineata* (as *D. elongata*) from Halwan (= Heluan), Egypt, a location from which we dissected *D. sublineata*. This record was apparently incorrectly cited by Laboissière (1934) as a collection from Sudan, and this error was followed by Ogloblin (1936).

Below are listed 25 unconfirmed locality records that we assign to *D. sublineata* (Map 4):

ALGERIA: Hippône [Annaba; 36.9000°N, 7.7667°E] (Lucas 1849); Djamaa [33.5333°N, 6.0000°E], on *Tamarix boveana* (as *T. bounopaea*), III; Maison Carree [El Harrach; 36.7203°N, 3.14500°E], on *Tamarix africana*, IX (Peyerimhoff 1926); Aurès Mountains, Beni Imloul Forest, Sidi Ali [=Ain Sidi Ali; 35.2833°N, 5.4667°E], 14-VI-1981, S. Doguet, on *Tamarix*; Biskra, Oued Beraze, 24-VI-1981, S. Doguet, on *Tamarix*; Guelma, Djebel Taya [36.507°N, 7.0828°E], 1-II-1968, S. Doguet, on *Tamarix*; Kabylie, El Adjiba [36.3258°N, 4.1503°E], VI-1959, J.C. Bourdonné; Nemanchas Mountains, Khangat Sidi Nadji [Sidi Naji; 34.8167°N, 6.7000°E], 24-VI-1981, S. Doguet, on *Tamarix* (S. Doguet, pers. comm.); **EGYPT:** Asyut

[27.1828°N, 31.1828°E], IX; Cairo vicinity, V-X [*D. sublineata* dissected from same location]; Helwan [Halwan], wadis northeast, V (Alfieri 1976); Heluan [Halwan] [*D. sublineata* dissected from same location] (Weise 1925); Minya, IX [Al Minya; 28.1194°N, 30.7444°E]; Siala [Silah; 29.3561°N, 30.9689°E], VI [*D. sublineata* dissected from same location]; Sinnuris [29.4167°N, 30.8667°E], VI (Alfieri 1976, on *Tamarix* spp.); **FRANCE**: Narbonne [43.1833°N, 3.0000°], *D. e.* var. *carinata* (Laboissière 1934); **MOROCCO**: Essaouira, Ounara [31.5336°N, 9.5536°W], 3-V-1983, S. Doguet, on *Tamarix*; Tamelelt [Tamelelt Jdida; 31.8189°N, 7.5089°W], Marrekech [*D. sublineata* dissected from same location], 11-V-1983, S. Doguet, on *Tamarix* (S. Doguet, pers. comm.); Melilla area [33.3881°N, -7.14500°E], on *Tamarix* sp.; Sidi Mouna el Harati [Sidi Moussa el Harrati shrine; 34.0800°, -5.9600°E], on *T. africana* (Jolivet 1967); South Essaouira, Tamri [30.6780°N, 9.8253°W], 4-V-1983, S. Doguet, on *Tamarix* (S. Doguet, pers. comm.); **SPAIN**: Empúries [Ampurias; 42.1333°N, 3.1167°E] (Petitpierre 1988); Huelva [Province in southwest Spain; specific locality not given; app. locality: 37.25830°N, -6.9508°E], *Tamarix gallica* (Hopkins and Carruth 1954); Torroella de Montgri [42.0333°N, 3.1333°E]; Valls [41.2833°N, 1.2500°N] (Petitpierre 1988); **TUNISIA**: Le Kef [El Kef; 36.1822°N, 8.7147°E], Kairouan [35.6744°N, 10.1017°E], Medjez-el-Baba [Majaz al Bab; 36.6500°N, 9.6167°E] (Normand 1937); 1 spmn., Douz, 20.2 km N, 33° 37' 52" N, 8° 59' 58" E [33.6311°N, 8.9994°E], 19-V-2000, A. Kirk, *Tamarix aphylla* (Alan Kirk, USDA/ARS, Montpellier, France, retired, pers. comm.).

***D. sublineata* × *D. elongata* Hybrid Morphology.** All six studied adult male *D. sublineata* × *D. elongata* laboratory hybrid F1 and F2 progeny (Figs. 46–47) obtained from D.C. Thompson and B. Peterson (NMSU) can be distinguished from parental pure lines (Figs. 44–45) by a variety of anomalous hybrid genitalic character combinations in the endophallic sclerites. These diagnostic character combinations are not seen in laboratory pure lines of *D. sublineata* and *D. elongata* (Figs. 44–45) or in field collected material anywhere in the Palearctic, including areas of marginal sympatry for *D. sublineata* and *D. elongata* such as Portugal, Spain and Egypt (Figs. 14, 16, 19, 21, 24, 26, 29, 31). Examples of anomalous character combinations in hybrids include: (1) length of blade (LB) of elongate endophallic sclerite (EES) is intermediate between the maximum length of blade for *D. elongata* (0.44 mm), and the minimum length of blade for *D. sublineata* (0.52 mm) (Figs. 46–48, NMSU 2006-1, 2); (2) length of spined portion (SL) of EES is intermediate between the maximum spined length for *D. elongata* (0.18 mm) and the minimum spined length for *D. sublineata* (0.38 mm) (Figs. 46–48, NMSU 2006-3, 4, 5); (3) length of blade of EES falls within the range for *D. sublineata*, but length of spined portion of the EES falls within the range for *D. elongata* (Figs. 47–48, NMSU 2006-6), or is intermediate between the species (NMSU 2006-3); (4) length of blade of EES falls within the range for *D. sublineata*, but connecting endophallic sclerite (CES) is absent as in *D. elongata* (Figs. 47–48, NMSU 2006-3, 4, 6); (5) palmate endophallic sclerite (PES) is broadly rounded with subdistal spines as in *D. elongata*, but length of blade of EES falls within the range of *D. sublineata* (Fig. 47—NMSU 2006-4); and (6) PES is truncate serrate with more than two spines being distal as in *D. sublineata*, but length of blade of EES falls within the range of *D. elongata* (Fig. 47—NMSU 2006-5). All hybrids examined lack the CES (Figs. 46–47) which is indicative of *D. sublineata* (Fig. 45). Of the six *D. sublineata*/*D. elongata* hybrids illustrated, most bear the external coloration and pattern of elytral vittae found in *D. elongata*, and only one hybrid (Fig. 47—NMSU 2006-5) had submarginal and subsutural elytral vittae extending into the base of the elytra as is sometimes found in *D. sublineata*. The morphologies of later generation hybrids or various types of backcross hybrids are not characterized.

Many of the male *D. sublineata* × *D. elongata* hybrids possess genitalic abnormalities in the form of conspicuous abnormal sclerites (AS) of varying number, size, shape and location on the endophallus (Figs. 46–47). Abnormal sclerites are not seen or are small and inconspicuous in parental pure lines (Fig. 44–45). Externally normal appearance with genitalic abnormalities is commonly observed in interspecific hybrids between some sibling species of *Drosophila* fruit flies (e.g., Hollocher *et al.* 2000). Abnormal endophallic sclerites in *D. sublineata* × *D. elongata* hybrids are evidence of genetic incompatibilities and possibly some level of reduced hybrid fitness and postzygotic reproductive isolation.

Discussion. Taxonomy. *Galeruca sublineata* Lucas (1849) (as *Galleruca sublineata*) was described from Hippône (= Annaba), Algeria, and synonymized under *G. elongata* by Reiche and Saulcy (1858). Weise (1890) proposed *D. elongata* var. *sublineata* as extending in range from North Africa to Mongolia. Weise (1924) later proposed the aberration *D. e. ab. sublineata* and this has been followed by several taxonomists (Ogloblin 1936, Normand 1937, Alfieri 1976, Warchalowski 2003). Chen (1961) excluded *D. e. ab. sublineata* from Mongolia and included the Mongolian population under the new subspecies *D. e. deserticola* described from western China. Apparently unaware of Chen's designation, Gressitt and Kimoto (1963) proposed the subspecies *D. e. sublineata* as occurring from Mongolia and western China west to North Africa. The catalogue of Lopatin *et al.* (2004) lists *D. e. sublineata* as a junior synonym of *D. e. elongata*.

In order to characterize the genitalia of *G. sublineata*, we examined specimens that matched the species description of *G. sublineata* from Algeria and Tunisia, in the broad vicinity of the type locality of Annaba, Algeria. In the color habitus illustration accompanying the species description for *G. sublineata* by Lucas (1849, Plate 44, Fig. 8), the submarginal and subsutural elytral vittae extend well into the basal half of the elytra (as in Fig. 5). This characteristic of the elytral vittae can be used to distinguish *G. sublineata* from *D. elongata*. In *D. elongata*, the elytral vittae are often absent, as in the color habitus illustration with the species description by Brullé (1832, Plate 44, Fig. 10), and, when present, the elytral vittae are confined to the apical half of the elytra (Fig. 1, see *D. elongata* - **Discussion-Taxonomy** above). From 12 locations in Algeria and Tunisia, we selected ten male and seven female specimens matching the description of *G. sublineata* with elytral vittae extending well into the basal half of the elytra. We are confident that these 17 specimens represent *G. sublineata* as described by Lucas (1849).

We studied the genitalia in the 17 above specimens matching *G. sublineata* from Algeria and Tunisia. In the ten males, the endophalli bear a combination of five characteristics distinguishing them from those of *D. elongata* (characterized above) and the holotypes of *D. carinulata*, *D. meridionalis*, and *D. carinata* (Figs. 18–19 of Berti and Rapilly 1973) (see **Male-Genitalia** above; Figs. 14–33). In the seven females matching *G. sublineata*, the vaginal palpi were triangulate and narrowly rounded, as in *D. carinata*, and distinct from the broadly rounded vaginal palpi of *D. elongata*. The distinct male and female genitalic characters of specimens matching *G. sublineata* are strong evidence of reproductive isolation from other species in the group, and especially from the two species with which it is marginally sympatric, *D. elongata* and *D. carinata* (see **Biogeography** below; Map 1, Table 8). Therefore, we remove *G. sublineata* from synonymy with *D. elongata* and restore the species *D. sublineata* (Lucas) REVISED STATUS. Although *D. sublineata* is allopatric with *D. carinulata* and *D. meridionalis*, their status as reproductively isolated is supported by the number of diagnostic genitalic characters separating *D. sublineata* from *D. carinulata* and *D. meridionalis* (6–8 characters) being greater than the number of characters separating the moderately sympatric *D. carinata* from *D. carinulata* (5 characters) (Table 5). Further evidence for reproductive isolation between *D. sublineata* and *D. elongata* is also found in previously discussed differences in component ratios of putative aggregation pheromones and reduced F2 hybrid egg viability. The elytral vittae of *D. sublineata* can resemble that of *D. elongata* in being confined to the apical half of the elytra or entirely lacking. The color habitus illustration of “*D. elongata*” from southern Europe in Plate 29, Figure 7 of Chatenet (2002), with the elytral striping extending through the entire basal half of the elytra, is actually of a specimen of *D. sublineata*.

If *D. sublineata* interbreeds as a subspecies with *D. elongata* where these species are marginally sympatric in Portugal, Spain and Egypt, we would expect intermediate hybrid forms to be evident in areas of range contact as seen in other chrysomelid subspecies, such as *Diabrotica virgifera virgifera* and *D. v. zeae* Krysan and Smith (Krysan *et al.* 1980). For example, we would expect hybrid characteristics such as varying degrees of development of the connecting endophallic sclerite and the lateral appendage of the palmate endophallic sclerite and intermediate lengths in the blade of the elongate endophallic sclerite. Diagnostic hybrid characteristics are found in examined laboratory produced *D. sublineata* × *D. elongata* hybrids (Figs. 46–47; see ***D. sublineata* × *D. elongata* Hybrid Morphology** above). However, we find no specimens with diagnostic hybrid characteristics in field collections of 157 male *D. elongata* and 89 male *D. sublineata*. These include 37 specimens from the areas of range overlap; 6 male *D. elongata* in Egypt, (Figs. 19, 24,

29—Cairo), Portugal (Fig. 19—Portugal), and Algeria (Fig. 19—Algeria) and 42 male *D. sublineata* in Egypt (Figs. 21, 26, 31—Cairo), Algeria (Fig. 21—Algiers), Spain (Fig. 21—Valencia), and Portugal. The lack of intermediate hybrid forms in areas of sympatry is firm evidence of reproductive isolation between *D. elongata* and *D. sublineata*, and we are confident that *D. sublineata* is not a subspecies of *D. elongata*.

The diagnostic characters separating *D. sublineata* from *D. elongata* comprise three discrete and two near discrete male genitalic characters and one discrete female genitalic character for a total of six diagnostic genitalic characters, four of which are discrete (see keys and Table 5). In comparison, a total of five discrete genitalic characters are diagnostic in distinguishing the moderately sympatric species *D. carinata* and *D. carinulata* (Table 5). Even if *D. elongata* and *D. sublineata* were allopatric rather than marginally sympatric, their degree of divergence in genitalic characters is similar to that found in the related sympatric species pair *D. carinata*/*D. carinulata* (see also *D. elongata* group *Stenophenetic Analysis*, Fig. 49), further justifying their status as separate species (see Helbig *et al.* 2002).

As noted with other members of the *D. elongata* group, we find that the external characters that have been used in separating *D. sublineata* from other sibling species are inadequate and that genitalic characters must be used. Weise (1890) proposed that two sharply defined stripes on the elytra (elytral vittae) that joined apically on *D. sublineata* (as *D. e. var. sublineata*) is a distinguishing character from *D. elongata*. The use of this character as diagnostic has been followed by Laboissière (1934) and Warchalowski (2003). However, apically joined elytral vittae variably occur in both *D. sublineata* and *D. elongata*. Chen (1961) noted that the ventral tarsal pubescence was generally distributed in *D. e. ab. sublineata*, as opposed to being medially absent (leaving a median glabrous area) in *D. e. deserticola*. However, we found that the pattern of ventral tarsal pubescence in specimens of *D. sublineata* from North Africa is the same as that described by Chen for *D. e. deserticola*, and regard this character as unsuitable for taxonomic diagnosis. We have dissected specimens of *D. sublineata* that were misidentified by taxonomists using external diagnostic characters as *D. elongata* from five countries and *D. e. var. carinata* from Algeria (see **Material Examined**).

We examined four specimens (from ZMHB) with old hand-written determination labels of *D. e. var. sublineata* from Weise's collection that were collected by Potanin from Mongolia. All four of these specimens are *D. carinulata*. These specimens are probably from the same series listed by Weise (1890) as *D. e. var. sublineata* and collected by G.N. Potanin from central Mongolia. All material we have examined from Mongolia and China are conspecific with *D. carinulata* (discussed below), and *D. sublineata* is absent from these areas, the easternmost occurrence of *D. sublineata* being in Baghdad, Iraq (Map 1).

Normand (1937) described the aberration *D. elongata ab. bipustulata* Normand from Kairouan, Tunisia in the area where *D. sublineata* is common (Maps 1 and 4). This aberration is distinguished by two dark spots near the base of the elytra on either side of the scutellum. We saw this uncommon color variant in one specimen (from Morocco) of over 150 examined specimens of *D. sublineata*. It was also seen in six specimens (from Greece and Cyprus) of 200 examined specimens of *D. elongata*, two specimens (from Ash Sharqat, Iraq) of over 150 examined *D. carinata*, and one specimen (from 74–164 km NW Turpan, China) of over 300 examined *D. carinulata*. *Diorhabda elongata* apparently is rare in Algeria and probably rarely occurs, if at all, in Tunisia, from which all 17 dissected specimens from all 12 available locations were *D. sublineata*. Therefore, we consider *D. e. ab. bipustulata* as a junior synonym of *D. sublineata* **NEW SYNONYMY**.

Diorhabda sublineata and *D. carinata* are the most morphologically similar species in the *D. elongata* group, and we considered the possibility that *D. sublineata* might be a subspecies of the earlier described *D. carinata*. The only character for consistent separation of *D. sublineata* from *D. carinata* is the presence of the connecting endophallic sclerite in the male (Figs. 16, 21, 26, 31). This connecting sclerite is not a trivial character in that it influences the three dimensional configuration of the inflated endophallus. In *D. sublineata* killed and preserved while copulating, the inflated endophallus is bent at the connecting sclerite and this is not seen in inflated endophalli of *D. carinata*. If *D. sublineata* and *D. carinata* were interbreeding subspecies, we should have observed intermediate forms in the critical distinguishing morphological character of the presence or absence of the connecting endophallic sclerite. Intermediate forms should increase along a

geographic cline approaching the point of range contact in Iraq. Specifically, we should have observed a transition from the fully developed connecting endophallic sclerite of *D. sublineata* to increasing incidence of faint lines in place of a connecting endophallic sclerite, to the total lack of connecting endophallic sclerite found in *D. carinata*. From Baghdad, Iraq, we examined a single male *D. sublineata* with a normal connecting endophallic sclerite (Fig. 21 – Baghdad) and 6 male *D. carinata*, none of which bore even a faint line where the connecting endophallic sclerite would be found (Fig. 20—Baghdad). The lack of intermediate forms in field collected material of 98 male of *D. carinata* and 69 male of *D. sublineata*, is evidence of reproductive isolation. Neither males nor females of *D. sublineata* and *D. carinata* were more difficult to identify to species near the contact zone of Iraq as would be expected were these to be interbreeding subspecies. Previously discussed differing component ratios in the putative aggregation pheromones of *D. carinata* and *D. sublineata* and the contrasting results of crossing each of these species with *D. elongata* are additional evidence of reproductive isolation.

Common Name. The vernacular name “subtropical tamarisk beetle” refers to most of the main distribution of *D. sublineata* (31–38°N; Fig. 51B) falling within the subtropical climates of North Africa (region from ca. 23.5–35°N with mild winters). This subtropical distribution contrasts with that of the marginally sympatric sibling species, *D. elongata*, which has its main distribution (37–41°N) entirely north of 35°N and which is rarely found below 35°N (Fig. 51B). *Diorhabda sublineata* has the strongest presence of any *Diorhabda* sibling species in subtropical to tropical biomes, including the Flooded Grasslands and Savannas and the Tropical and Subtropical Grasslands, Savannas and Shrublands (Table 9; Fig. 52B).

Biology. Host Plants. *Diorhabda sublineata* (as *D. elongata*) is reported from *T. africana* Poiret and *T. boveana* Bunge (as *T. bounopaea* Gay) in Algeria (Peyerimhoff 1926) and *T. africana* and *Tamarix* sp. in Morocco (Jolivet 1967) (Table 1). Reports of *T. gallica* as a host of *D. elongata* in France (Laboissière 1934) and Spain (Huelva Province, Hopkins and Carruth 1954) should also refer to *D. sublineata*. *Tamarix senegalensis* de Candolle is a new host record from collections in Ndiol Nar, Senegal by P. Jolivet (BMNH collection). *Tamarix aphylla* is a new host for *D. sublineata* (as *D. elongata*) derived from a single adult collected by A. Kirk (pers. comm.) 20.2 km north of Douz, Tunisia. We examined other specimens of *D. sublineata* that Kirk collected from *Tamarix* sp. (not *T. aphylla*) at six locations in Tunisia. *Diorhabda sublineata* is reported from *Tamarix* spp. in Egypt (Boehm 1908, Alfieri 1976) and has been found in several locations along the Nile River where *T. mannifera* (Ehrenberg) Bunge and *T. nilotica* (Ehrenberg) Bunge, close relatives of *T. senegalensis* (Baum 1978) are common, and these species may also serve as hosts. The center of distribution of *T. canariensis* is in Algeria, Morocco and Spain (Baum 1978), and it is another likely host (Map 4). *Tamarix arabica* Bunge occurs in Yemen (Baum 1978), where it could serve as a host of *D. sublineata*.

No-choice larval host suitability studies by Milbrath and DeLoach (2006a) confirm that *D. sublineata* larvae from Tunisia can survive to adulthood only on plants of the order Tamaricales, including *Tamarix* (Tamaricaceae) and, to a significantly lesser degree, on three North American *Frankenia* spp. (Frankeniaceae): *F. salina*, *F. johnstonii*, and *F. jamesii*. In field cage no-choice studies, oviposition by *D. sublineata* on *F. jamesii* and *F. johnstonii* was not different from that on non-host coyote willow (*Salix exigua* Nutt.) and adults experienced increased mortality compared to *T. ramosissima* × *T. chinensis* treatments (Milbrath and DeLoach 2006a). Multiple-choice adult oviposition studies in field cages (Milbrath and DeLoach 2006a) revealed that the three North American *Frankenia* spp. provide a little attraction for oviposition compared to *Tamarix*. However, surveys by Alan Kirk in Tunisia of May 2000 revealed *D. sublineata* (as *D. elongata*) on *Tamarix* spp. from five of eight collection sites, but no *Diorhabda* were found on *Frankenia* at six collection sites in areas near *Tamarix*, even where *Frankenia* was found adjacent to *Tamarix* on which *D. sublineata* was abundant (DeLoach *et al.* 2003b; A. Kirk, pers. comm.). In field cage multiple-choice studies, *D. sublineata* oviposited significantly less on *T. aphylla* than on most of the invasive North American tamarisks, including *T. ramosissima*, *T. ramosissima* × *T. chinensis*, *T. ramosissima* × *T. canariensis*/*T. gallica*, *T. chinensis* × *T. canariensis*/*T. gallica*, and *T. parviflora* (Milbrath and DeLoach 2006a, Milbrath and DeLoach 2006b). Oviposition did not differ between *T. aphylla* and *T. canariensis*/*T.*

gallica in one of these field cage tests (Milbrath and DeLoach 2006b) while oviposition was significantly lower on *T. aphylla* than on *T. canariensis*/*T. gallica* in the other test (Milbrath and DeLoach 2006a). For oviposition, *T. aphylla* is accepted by *D. sublineata* to the same degree as *T. ramosissima* × *T. chinensis* in no-choice field cage studies (Milbrath and DeLoach 2006b). *Tamarix aphylla* is at moderate risk to damage by *D. sublineata* in the field and the degree to which *D. sublineata* would damage *T. aphylla* is difficult to predict, especially in the absence of other *Tamarix* spp. (Milbrath and DeLoach 2006b). Moran *et al.* (in press) found that *D. sublineata* (ex: Sfax, Tunisia) × *D. elongata* (ex: Sfakaki, Crete, Greece) hybrids demonstrate a clear preference to *T. canariensis*/*T. gallica* over *T. aphylla* in open-field tests near Kingsville, Texas. *Frankenia* is at very low risk of damage from *D. sublineata* (Milbrath and DeLoach 2006a). Risk of damage to both *T. aphylla* and *Frankenia* by *D. sublineata* is probably much lower when these plants are not in the proximity of preferred *Tamarix* spp. (e.g., Blossey *et al.* 2001).

Ecology and Phenology. We found no reports on the ecology and phenology of *D. sublineata* in the Palearctic. Adult collection dates in the literature and our examined material are from January to November in Egypt, 22 January to 14 December in Tunisia (both from examined material), January to September in Algeria (Peyerimhoff 1926, Doguet, pers. comm.) and April to October in France and Spain (this study). From these data, adults are found almost year round in North Africa.

Milbrath *et al.* (2007) found that *D. sublineata* (as *D. elongata* from Sfax, Tunisia) overwintering at Temple, Texas had ca. 92% survival from early November through the beginning of March but survival dropped to ca. 62–67% by mid-March when the tamarisk leaves were just budding. Overwintered adults began ovipositing in late March giving rise to five generations and a partial sixth generation. Fifth generation adults emerging in early September oviposited for several weeks before ceasing oviposition in November when they appeared to enter diapause.

Development and Reproduction. Milbrath *et al.* (2007) found that, at 28°C, *D. sublineata* (as *D. elongata* from Sfax, Tunisia) had a development time of 18.6 days from egg to adult (with 89% survival), a fecundity of 208 eggs, and a population doubling time of 5.5 days. These values were all very similar to those found for *D. carinulata* (Turpan and Fukang), *D. elongata* (Crete), and *D. carinata* (Uzbekistan) (all as *D. elongata*) in the same study.

Natural Enemies. *Nosema* sp. microsporidians infected *D. sublineata* larvae and adults collected southeast of Marith, Tunisia in 2008 (shipment EBCLGR-JK-2008-004) (D. Bean, pers. comm.).

Biogeography. **Comparative.** *Diorhabda sublineata* differs from other tamarisk beetles by the following combination of biogeographic characteristics: (1) strongly maritime and generally found within ca. 200 km from a sea coast, usually below 300 m elevation (but can range to 2,600 m elevation); (2) favors subtropical Mediterranean woodlands or Flooded Grasslands, Savannas and Shrublands biomes; and (3) latitudinal range of 16–44°N and most commonly collected from 31–38°N (Table 7; Figs. 51–52). In contrast, the marginally sympatric *D. elongata* has a southern range limited to 30°N and it is much less common south of 35°N. In addition, *D. elongata* is rare or lacking in flooded grassland and desert biomes in which *D. sublineata* is found. Although both *D. elongata* and *D. sublineata* share *T. gallica* as one of their hosts (Table 1), we have seen no mixtures of *D. sublineata* and *D. elongata* within series collected from specific localities such as are found with *D. carinata* and *D. carinulata*, or *D. carinata* and *D. meridionalis*. This may be the result of *D. sublineata* dominating in areas where it is marginally sympatric with *D. elongata* in Spain, Algeria, Egypt and probably elsewhere along the Mediterranean coast of North Africa (Map 1, Table 8; see also discussion under **Biogeography** for *D. elongata*). The possibility that *D. sublineata* may occur in Italy where it may be rare and dominated by *D. elongata* should be investigated.

Diorhabda sublineata is marginally sympatric with *D. carinata* in Baghdad, Iraq, where their ranges meet, and it is allopatric with *D. carinulata* (Map1; Table 8). Both *D. carinata* and *D. carinulata* differ from *D. sublineata* in being primarily continental in distribution, mostly found in desert and grassland biomes rather than the Mediterranean biome, and being common north of 38°N (Figs. 51–52). *Diorhabda sublineata* is also allopatric with *D. meridionalis* (Map 1; Table 8). *Diorhabda meridionalis* differs from *D. sublineata* in

being more commonly collected further south at 26–30°N, and in preferring the desert biome over the Mediterranean biome (Figs. 51–52).

Descriptive. *Diorhabda sublineata* primarily inhabits the southwestern Palearctic realm and is the only member of the *D. elongata* group known to occur in the Afrotropical biogeographic realm (in Senegal and Yemen) (Map 1). It has most commonly been collected from the Mediterranean Forests, Woodlands and Scrub biome from 31–38°N (Fig. 52B). The next most important biome for *D. sublineata* is the Flooded Grasslands and Savannas biome from ca. 24–34°N (Map 4; Fig. 42B). *Diorhabda sublineata* is also found in two additional biomes: the Deserts and Xeric Shrublands biome from 25–33°N in North Africa and Iraq (at ca. 20–600 m elevation), and the Montane Grasslands and Shrublands biome to ca. 2,600 m elevation at Tacheddirt, Morocco (latitude 31°N) (Map 4; Table 7).

Diorhabda sublineata occurs primarily in three ecoregions of the Mediterranean Forests, Woodlands and Scrub biome (Olson and Dinerstein 2002), based on frequency of collections (Map 4): Mediterranean Woodlands and Forests of coastal Morocco, Algeria and Tunisia (at ca. 0 to 1,700 m), Mediterranean Acacia-Argania Dry Woodlands and Succulent Thickets of Morocco (at ca. 0 to 600 m), and Mediterranean Dry Woodlands and Steppe of Algeria and Tunisia (at ca. 0 to 600 m). Primary ecoregions of *D. sublineata* in the Flooded Grassland and Savanna biome are the Nile Delta Flooded Savanna of Egypt (at ca. 0 to 80 m elevation) and Saharan Halophytics of Algeria and Tunisia (at ca. 20 to 120 m elevation). *Diorhabda sublineata* was the most common galerucine reported in Egypt in 1908 (Boehm 1908).

Diorhabda sublineata is found only in the Mediterranean Forests, Woodlands and Scrub biome in the northern portion of its range at ca. 37–42°N in France and Spain (Map 4). *Diorhabda sublineata* (as *D. elongata*) is common but not damaging in parts of southern Spain (Hopkins and Carruth 1954) and it is uncommon along Mediterranean coast of northeastern Spain (Petitpierre 1988) and southern France (Laboissière 1934, Chatenet 2002).

We found few reports of *D. sublineata* in the southern portion of its range from 16–25°N in Africa and the Arabian Peninsula (Map 4). Additional collection efforts may reveal it to be more common in these areas. P. Jolivet (pers. comm.) reported August populations in Senegal reaching the thousands where he collected material that we examined from the Tropical and Subtropical Grasslands, Savannas and Shrublands biome.

The northwestern portion of the range of *D. sublineata* (France, Spain, Morocco, Algeria and Tunisia) closely follows that of known host *T. boveana* and the suspected host *T. canariensis* (Map 4). Both hosts *T. gallica* and *T. africana* widely overlap the northwestern range of *D. sublineata*, but extend further east into Italy from which *D. sublineata* is not known. In Egypt, the distribution of *T. nilotica* and *T. mannifera* along the Nile River (Baum 1978) corresponds well with that of *D. sublineata*.

Potential in Tamarisk Biological Control. *Summary.* The subtropical tamarisk beetle can potentially be effective in biological control of *T. ramosissima*/*T. chinensis* and hybrids with *T. canariensis*/*T. gallica* in the extreme southwestern U.S. *Diorhabda sublineata* may be the most suitable *Diorhabda* species for introduction into the Mediterranean biome below 37°N in California and the southern Chihuahuan Desert in Mexico (Map 13) (including the Mapimian and Saladan regions of Map 6 in Morafka [1977]). In the absence of *D. meridionalis*, *D. sublineata* is probably the most suitable species for a major portion of maritime subtropical deserts such as the Sonoran Desert and Tamaulipan Mezquital xeric shrubland.

Discussion. We find no anecdotal reports of the subtropical tamarisk beetle damaging *Tamarix* in the Old World, but this species can be locally abundant in places such as Senegal and Kom Ombo, Egypt, from which a large series of 106 specimens was collected in November. *Tamarix ramosissima* and its relatives are not recorded hosts of *D. sublineata*. Hybrids of *T. ramosissima*/*T. chinensis* with *T. canariensis*/*T. gallica* are common in Texas (J. Gaskin, pers. comm.), and *D. sublineata* may prefer these hybrids more than would other *Diorhabda*. *Diorhabda sublineata* has a moderate risk of damaging *T. aphylla* (Milbrath and DeLoach 2006b) and very low risk of damaging *Frankenia* (Milbrath and DeLoach 2006a), and both these risks are probably much reduced at less proximity to preferred *Tamarix* spp. (e.g., Blossey *et al.* 2001).

The subtropical tamarisk beetle is most commonly found in the Mediterranean Forests, Woodlands and Scrub biome at 31–38°N (Map 4, see **Biogeography**). In North America, Mediterranean ecoregions

corresponding to this area include the California Coastal Sage and Chaparral ecoregion of California and Baja California, the California Montane Chaparral and Woodlands and southern portions of the California Interior Chaparral and Woodlands (Map 13). Additional North America habitats should be similar to where *D. sublineata* is found in the subtropical maritime Flooded Grassland and Savannah biome from 24–34°N in North Africa that are surrounded by the subtropical maritime Deserts and Xeric Shrublands biome. In North America, this habitat particularly includes lower elevation (below 300m) portions of maritime subtropical Deserts and Xeric Shrublands biome from ca. 24–35°N in the following ecoregions: southern Mojave Desert, Sonoran Desert, Tamaulipan Mezquital along the lower Rio Grande, and Tamaulipan Mattoral (Map 13). Along the Rio Grande near Presidio in the Big Bend region, the distribution of the Rio Grande cottonwood (*P. deltoides* subsp. *wislizenii*) more common in the Trans-Pecos Chihuahuan transitions to the more southern Chihuahuan desert species, Meseta cottonwood (*Populus fremontii* subsp. *mesetae*) (Powell 1998). Correspondingly, the Big Bend area near Presidio may correspond with a transition zone for more northern desert *D. carinata* and *D. carinulata* into more southern desert *D. sublineata*. Morafka (Map 6 of Morafka 1977) mapped a transition from northern Trans-Pecos Chihuahuan Desert to more southern Mapimian Chihuahuan Desert at approximately the interface of our predicted ranges of *D. carinata*/*D. carinulata* and *D. sublineata* in the Big Bend region (Map 13). *Tamarix aphylla* is not a primary host for *D. sublineata*, but it is an indicator of the subtropical climate in North Africa where *D. sublineata* is most common (Map 4), and the most suitable areas in North America for *D. sublineata* may also occur within the area warm enough for *T. aphylla* to flourish (see Map 7). In the absence of *D. meridionalis*, *D. sublineata* would be the most suitable species for all of the Tamaulipan Mezquital in Texas according to our HSI model. *Diorhabda sublineata* appears to be well adapted to more southern latitudes in terms of initiation of diapause at shorter photoperiods (later in season) in the south (Bean and Keller in prep.) and can have high overwintering survival (ca. 65%) at Temple (Milbrath *et al.* 2007). Species distribution models incorporating climatic data are in preparation to better predict habitat suitability.

Efforts to establish populations of *D. sublineata* from near Sfax, Tunisia near Ricardo, Texas on *T. canariensis*/*T. gallica* were not successful, possibly partly due to the small isolated poorly vigorous stand of tamarisk at this site. Plans are being made to release *D. sublineata* from near Marith, Tunisia in 2009 at better quality release sites with larger and more vigorous *T. chinensis*/*T. canariensis* stands along the Rio Grande and tributary streams in west and south Texas, such as at Ruidosa. Releases of any *Diorhabda* in southern California are awaiting clearance with USDA-APHIS (T. Dudley, pers comm.).

***Diorhabda carinulata* (Desbrochers, 1870)**

northern tamarisk beetle

(Figs. 7, 8, 17, 22, 27, 32, 37, 42)

Galeruca carinulata Desbrochers, 1870:134 (Type locality: Sarepta, Russia).

Diorhabda elongata var. *sublineata*: Weise, 1890:484 (part, central Mongolia).

Diorhabda elongata var. *carinata*: Weise, 1893:635 (part, Sarepta, Russia).

Diorhabda elongata ab. *carinata*: Weise, 1924:78 (part; world catalog; Sarepta, Russia); Winkler, 1924–1932:1307 (part; Palearctic catalog; southern Russia)

Diorhabda elongata ab. *sublineata*: Weise, 1924:78 (part; world catalog; Mongolia); Laboissière, 1934:54 (part, Mongolia); Winkler, 1924–1932:1307 (part, Palearctic catalog, Mongolia); Medvedev and Voronova, 1977b:238 (part, keys, Mongolia); Medvedev, 1982:259 (part, keys to adults and larvae, Mongolia).

Diorhabda koltzei ab. *basicornis* Laboissière, 1935:324 (Type locality: Khotan, Taklamakan Desert, Turkestan [Hotan, Xinjiang Uygur Zizhiqu, China]) (NEW SYNONYM); Wilcox 1971:63 (world catalog, Karakorum [western China]).

Diorhabda elongata: Ogloblin, 1936:79 (part, Russia, transcaucasus, Iran, central Asia, central Mongolia); Rusanov, 1949:118 (part, Central Asia, as *Diorhabda*); Kyrzhanovskiy, 1952:198 (part, Turkmenistan), 1965:392 (part, middle Asia); Pavlovskii and Shtakelberg, 1955:566 (part, southwest Russia, transcaucasus, central Asia, Iran, Mongolia, as *Diorhabda*); Yakhontov and Davletshina, 1955:58 (part, biology, Amu Darya Delta, northern Uzbekistan); Sinadsky, 1957:950, 1963:84, 1968:64 (part, biology, Amu Darya Valley, Uzbekistan, as *Diorhabda*); Yakhontov,

1959:338 (part, biology, Uzbekistan); Medvedev, 1959:118 (part, Turkmenistan); Kulinich, 1962:73 (part, biology, Tajikistan); Kryzhanovsky, 1965:392 (part, middle Asia); Pripisnova, 1965:83 (part, biology, Tajikistan); Kulenova 1968:171 (part, southeastern Kazakhstan); Lopatin and Tadzhibaev, 1972:591 (part, Tajikistan); Lopatin, 1977a:282 (part, keys, Asia); Medvedev and Voronova, 1977a:339 (Mongolia), 1977b:238 (part, keys, Mongolia), 1979:119 (catalog for Mongolia, hosts); Davletshina *et al.*, 1979:79 (part, southwest Kyzyl–Kum Desert, central Uzbekistan); Ogloblin and Medvedev, 1971:83, 89 (part, key to larva, European Russia); Medvedev, 1982:99 (part, keys to adults and larvae, Mongolia); Samedov and Mirzoeva, 1985:712 (part, Azerbaijan); Lopatin and Kulenova, 1986:129 (part, Kazakhstan); Kovalev, 1995:78 (part, south central Palearctic); Myartseva, 1995:4, 1999:1, 2001:1 (part, biology, Turkmenistan); DeLoach *et al.*, 1996:253 (part, China); Ishkov, 1996:30 (part, Ili River Valley, Kazakhstan); White, 1996:392 (part, China); Mityaev and Jashenko, 1997:4, 1998:7, 1999:6, 2000:14, 2001:9, 2007:3 (part, biology, ecology; southeast Kazakhstan); Gruev and Tomov, 1998:70 (part, Transcaucasus, mid-Asia, Mongolia); USDA-APHIS, 1999:13395 (Fukang, China; approval of initial introduction into U.S.); Anonymous, 2001:52N (part, Kazakhstan, China); Gould and DeLoach, 2002:302 (part, biological control, North America); Dudley *et al.* 2000:346 (part, biological control, North America), 2001:260 (part, biological control, North America); Stenquist, 2000:492 (Kazakhstan); Jolivet, 2001:134 (part, U.S. introduction); Vail *et al.* 2001:37 (part, U.S. introduction); DeLoach *et al.*, 2003a:230 (part, China, Kazakhstan), 2003b:126 (part, host range; Uzbekistan, Turkmenistan, Iran); Khamraev, 2003:11 (part, Uzbekistan); Petroski, 2003:3234 (synthesis of aggregation pheromone components); Milbrath *et al.*, 2003:225 (part, China, Kazakhstan); Riley *et al.*, 2003:69,189 (part, catalog, North America [introduced]); Warchalowski, 2003:328 (part, taxonomic keys, Caucasus, Central Asia, and Mongolia); Bieñkowski, 2004:76 (part, keys, eastern Europe (part, southern Russia, Caucasus, Iran, Iraq, Central Asia, Kazakhstan, Mongolia); DeLoach and Carruthers, 2004b:311 (part, China and Kazakhstan); Dudley and DeLoach, 2004:1542 (part, biological control, North America); Lopatin *et al.*, 2004:127 (part, central Asia); Cossé *et al.*, 2005:657 (aggregation pheromone, Fukang, China, population), 2007:2695 (Fukang, China; attraction to green leaf volatiles); Dudley, 2005a:13, 2005b:42N (part, biological control, ex: China and Kazakhstan); Herrera *et al.*, 2005:775 (part, developmental rates, Fukang, China, population); Carruthers *et al.* 2006:71, 2008:258 (part, biological control, ex: China and Kazakhstan); Milbrath and DeLoach, 2006a:32 (part, host specificity, Turpan, China, populations); Geraci *et al.* (in press) (remote sensing of defoliation, Nevada); Milbrath *et al.* (2007) (part, biology, Fukang, China, population); Dudley *et al.*, 2006:137 (part, releases in Nevada, Fukang, China; host range, Fukang and Turpan, China); Longland and Dudley (2008) (ecology, North America); Dudley *et al.* (in prep.) (host range, Nevada); Thompson *et al.* (in prep.) (part, laboratory hybridization, Fukang, China).

Diorhabda rybakovi: Mityaev, 1958:86 (part, biology, Kazakhstan, as *rybakovi*).

Diorhabda elongata deserticola Chen, 1961 (Type locality: Yuli (= Wei–li), Xinjiang Uygur Zizhiqu, China) (NEW SYNONYM); Gressitt and Kimoto, 1963b:930 (China); Wilcox, 1971:63 (world catalog, Xinjiang Uygur Zizhiqu, China); Tian *et al.*, 1988:24 (biology, ecology; Ningxia Province, China); Bao, 1989:45 (biology and control as pest; Nei Mongol Zizhiqu, China); Xiao, 1992:537 (biology, China); Sha and Yibulayin, 1993:7 (biology, ecology, control as pest, China, Xinjiang Prov.); Chen *et al.*, 2000:44 (control as pest; Alashan Meng, Nei Mongol Zizhiqu, China); USDA-APHIS, 2005:1 (Fukang, China; large-scale introduction to 13 states in northwestern U.S.); Li *et al.*, 2000:48 (biology, ecology; China, Xinjiang Prov., Fukang); Eberts *et al.*, 2001:3 (Fukang, China, establishment in Colorado); Lair and Eberts, 2001:3 (China, potential introduction into north Texas); Zhang 2002:1 (biology and ecology, Xinjiang Uygur Zizhiqu, China); DeLoach *et al.*, 2003a:229 (China, Kazakhstan), 2003b:117 (host specificity; Turpan and Fukang, China and Chilik, Kazakhstan; host range; China, Kazakhstan, Mongolia), 2004:505 (field establishment in North America from populations in Fukang, China and Shelek, Kazakhstan), (2008, in prep.) (part, China); Lewis *et al.*, 2003a:148 (host specificity; Fukang, China and Chilik, Kazakhstan), 2003b:101 (developmental and reproductive biology; Fukang, China and Chilik, Kazakhstan); Meng and Baoping, 2003:99, 2005:192 (biological control; Xinjiang Uygur Zizhiqu, China), 2006:189 (ecology; Xinjiang Uygur Zizhiqu, China); DeLoach and Carruthers, 2004a:10 (field establishment in North America from populations in Fukang, China and Shelek, Kazakhstan); Ding, 2004:57 (control as pest; Anxi County, Gansu Sheng, China); Ming *et al.* 2004:283 (Xinjiang Uygur Zizhiqu, China); Lopatin *et al.*, 2004:127 (east Kazakhstan, northwest China); Aber *et al.*, 2005:63 (field monitoring in Colorado; ex: Fukang, China); Dudley and Kazmer, 2005:265 (host specificity, Fukang, China, population); Peng *et al.*, 2005:63 (control as pest; Gansu Sheng, China); Zheng *et al.*, 2005:136 (China); Ding *et al.*, 2006:1442 (biological control, ex: Kazakhstan, China); Li and Wang, 2006:27 (biology, control as pest; Gansu Sheng, China); Bean *et al.*, 2007a:15 (diapause, Fukang, China); Mityaev and Jashenko, 2007:8 (biological control, ex: Kazakhstan, China); Bean *et al.*, 2007b:531 (diapause, Fukang, China); Hudgeons *et al.*, 2007a:158 (biological control; Fukang, China, Chilik, Kazakhstan), 2007b: 215 (part, tamarisk damage in Nevada, ex: Fukang, China); Dalin *et al.* (in press) (host range; Turpan, China).

Diorhabda elongata sublineata: Gressitt and Kimoto, 1963a:407 (part; keys; northwestern China and Mongolia); Lopatin, 1968:214 (Mongolia); 1970:254 (Mongolia, on *Tamarix*); 1975:219 (Mongolia); 1977b:154 (Mongolia).

Diorhabda carinulata carinulata: Berti and Rapilly, 1973:881 (restored species; Sarepta, Russia); DeLoach *et al.*, 2003b:126; Warchalowski, 2003:328 (taxonomic keys, southern Russia).

Diorhabda deserticola: Yu *et al.*, 1996:94 (taxonomic keys and descriptions, China); Meng *et al.*, 2005:27 (ecology, Xinjiang Uygur Zizhiqu, China); Zhang and Baoping, 2006:109 (behavior and reproductive biology, Xinjiang Uygur Zizhiqu, China).

Male. Genitalia. Male *D. carinulata* can be distinguished from all other species in the *D. elongata* group by two unique characteristics of the palmate endophallic sclerite (PES): (1) the distal margin is acutely rounded and generally smooth, with one or two small subdistal spines, and (2) the PES has a length to width ratio of 0.61–1.02 (Figs. 17, 32; Table 3). In contrast, the distal margin of the PES is truncate or more broadly rounded with larger distal or subdistal spines in *D. elongata*, *D. carinata*, and *D. sublineata* (Figs. 14–16, 29–31), and the PES is narrowly rounded with a length to width ratio of 0.35–0.63 in *D. meridionalis* (Figs. 18, 33). The length of the spined area (SL) of the elongate endophallic sclerite (EES) is greater than or equal to 0.33 times (or greater than about one third) the length of the EES in *D. carinulata* (Figs. 17, 22), compared to the spined area being less than or equal to 0.16 times (or less than about one fifth) the length of the EES in *D. elongata* (Table 3; Figs. 14, 19, 24, 48). In *D. carinulata*, the blade of the EES extends less than 2/3 the total length of the sclerite (Figs. 17, 22), and the EES lacks a strong hook at the apex in dorsal aspect (Fig. 27). In contrast, the blade of the EES extends for more than 2/3 the total length of the EES in *D. meridionalis* (Figs. 18, 23), and the apex of the EES is strongly hooked in dorsal aspect (Fig. 28).

Measurements. See Tables 2 and 3.

Female. Genitalia. Female *D. carinulata* can be distinguished from all other members of the *D. elongata* group by the following combination of characters in the vaginal palpi (VP) and internal sternite VIII (IS VIII): (1) the vaginal palpi are broadly rounded and about as long as wide or longer with a width to length ratio (LP/WP) of 0.94–1.36 (Fig. 37; Table 4), (2) if the width to length ratio of the vaginal palpi is 0.94, then the width of the widest lobe of the stalk (WLS) of IS VIII is greater than or equal to 0.11 mm (Fig. 37), and (3) the width of the stalk (WST) of IS VIII is 0.36–0.57 mm and this width is 0.49–0.77 times the width of the apical lobe (WAL) (Figs. 37, 42; Table 4). In contrast, the vaginal palpi are triangulate and wider than long with a width to length ratio of 0.46–0.89 in *D. carinata* and *D. sublineata* (Figs. 35–36). In *D. elongata* the vaginal palpi are also broadly rounded but are wider than long with a length to width ratio of 0.52–0.94, and when the width to length ratio of the vaginal palpus is 0.94, the width of the widest lobe of IS VIII is less than or equal to 0.10 mm (Fig. 34). In *D. meridionalis*, the width of the stalk of IS VIII is narrower than in *D. carinulata*, measuring 0.22–0.33 mm and this width is from 0.33–0.48 times the width of the apical lobe (Fig. 38, 43). In addition, the width of the widest lobe of the stalk of IS VIII is usually greater than 0.10 mm in *D. carinulata* (Figs. 37, 42); whereas, in *D. meridionalis* the width of the widest lobe of the stalk is from 0.04–0.09 mm (Fig. 38, 43; Table 4).

Measurements. See Tables 2 and 4.

Coloration. Coloration and elytral vittae of dead (Fig. 7) and living (Fig. 8) *D. carinulata* is very similar to that discussed above for *D. sublineata* (Figs. 5, 6). Chen (1961) also noted the similar appearance of *D. carinulata* (as *D. e. deserticola*) and *D. sublineata* (as *D. e. ab. sublineata*) from North Africa.

Type material. According to Berti and Rapilly (1973), the Desbrochers type material for *D. carinulata*, consisting of a male holotype, is deposited in the Demaison Collection at MNHN. As discussed above (see *D. elongata* – **Type material**), we were unable to obtain type materials from MNHN. We studied the original description by Desbrochers (1870), which he based on a single individual 5.5 mm in length, the illustrations of the endophallus of the male holotype by Berti and Rapilly (1973), and topotypes from Sarepta, Russia and the neighboring area.

Chen's (1961) type material for *D. e. deserticola* consists of a holotype male and allotype female from Wei-li (=Yuli), Xinjiang Uygur Zizhiqu, China, and 25 paratypes (8 ♂♂, 17 ♀♀) in Xinjiang from Akesu (= Aksu), Atushen (= Atux), Baicheng, K'u-ch'e (Kuqa), Miqan, Turtiaogou, Shajingzi, Yecheng (= Kargilik), and Wei-li. These are deposited at the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZAS). We studied four paratypes (2 ♂♂, 2 ♀♀) from Wei-li County, Xinjiang Uygur Zizhiqu, China (from IZAS), and the original description of *D. e. deserticola* by Chen (1961).

We studied the type material of *D. koltzei* ab. *basicornis* Laboissière from Khotan (=Hotan), Turkestan (now in Xinjiang Uygur Zizhiqu, China) which consists of a single female according to Laboissière (1935) that Ron Beenen kindly located for us in the Zoological Museum Amsterdam (ZMAN).

Material examined. 120♂♂ dissected (diss.), 52♀♀ diss., 199♂♂, 230♀♀, 128 unsexed specimens. **AZERBAIJAN:** 1♂ diss., Gobustan [Qobustan; 40.08416°N, 49.41583°E], 9-10-VII-2001, V. Dolin, MBPF [2003-07]; 2♀♀ diss., Ordubat [Ordubad; 38.9081°N, 46.0278°E], [19]14, Dr. Veselý, NMPC [2004-26, 2005-37]; 1♀ diss., Ordubat, Araxes [Aras River] Road, Dr. J. Veselý, 9131, NMPC [2004-18]; **CHINA: Nei Mongol Zizhiqu (Inner Mongolia):** 1♂ diss., Erjina County [specific location not given], 15-VII-1960, Forest Department, Forest Science Institute, Erjina Co., on *Tamarix*, IZAS [2005-05]; **Gansu Sheng:** 1♂ diss., 1♀ diss., 1♀, Jiayuguan, 3 km southeast [39.7900°N, 98.3200°E], north side road, 40,238 km odom., 29-VII-1993, C.J. DeLoach, on *T. ramosissima*, *Diorhabda elongata deserticola* det. I. Lopatin 2000, 6682–6684, GSWRL [2003-53, 54]; 1♂ diss., 9♀♀, Lanzhou, 4 km east [36.05639°N, 103.84000°E], 39,249 km odom., 26-VII-1993, C.J. DeLoach, on *T. hohenackeri* [= *T. smyrnensis*]/*T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000 [1♂ diss., 6♀♀], 6677–6681, 6729, 8980, GSWRL [2003-48]; **Xinjiang Uygur Zizhiqu:** 1♂ diss., Bogda Shan Mtns., 80 km northeast Urumqi [Urumchi; 43.81850°N, 87.97160°E]; 4-VI-1993, Mityaev, on saksaul [*Haloxylon ammondendron* (C.A. Meyer) Bunge (Chenopodiaceae), apparently incidental occurrence], USNM [2003-15]; 1♀ diss., 5♂♂, 8♀♀, Fukang [44.1667°N, 87.9833°E], 8-VIII-1995 [not 13-VIII-1995 as in some records], Lu Qing-guang, M.T. Liu & Jiang Xi Liang, on *T. ramosissima*, *D. e. deserticola* Chen det. I. Lopatin 2000 [1♀], 8584–8586, 8588, 8591–8593, GSWRL(CJD)-1995-25, GSWRL [2005-20] [11 specimens from Lot GSWRL(CJD)-1995-9 identified as prob. *D. e. deserticola* by R.E. White on 15-XI-1995 at USDA SEL, SEL Lot # 95-10233]; 1♂ diss., 1♂, 2♀♀, Fukang, 8-IX-1996, Li Bao Ping, on *T. ramosissima*, voucher shipment GSWRL(CJD)-1996-27, GSWRL [2005-90] [9 specimens from Lot GSWRL(CJD)-1996-4 identified as *D. elongata* by S.M. Clark on 28-X-1996 at West Virginia Dept of Agric.]; 1♂ diss., 1♂, 1♀, Fukang, 8-VI-1996, Li Bao Ping, on *Tamarix* sp. prob. *ramosissima*, GSWRL [2006-02]; 1♀ diss., Fukang, southwest, 9-VI-1996, P.E. Boldt, on *T. karelinii* [*T. hispida* var. *karelinii*], GSWRL [2006-01]; 1♂ diss., 11♂♂, 7♀♀, Fukang, Tamarix Park, 1-IX-1997, Li Bao Ping, on *Tamarix* sp., voucher shipment GSWRL(CJD)-1997-22, GSWRL [2005-100]; 1♂ diss., 1♀ diss., 15♂♂, 10♀♀, Fukang, Tamarisk Park, 18-IV-1998 [not 11-V-1998 as on some shipment records and labels], Li Bao Ping, on *T. ramosissima*, 805, 806, 808, 811, 812, 814–815, 820, 821, 823–825, voucher shipment GSWRL-1998-05, GSWRL [2005-67, 68] [parasite *Erynniopsis antennata* Rondani (Diptera: Tachinidae) emerged from 21 adult specimens in Lot GSWRL-2000-04 identified by N. E. Woodley on 23-II-2000 at USDA SEL, SEL Lot # 0001060]; 1♂ diss., 4♂♂, 8♀♀, Fukang, 13-VII-1999, Li Bao Ping, on *Tamarix* spp., voucher shipment BCW/WRRC-99-04 received 21-VII-1999, GSWRL [2005-75] [7 specimens from Lot GSWRL-1999-2 identified as *D. e. deserticola* by S. Lingafelter on 23-VII-1999 at USDA SEL, SEL Lot # 9904542] [USDA lab colony at Albany, CA] [introduced into cages in Nevada, Colorado, and Wyoming in 1999; released in 2001] [used in biological studies of DeLoach *et al.* (2003b), Lewis *et al.* (2003a, 2003b), Petroski (2003), Cossé *et al.* (2005), Herrera *et al.* (2005), Milbrath and DeLoach (2006a), Herr *et al.* (in prep.), Bean and Keller (in prep.), and Thompson *et al.* (in prep.)] [in field studies by DeLoach *et al.* (2004), Dudley and Kazmer (2005), Aber *et al.* (2005), USDA-APHIS (2005), and Dudley *et al.* (in prep.)]; 1♂ diss., 2♀♀ diss.; Fukang, 13-VII-1999, Li Bao Ping, on *Tamarix* spp., voucher shipment BCW/WRRC-99-04, USDA/ARS lab colony at Temple, Texas (ex Lovell, WY, 2002, J.L. Tracy), GSWRL [2003-28, 29, 32]; 1♂ diss., 1♂, 3♀♀, Fukang, ca. 3 km west [44.14240°N, 87.92806°E], km marker 748, 15-VII-1992, R. Wang & C.J. DeLoach, on *T. arceuthoides* [1♂ diss.], on *T. hispida* var. *karelinii* – no flowers [1♂, 2♀♀], on *T. laxa* – no flowers [1♀], *D. e. deserticola* det. I. Lopatin 2000 [1♂ diss., 1♂, 2♀♀], 8974, GSWRL [2005-18]; 2♀♀ diss., Fukang, ca. 3 km west, km marker 749, 15-VII-1992, R. Wang & C.J. DeLoach, on *T. ramosissima* very few flowers [1♀ diss.], on *T. ramosissima* foliage [1♀ diss.], *D. e. deserticola* det. I. Lopatin 2000, 6728, 6659, GSWRL [2005-12,13]; 1♂ diss., 3♂♂, 2♀♀, Fukang, 7 km west [44.13658°N, 87.87737°E], 10,406 km odom., 7-VII-1992, R. Wang & C.J. DeLoach, on *T. ramosissima* [1♂ diss., 2♂♂, 1♀], on *T. laxa* - no flowers [1♀], *D. e. deserticola* det. I. Lopatin 2000 [1♂ diss., 2♂♂, 1♀], 6646–6649, GSWRL [2005-17]; 4♂♂ diss., 6♂♂, 6♀♀,

Fukang, 18 km west [44.11252°N, 87.77169°E], 14,731 km odom., 9-VIII-1993, C.J. DeLoach, on *T. leptostachya* [1♂ diss., 2♂♂, 1♀], on *T. karelinii* [*hispidus* var. *karelinii*]-some flowers (red) [1♂ diss., 1♂, 2♀♀], on *T. ramosissima*-some flowers [1♂ diss., 1♂, 1♀], on *T. elongata* [1♂ diss., 1♂, 1♀], *T. laxa* – no flowers [1♂, 1♀], *D. e. deserticola* det. I. Lopatin 2000 [4♂♂ diss., 3♂♂, 4♀♀], 6662–6669, 6693, 6694, GSWRL [2003-47, 2005-07, 19, 22]; 1♂ diss., Jiashi [39.4883°N, 76.7125°E], 11-VII-1992, R. Wang & C.J. DeLoach, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000, 6515, GSWRL [2005-04]; 1♀ diss., Jiashi, 9 km west [39.45198°N, 76.61615°E], 11-VII-1992, R. Wang and C.J. DeLoach, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000, 6658, GSWRL [2005-05]; 1♂ diss., Khotan [Hotan; 37.09972°N, 79.92694°E], *D. elongata* ab. *sublineata* Lucas, HNHM [2003-14]; 1♂ diss., 1♂, 1♀, Khotan [Hotan], Kashgar, 13-VI-1890, B. Grombchevskii, ZIN [2005-02]; 1♀, Khotan [Hotan], 6-12-V-1930, J.A. Sillem, *Diorhabda koltzei* Weise ab. *basicornis* Laboissière, TYPE [Laboissière 1935], Nederlandsche Karakorum Expeditie, ZMAN [2008-01]; 1♂ diss., 2♂♂, 4♀♀, Kuldsha [Yining; 43.9000°N, 81.35000°E], Daharkent, NHMB [2003-27]; 1♂ diss., Sanchakou, 50 km west [39.93778°N, 77.8600°E], 10-VII-1992, R. Wang & C.J. DeLoach, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000, 6657, GSWRL [2003-57]; 2♂♂ diss., 1♂, 4♀♀, Shanshan [42.8667°N, 90.1667°E], edge of, 41,571 km odom., 5-VIII-1993, C.J. DeLoach, on *T. laxa*, *D. e. deserticola* det. I. Lopatin 2000, 6671, 6673, 6674, 6676, 6689, 6690, 6730, GSWRL [2005-10, 96]; 1♂ diss., 4♂♂, 1♀, Turpan [Turpan Botany Station; 10 km SE Turpan; 42.863°N, 89.222°E], 17-VII-1992, C.J. DeLoach, on *T. arceuthoides*, *D. e. deserticola* det. I. Lopatin 2000 [1♂ diss., 1♂], 8975, 8978, voucher shipment GSWRL(CJD)-1992-21, GSWRL [2005-15] [12 specimens from Lot GSWRL(CJD)-1993-11 identified as prob. *D. e. deserticola* by R.E. White on 15-X-1993 at USDA SEL, SEL Lot # 93-10349]; 1♂ diss., 2♂♂, 1♀, Turpan Botany Station [10 km SE Turpan], 17-VII-1992, R. Wang & C.J. DeLoach, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000 [1♂ diss., 1♂, 1♀], 6660–6662, voucher shipment GSWRL(CJD)-1992-21, GSWRL [2005-16] [used in biological studies of DeLoach *et al.* (2003b)]; 3♂♂ diss., 2♀♀ diss., Turpan Botanical Garden, 10 km SE Turpan, 19-VI-2002, Li Bao Ping, on *Tamarix* spp., voucher USDA/ARS lab colony at Temple, Texas (4-IX-2002, J.L. Tracy; 1♂, 1♀, 25-26-VIII-2003, L. Milbrath [nos. 1265, 1268]), shipment EIWRU-2002-1005, GSWRL [2003-21, 31, 33, 2004-04, 2005-84] [released in Colorado in 2004] [used in biological studies of Milbrath and DeLoach (2006a, 2006b), Herr *et al.* (in prep.), and Bean and Keller (in prep.)]; 1♂, Turpan, ca. 30 km east, 41,751 km odom., 5-VIII-1993, C. J. DeLoach, 20 sweeps on *T. laxa*, GSWRL; 1♀, Turpan, 74 km northwest [43.20415°N, 88.46102°E], White Poplar Valley, rd. km 687, 7-VIII-1993, C.J. DeLoach, on *T. arceuthoides*, *D. e. deserticola* det. I. Lopatin 2000, 6691, GSWRL; 1♂ diss., 1♂, 4♀♀, Turpan, 76 to 164 km northwest, 7-VIII-1993, C.J. DeLoach, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000 [1♂ diss., 1♂, 3♀♀], 8981–8984, voucher shipment GSWRL(CJD)-1993-15, GSWRL [2005-76] [11 specimens from Lot GSWRL(CJD)-1993-11 identified as prob. *D. e. deserticola* by R.E. White on 15-X-1993 at USDA SEL, SEL Lot # 93-10349] [used in biological studies of DeLoach *et al.* (2003b)]; 1♂ diss., 5♂♂, 9♀♀, Turpan, 74 to 164 km northwest, White Poplar Valley, 7-VIII-1993, C.J. DeLoach, on *T. arceuthoides* and *T. ramosissima*, GSWRL [2004-14]; 1♂ diss., Urumqi [43.8000°N, 87.58333°E], water reservoir in suburb, VII-1998, Li Bao Ping, on *Tamarix* sp., voucher shipment GSWRL-1998-12, received 4-VIII-1998, GSWRL [2005-24]; 1♂ diss., 2♂♂, 2♀♀, Urumqi, 12 km northeast [43.89406°N, 87.61073°E], by fertilizer factory, 42,403 km odom., 8-VIII-1993, C.J. DeLoach, *T. hispidus*, *D. e. deserticola* I. Lopatin 2000 [1♂ diss., 2♂♂, 1♀], 6685–6688, GSWRL [2005-01]; 1♂ diss., 1♀, Urumqi, 47 km southeast [43.54156°N, 87.96419°E], 10,525 km odom., 8-VII-1992, R. Wang & C.J. DeLoach, on *T. ramosissima* - flowers, *D. e. deserticola* det. I. Lopatin 2000, 8973, GSWRL [2005-11]; 1♂ diss., 2♂♂, 4♀♀, Urumqi, 57 km east [43.56707°N, 88.07503°E], 8-VII-1992, R. Wang & C.J. DeLoach, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000 [1♂ diss., 2♂♂, 3♀♀], 6645, 6650, 6651, 6653–6656, GSWRL [2005-06]; 1♂ diss., Urumqi, 47 km southwest [43.44176°N, 87.23066°E], 10,525 km odom., 8-VII-1992, C.J. DeLoach, on *T. ramosissima*, GSWRL [2005-37]; 1♀ diss., Wei Lei Co. Farm 6 [near Yuli; 41.33060°N, 87.25780°E], 14-V-1960, Wang Shuyong, *D. e. deserticola* det. Chen, PARATYPE, IZAS [2005-04]; 1♂ diss., Wei Lei Co. Farm 6 [near Yuli], 14-V-1960, Zhang Facai, *D. e. deserticola* det. Chen, PARATYPE, IZAS [2005-03]; 1♀ diss., Wei Lei Co. Farm 4 [near Yuli], 17-V-1960, Wang Shuyong, *D. e.*

deserticola det. Chen, PARATYPE, IZAS [2005-02]; 1♂ diss., Wei Lei Co. Farm 4 [near Yuli], 17-V-1960, Zhang Facai, *D. e. deserticola* det. Chen, PARATYPE, IZAS [2005-01]; **IRAN**: 3♂♂ diss., 4♀♀ diss., 1♂, 3♀♀, 124 specimens [NMPC], Abaregh [Abareq; 29.31667°N, 57.91667°E; irrigation channel in semi-desert; *T. leptopetela* (= *T. kotschy*) present (Hoberlandt 1981)], 53 km northwest Bam, 25-IV-1973, Exp. Nat. Mus. Praha Loc. No. 178, NMPC [2004-30, 31, 40, 2005-04, 05], USNM [2003-06, 2004-04]; 1♂ diss., 1♀ diss., Bareng [Berang] to Nasratabad [Nosratabad] [app. location: 30.23670°N, 61.00170°E], Sistan, 11-V-1898, N. Zarudnyl, ZIN [2004-18, 21]; 1♂ diss., Bendun [Bandan] [to] Nayzar [Naizar marsh] [app. location: 31.3033°N, 60.8292°E], Sistan, east Persia, 8-V-1898, N. Zarudnyl, 17585, ZIN [2005-05]; 2♂♂ diss., 5♂♂, Kashan, 25 km toward Natanz [Natanz] [33.81444°N, 51.74361°E], 3,200 m elev. 2-V-2000, J. Gaskin, on *Tamarix* sp., #772, GSWRL [2003-06, 37]; 1♂ diss., 1♀, Khatunabad [29.46667°N, 57.80000°E; stony semi-desert; *Tamarix* sp. not recorded (Hoberlandt 1981)], 70 km northwest Bam, 25-IV-1973, Exp. Nat. Mus. Praha Loc. No. 179, NMPC [2004-35b]; 1♂ diss., Khorassan [Ostan-e Khorasan Province; on northeast border of Iran; specific locality not given], 12-13-VIII-1901, N. Zarudnyl, ZIN [2004-01]; 1♂ diss., 1♀, Minu Dasht, 60 km east [37.39°N, 55.85°E], MRSW Park [Mohammed Reza Shah Wildlife Park (= Golestan Biosphere Reserve)], 28-VIII-1972, [on *T. ramosissima* (Gerling and Kugler 1973)], *D. elongata* det. S.L. Shute 1973, P27-29, TAUJ [2003-03]; 1♂ diss., 1♀ diss., Shakhrud K. [Sharud Kola; 36.41670°N, 52.85000°E], north of Gorgan [southeast of Astrabad], Christof, ZIN [2004-17, 20]; **KAZAKHSTAN**: 1♂ diss., 2♂♂, 2♀♀, Chilik [Shelek], near [2♂♂, 2♀♀], or 25 km east [43.6715°N, 78.5050°E], Buryndysu environs [1♂ diss.], 6-VI-1999, Mityaev & Jashenko, on *T. ramosissima*, voucher shipment GSWRL-1999-8, GSWRL [2004-03] [introduced near Delta, Utah in 1999] [28 specimens from Lot GSWRL-1999-1 identified as *D. elongata* by A. Konstantinov on 20-VII-1999 at USDA Systematic Entomology Laboratory (SEL), SEL Lot # 9904498]; 1♂ diss., 4♂♂, 5♀♀, Bzandy-Su [Buryndysu] Campsite, 3-4 km north [43.70650°N, 78.68490°E], 186 km east northeast Almaty, 99,921 km odom., 4-VI-1995, C.J. DeLoach, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000 [2♂♂, 1♀], 8989–8891, GSWRL [2003-56]; 1♂ diss., 9♂♂, 6♀♀, Chilik [Shelek; 43.60030°N, 78.29630°E], near, 106 east of Almaty, 8-VIII-1995, I.D. Mityaev, on *T. ramosissima*, *D. elongata* det. I.D. Mityaev [1995; 3♂♂, 4♀♀], voucher shipment GSWRL(CJD)-1995-23, GSWRL [2005-91]; 1♂ diss., Chilik, near, 4-VI-1997, I.D. Mityaev and P.E. Boldt, on *T. sp. prob. ramosissima*, voucher shipment GSWRL(CJD)-1997-13, GSWRL [2005-92]; 1♂ diss., 5♂♂, 8♀♀, Chilik [Shelek], near, 1-VIII-1999, I. Mityaev & R. Jashenko, on *T. ramosissima*, voucher shipment GSWRL-1999-15, GSWRL [2005-98]; 1♂ diss., 3♂♂, 1♀, Chilik [Shelek], environs, 21-V-2000, Mityaev & Jashenko, on *T. ramosissima*, voucher shipment GSWRL-2000-9, GSWRL [2005-80, 97] [used in biological studies by DeLoach *et al.* 2003b and Lewis *et al.* (2003a)]; 2♂♂ diss., 8♂♂, 8♀♀, Chilik [Shelek], 7 km before [southwest; 43.49000°N, 78.25000°E], 130 km east Almaty, site 1, 99,865 km odom., 3-VI-1995, C.J. DeLoach, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000 [6♂♂, 2♀♀], 8595–8664, 8985, 8987, 8988, voucher shipment GSWRL(CJD)-1995-11, GSWRL [2003-45, 2005-14] [10 specimens from Lot GSWRL(CJD)-1995-9 identified as *prob. D. e. deserticola* by R.E. White on 15-XI-1995 at USDA SEL, SEL Lot # 95-10233]; 2♂♂ diss., 2♂♂, 5♀♀, Chilik [Shelek], 38 km east [Buryndysu; 43.69710°N, 78.66300°E], 15-VI-1996, P.E. Boldt, on *T. ramosissima*, *D. e. deserticola* det. I. Lopatin 2000 [1♂ diss., 2♀♀], 9013 [1♂ diss.], 9015, 9016, voucher shipment GSWRL(PEB)-1996-9, GSWRL [2003-83, 2005-23]; 1♂ diss., Chilik [Shelek], 23 km east [odometer reading 9,465 km] and 38 km east [odometer reading 9,480 km; Buryndysu; not west Chilik as in some shipment records], 15-VI-1996, I.D. Mityaev & P.E. Boldt, on *T. ramosissima*, voucher shipment GSWRL(PEB)-1996-9, GSWRL [2005-99] [8 specimens from Lot GSWRL(CJD)-1996-4 identified as *D. elongata* by S.M. Clark on 28-X-1996 at West Virginia Dept of Agric.] [8 specimens (no. 9205) from Lot GSWRL(CJD)-1997-1 identified as *D. e. prob. elongata* by A. Konstantinov on 21-V-1997 at USDA SEL, SEL Lot # 9704023]; 2♂♂ diss., 5♀♀ diss., 3♂♂, 3♀♀, Chundzha, 40 km west [43.47035°N, 79.02773°E], desert near Boguty Mtns., 9-VI-1999, Mityaev & Jashenko, on *T. ramosissima*, voucher shipment GSWRL-1999-9, GSWRL [2003-62, 63, 64, 2005-02, 48, 73, 74] [subject of field studies by Mityaev and Jashenko (1999, 2007)]; 2♂♂ diss., 3♂♂, 3♀♀, Chundzha, 40 km west, desert near Boguty Mtns., 1-VIII-1999, I.D. Mityaev & R. Jashenko, on *T. ramosissima*, voucher shipment GSWRL-1999-15,

GSWRL [2005-93, 95]; 1♂ diss., Dzhulek [Zhulek; 44.28330°N, 66.43330°E], Syrdar'indkaya Oblast, VII-1910, Kozchanchikov, ZIN [2004-15]; 1♂ diss., Indersk [Ynderbor; 48.55000°N, 51.78330°E], Reitter, *D. e. ab. sublineata*, HNHM [2003-10]; 7♂♂ diss., 2♂♂, 1♀, Kerbulak [43.9311°N, 77.6019°E], ca. 150 km north northeast Almaty, Ili River Valley, 2-VI-1999, Mityaev & Jashenko, on *Tamarix* sp., voucher shipment GSWRL-1999-7, GSWRL [2004-19; 2008-06, 07, 08, 09, 10, 11] [subject of field studies by Mityaev and Jashenko (1999, 2007)]; 1♂ diss., Lavar [43.56860°N, 78.13360°E], 10 km west Chilik [Shelek], 21-V-2000, Mityaev & Jashenko, on *T. ramosissima*, voucher shipment GSWRL-2000-9, GSWRL [2004-21] [introduced near Delta, Utah in 2000]; 1♂ diss., 10♂♂, 3♀♀, Masaq [43.62028°N, 78.30556°E] [not Marak as in some shipment records and labels], near, Ili Desert, 4-VI-1997, I.D. Mityaev and P.E. Boldt, on *Tamarix* sp., voucher shipment GSWRL(CJD)-1997-13 [1♂], GSWRL [2004-18]; 1♂ diss., Sarytogay, Charyn Canyon [43.43240°N, 79.15040°E], 13-VI-1998, Mityaev, on *Tamarix* sp., voucher shipment GSWRL-1998-10, GSWRL [2004-20]; 1♂ diss., Shelek, near, Shelek River, 6-VI-1999, Mityaev & Jashenko, on *T. ramosissima*, voucher shipment GSWRL-1999-8, GSWRL [2004-02] [introduced near Delta, Utah in 1999] [used in biological studies of DeLoach *et al.* (2003b) and Lewis *et al.* (2003b); subject of field studies by Mityaev and Jashenko (1999, 2007)]; **KYRGYZSTAN**: 1♂ diss., 1♀ diss., Dostuk [41.36972°N, 75.63667°E], environs, At-Bash River bed, Naryn Region, 20-VIII-1995, S. Saluk, USNM [2003-14, 16]; 1♂ diss., Naryn, 80 km west [41.36972°N, 75.3799°E], Central Tian Shan Mts., 3-VII-1966, E. Gurieva, ZIN [2004-14]; **MONGOLIA**: 1♂ diss., Mongolia [specific locality not given], Potanin, Coll[ection] Weise, [*D.*] *e. var. sublineata* [1♂ diss.], ZMHB [2006-05] [probably from series collected by G.N. Potanin from 22-VII to 3-VIII-1886 from Central Mongolia listed as *D. e. var. sublineata* by Weise (1890)]; 1♂ diss. 1♀ diss., southwestern Mongolia [specific locality not given], 17-VI [1♂ diss.], 18-VI [1♀ diss.] [circa 1928 (Hedin 1943)], Söderbom, *D. elongata* [1♂ diss.], Sven Hedins Expedition Central Asia, NHRS [2003-02, 03]; **Bayanhongor Aymag**: 1♂ diss., Tooroy Bulag spring [42.76745°N, 98.96116°E], 13 km east Tsagan Bulag, Bayanhongor Aymag, 16-VIII-1969, Zaitsev, ZIN [2004-16]; **Hovd Aymag**: 1♂ diss., Baruun Hurray [Barun Khurai Tract; 45.66667°N, 91.66667°E], 50 km southwest of Uench [Uyonch], 3-4-VIII-1976, L.N. Medvedev, *D. elongata* det. L. Medvedev, MRSN [2003-01] [from series listed as *D. elongata* by Medvedev and Voronova (1979)]; 2♂♂ diss., 2♀♀, Bulgan Somon [Burenhayrhan; 45.99394°N, 91.55267°E], 10 km south southwest, Chovd Aimak [Hovd Aymag], 4-5-VII-1966, Exp. Dr. Z. Kaszab, Nr. 628, *D. elongata sublineata* det. K. Lopatin [1♂ diss., EGRC], USNM [2003-08], EGRC [2005-05] [from series listed as *D. e. sublineata* by Lopatin (1968)]; 1♂ diss., Yelkhon, 20 km southeast [sic; should be southwest along Bodochiin Gol from Altai] Altai [Bor-Udzuur], on Bodonchiyn [Bodochiin Gol stream] [45.7008°N, 92.0836°E], 27-VII-1970, Emeljanov, ZIN [2004-05]; **RUSSIA**: 1♂ diss., 1♂, 1♀, Astrachan [Astrakhan; 46.34944°N, 48.04917°E], coll[ection] Koltze, 10883, DEI [2003-25]; 1♀ diss., *signata* [designated] Astrachan, Becker, coll[ection] L.V. Heyden, [*Galeruca*] *carinulata* Desbr., DEI [2003-04]; 1♀ diss., 2♂♂, 1♀, Astrachan, Coll[ection] Kraatz, [*Galeruca*] *carinulata* Desbr. [1♀ diss.], DEI [2005-11]; 1♂, 1♀, Astrakhan [Astrakhan], Becker, *D. e. ab. carinata* det. Le Moul, IRSNB; 1♂ diss., 1♀, Astrakhan, Letzner, coll[ection], *Gal[eruca] carinulata* Desbr. [1♂ diss.], DEI [2003-03]; 1♂ diss., 1♂, 2♀♀, Astrakhan, Becker, coll[ection] Reitter, *D. elongata*, HNHM [2003-01]; 1♂ diss., 1♀, Astrakhan. [region; specific locality not given], Bekker, ZIN [2005-04]; 1♂ diss., Derbent [42.06278°N, 48.29583°E], Coll[ection] Koltze, 10884, DEI [2003-05]; 1♀ diss., Derbent, Becker, DEI [2004-01]; 1♂ diss., 1♂, 1♀, Malaya Areshkeva [44.02083°N, 46.82305°E], northern Daghestan [Respublika Dagestan], 31-V-1925, A.N. Kiritschenko, ZIN [2004-03]; 1♂ diss., 1♀ diss., Sarepta [48.52778°N, 44.48361°E], *G. carinulata* Desbrochers [1♂ diss.], Coll[ection] Stierlin, DEI [2003-07, 26]; 1♀ diss., Sarepta, Becker, [*G.*] *carinulata*, NHRS [2003-01]; 1♀ diss., Sarepta, D. Becker, ex. coll. J. Weise, ZMHB [2003-01]; 1♀ diss., Sarepta. Schioda [?], 896, Collectie C. et O. Vogt Acq. 1960, ZMAN [2008-13]; 2♂♂ diss., 1♀ diss., Ikrianoe [Ikryanoye; 46.09440°N, 47.73470°E] Village, Astrakhan region, 22-28-VIII-2002, Osipov collection, GSWRL [2003-70, 2004-25, 26]; **TAJIKISTAN**: 1♂ diss., 1♀ diss., Vakhsh River, Tigrovaya Balka State Reserve [37.10528°N, 68.30389°E], Dzhilikul District, Kurgan-Tube [Kurgan Tyube] Region, 9-V-1992, Osipov collection, GSWRL [2003-77, 2004-08]; **TURKMENISTAN**: 2♂♂ diss., 2♀♀ diss., Ashgabat, 2-IX-2002, S.N. Myartseva, on *T. ramosissima*, GSWRL [2003-01, 03, 05, 2006-06]; 1♀

diss., Ashgabat, Dry Sport Lake, 11-V-1997, S. N. Myartseva, on *Tamarix ramosissima* [prob. *T. aralensis* J. Gaskin], voucher shipment GSWRL(CJD)-1997-11, GSWRL [2005-101] [8 specimens (nos. 9202, 9203) from Lot GSWRL(CJD)-1997-1 identified as *D. e.* prob. *elongata* by A. Konstantinov on 21-V-1997 at USDA SEL, SEL Lot # 9704023]; 2♀♀ diss., Ashgabat [37.95°N, 58.36667°E], Dry Sport Lake, 11-VI-1997, S. N. Myartseva and P. Boldt, on *T. ramosissima* [prob. *T. aralensis* J. Gaskin], voucher shipment GSWRL(CJD)-1997-12, *D. elongata* det. I. Lopatin 1999 [1♀], 9023, GSWRL [2005-08, 2006-07]; 2♂♂ diss., Ashgabat, Dry Sport Lake, 26-IX-2002, S.N. Myartseva, on *Tamarix* spp., GSWRL [2006-08, 09]; Ashgabat, near Quaragum Canal, 27-V-1994, C.J. DeLoach, on *Tamarix* sp., *D. e. deserticola* det. I. Lopatin 2000, 6731, GSWRL [2005-03]; 1♀ diss., 2♂♂, Ashgabat, canal [Quaragum], 11-VI-1997, S.N. Myartseva and P. Boldt, on *Tamarix* sp., *D. elongata* det. I. Lopatin 1999, 9017–9019, GSWRL [2005-21]; 3♂♂ diss., 4♀♀ diss., Ashgabat, Karakum [Quaragum] Canal, 12-IX-2002, S. N. Myartseva, on *T. ramosissima*, GSWRL [2003-13b, A5, A6, A7, A8, 2005-49, 63]; **UNKNOWN COUNTRY**: 1♀ diss., Araxesthal [Aras River of Armenia, Azerbaijan and Iran], Reitter, HNHM [2003-11]; 1♂ diss., Caucasus [specific locality not given; possibly Armenia or Azerbaijan], Reitter. Leder., NMPC [2005-41]; 1♀ diss., 1♀, Kammenaja retschka [Kamennaya Rechka, Russia?], 4-VI-1909, Collectie C. et. O. Vogt Acq. 1960, ZMAN [2008-03]; 1♀ diss., Tscholokai [Tschkalow/Orenburg, Russia?], 31-V-1909, Collectie C. et. O. Vogt Acq. 1960, ZMAN [2008-02]; **UNITED STATES OF AMERICA** (introduced): **Colorado: Pueblo Co.**: 1♂ diss., 4♂♂, 7♀♀, Arkansas River, Pueblo Reservoir, 38.270°N, -104.713°W, 7-IX-2005, D. Hosler and F. Nibling, on *T. ramosissima*, voucher [source: Fukang, China], GSWRL [2006-16]; **Nevada: Churchill Co.**: 1♂ diss., 5♂♂, 4♀♀, Carson Sink, Trinity Junction, 38.92°N, -118.75°W, 23-IX-2005, T. Dudley, on *T. ramosissima*, voucher [source: Fukang, China], GSWRL [2006-12]; **Mineral Co.**: 1♂ diss., 4♂♂, 5♀♀, Walker Lake, 38.88°N, -118.79°W, 21-IX-2005, T. Dudley, on *T. ramosissima*, voucher [source: Fukang, China], GSWRL [2006-13]; **Pershing Co.**: 1♂ diss., 3♂♂, 6♀♀, Humboldt Sink, 40.13°N, -118.42°W, 23-IX-2005, T. Dudley, on *T. ramosissima*, voucher [source: Fukang, China], GSWRL [2006-14]; **Utah: Millard Co.**: 1♂ diss., 5♂♂, 6♀♀, Sevier River west of Delta, 39.172°N, -112.903°W, 15-IX-2005, C.J. DeLoach, on *T. ramosissima*, voucher [source: Shelek, Lavar, and environs Buryndysu, Kazakhstan], GSWRL [2006-17]; **Wyoming: Big Horn Co.**: 1♂ diss., 4♂♂, 5♀♀, Big Horn Canyon National Recreation Area [44.857°N, -108.208°W, east of Lovell], 22-VIII-2005, D. Kazmer, on *T. ramosissima*, voucher [source: Fukang, China], GSWRL [2006-15]; **UZBEKISTAN**: 2♂♂ diss., 11♂♂, 2♀♀, Buchara [Buxoro], southeast [39.7555°N, 64.4867°E], 3-IV-1999, R. Sobhian, on *Tamarix* spp., *D. elongata* det. I.K. Lopatin 1999 [12♂♂, 2♀♀], 9036–9048, 9050, GSWRL [2003-82, 2008-20]; 2♂♂ diss., 1♀ diss., Buxoro, 5 km northwest [39.8228°N, 64.39134°E], along the road to Gazli, 27-IX-2002, R. Sobhian, on *Tamarix*, USDA lab [Buchara] colony at Albany, California, voucher (2002–2003, D. Bean), shipment EIWRU-2002-1010, GSWRL [2005-53, 54, 56]; 2♂♂ diss., 1♀ diss., 5♂♂, 2♀♀, Buchara [Buxoro], 10 km west [39.7614°N, 64.3011°E], 3-IV-1999, Kirk & Sobhian, on *Tamarix* sp., *D. elongata* det. I.K. Lopatin 1999 [2♂♂ diss. 4♂♂], 9028–9031, 9033, 9034, GSWRL [2003-80, 2004-05, 2008-21]; 1♂ diss., 1♂, Bukhara [Buxoro], 25 km west [39.69778°N, 64.18315°E], 20-V-1994, Osipov Coll., GSWRL [2004-22]; 1♂ diss., 1♂, Karshi [Qarshi], 10 km west [38.92278°N, 65.73307°E], 7-IV-1999, A. Kirk & R. Sobhian, on *Tamarix*, *D. elongata* det. I.K. Lopatin 1999, 9065, 9066, GSWRL [2003-78]; 1♂ diss., Tashkent [Toshkent], 140 km south [approximate location: 40.29057°N, 68.91332°E], 10-IV-1999, Kirk & Sobhian, on *Tamarix* spp., GSWRL [2004-17].

Distribution. General. The native distribution of *D. carinulata* ranges from Sarepta, Russia south to Iran and east to China and Mongolia (Map 5). Surveys by our colleague C. J. DeLoach reveal that *D. carinulata* populations are temporally sporadic in China and Kazakhstan, with outbreaks in some years and rarity in other years. Further collections might also reveal *D. carinulata* in Armenia, Afghanistan, Pakistan and northwestern Iraq.

Confirmed Records. We dissected specimens (see **Material examined**) from Russia, the single country with a previous literature record for *D. carinulata* (Desbrochers 1870) (Map 5).

New Records. We have dissected specimens from the following countries for which we find no previous specific reports of *D. carinulata* in the literature (Maps 5–6): Azerbaijan, Iran, Turkmenistan, Kazakhstan,

Uzbekistan, Tajikistan, Kyrgyzstan, China, Mongolia, and the United States of America (Nevada, Utah, Colorado, Wyoming; introduced; Map 7, see *Potential in Tamarisk Biological Control* below for additional details). Past reports of *D. elongata* from Azerbaijan, Turkmenistan, Kazakhstan, Uzbekistan, and the United States should refer, at least in part, to *D. carinulata*. Past reports of *D. e. deserticola* from China, Mongolia, Kazakhstan, and the United States should also refer to *D. carinulata* (see synonymy above). Past reports of *D. e. sublineata* and *D. e. ab. sublineata* in China and Mongolia are also *D. carinulata*.

Unconfirmed Records. We find no country distribution records that remain unconfirmed. We consider reports of *Diorhabda* from Littlefield, Arizona (L.D. Walker, USDI Bureau of Land Management, St. George, Utah) that spread south from Utah as *D. carinulata*. All available locations from which specimens were dissected from China (25) and Mongolia (6) were *D. carinulata*, with the exception of specimens of *D. carinata* from China near the border of Kazakhstan in the Ili Kazakh Autonomous Prefecture and Yining. Therefore, we consider all literature records of *D. elongata*, *D. e. sublineata* and *D. e. deserticola* from these countries to be *D. carinulata*, although *D. carinata* may also be present at sites in far western Xinjiang Uygur Zizhiqu, China. From 11 locations east of 75° E in Kazakhstan, *D. carinulata* was dissected from ten locations; while, *D. carinata* was dissected from four locations, two of which were series greatly predominated by *D. carinulata*. Therefore, we consider all literature reports of *D. elongata* east of 75°E in Kazakhstan to include *D. carinulata*, but it is probable that *D. carinata* occurs in lower frequency at many of these same sites. Only *D. carinulata* was dissected from all five locations available from north of 42°N in southern Russia and we consider all reports of *D. elongata* from this area to be *D. carinulata*.

Below are 33 unconfirmed locality records that we consider as *D. carinulata*, but are listed as *D. elongata* in Russia, Kazakhstan and Mongolia, *D. e. sublineata* in Mongolia (Lopatin 1970, 1977b), and *D. e. deserticola* in China (Map 5):

CHINA: Gansu Sheng: Anxi [Yuanquan; 40.500°N, 95.800°E], on *Tamarix*; Dunhuang [40.16667°N, 94.68333°E], on *Tamarix*; **Nei Mongol Zhizhiqu:** Dong He River [41.73647°N, 100.85793°E], on *Tamarix* (Bao Ping, Nanjing Agricultural University, Nanjing, China, pers. comm.); **Ningxia Huizu Zizhiqu:** Yanchi [37.7869°N, 107.3994°E], on *Tamarix* (B. Ping, pers. comm.); **Xinjiang Uygur Zizhiqu:** Akesu [Aksu; 41.1231°N, 80.2644°E]; Atushen [Atux; 36.7061°N, 76.1519°E]; Baicheng [41.7739°N, 81.8689°E] (Chen 1961); Hami [42.800°N, 93.4500°E] (Sha and Yibulayin 1993); Hotan (Sha and Yibulayin 1993); K'u-ch'e [Kuqa; 41.7278°N, 82.9364°E]; Miquan [43.96667°N, 87.7000°E]; Shajingzi [40.76667°N, 79.96667°E]; Turtiaogou [geocoordinates not locatable] (Chen 1961); Turpan [*D. carinulata* dissected from same location], on *Tamarix* (Sha and Yibulayin 1993); Yecheng [Kargilik; 37.88500°N, 77.4131°E]; Wei-li [Yuli; 41.3306°N, 86.25780°E] (Chen 1961); **KAZAKHSTAN:** Bakanas [Baqanas; 44.8081°N, 76.2772°E], Ili River, on *Tamarix* (Ishkov 1996); Boguty [desert near Boguty Mts., 40 km west of Chundzha; *D. carinulata* dissected from same location], on *Tamarix* (Mityaev and Jashenko 1999, 2007); Borokhudzhir [43.9667°N, 79.5833°E], on *Tamarix* (Kulnova 1968); Burundysu [Chilik, 38 km east; *D. carinulata* dissected from same location], on *Tamarix*; Chilik [Shelek; *D. carinulata* dissected from same location], near, in Chilik River Valley, on *Tamarix*; Kerbulak [*D. carinulata* dissected from same location], Ili River Valley, on *Tamarix* (Mityaev and Jashenko 1999, 2007); Koku [45.02780°N, 77.9460°E], on *Tamarix* (Kulnova 1968); Lavar [*D. carinulata* dissected from same location], on *Tamarix* (Mityaev and Jashenko 1999, 2007); Masak [Masag; *D. carinulata* dissected from same location] Town environs, Chilik [Shelek] riverbed, 22-VI-1995, *Myricaria* sp. (Mityaev and Jashenko 1997, 2007); Sarytogay [*D. carinulata* dissected from same location], Charyn Canyon, on *Tamarix* (Mityaev and Jashenko 1999, 2007); **MONGOLIA: Bayanhongor Aymag:** 2 specimens, Echin Gol Oasis [Ekhiin Gol, 43.30851°N, 98.99646°E], 90 km north of Capanbulag border post, 950 m, 27–28-VI-1967 (Nr. 855), on *Tamarix* (Lopatin 1970); Ezhiin Gola [Ekhiin Gol], 900 m, 3–4-IX-1976; Khatan–Sudlyn–Bulak [geocoordinates not locatable], 75 km west north west Tsagan–Bulak [Tsagaan Bulag spring], 1,450 m [elev.], 28-VII-1977 (Medvedev and Voronova 1979); Zxilin Gol oasis [geocoordinates not locatable], 150 km south Shine Dzhinsta [Dzalaa or Shinejinst], 900 m [elev.], 12–15-IX-1976 (Medvedev and Voronova 1977b); Talyn–Belgekh–Bulak spring [geocoordinates not locatable], 40 km south southeast of Ezhiin Gola [Ekhiin Gol], 1,250 m [elev.], 26-VII-1977 (Medvedev and Voronova 1979); **Govi–Altay**

Aymag: Dzahuy [44.950°N, 96.600°E]; Khatan Khaïrkhan environs [Hatan Hayrhan Mt.], 50 km east southeast Altay [geocoordinates not locatable] (Medvedev and Voronova 1977b); Khatan Khayrkhav [Hatan Hayrhan Mt.], north slope, 1,225 m [elev.] [44.9881°N, 96.1792°E], 13–14-VII-1976; Khatan Khayrkhav [Hatan Hayrhan Mt.], 20 km southwest, 1,300 m [elev.] [44.8505°N, 96.0897°E], 15-VII-1976 (Medvedev and Voronova 1977a); Shara–Xulsni–Bulak spring [Shara Hulasanii Bulag; 43.3°N, 97.75°E], 100 km west Ezhiin Gola [Ekhiin Gol], 29-VII-1977; **Hovd Aymag:** Bodonchiyn Gol [Bodochiin Gol stream], 15 km southeast [sic; should be southwest along Bodochiin Gol from Altai] Altai [Bor–Udzuur] [45.7367°N, 92.1217°E], 4-VII-1976, on *Myricaria alopecuroides* (Medvedev and Voronova 1979); Jarantaj [geocoordinates not locatable], Wuste, 15-V-1974, R. Piechocki (Lopatin 1977b); Uench Gol [Uyonch Gol stream], 25 km southwest Uencha [Uyonch], 1,300 m [elev.] [45.8861°N, 91.7807°E], 28-VII-1976 (Medvedev and Voronova 1977a); **Omnogovi Aymag:** Obooto Hural, 50 km west [43.02078°N, 100.90040°E], 1600 m [elev.], 25-VII-1977 (Medvedev and Voronova 1979); **RUSSIA:** Dosang [46.9044°N, 47.9111°E], Astrakhan Province, VI-2003, K.A. Grebennikov (with photograph, Berlov 2006).

From our habitat suitability index models (Maps 8b and 9a) and our preliminary species distribution models based on 10' climate grids (Tracy and DeLoach, unpublished data), we estimate northern Uzbekistan as much more suitable habitat for *D. carinulata* than *D. carinata*. Therefore, we consider reports of *D. elongata* along the Amu Darya (river) in northern Uzbekistan by Yakhontov and Davletshina (1955, 1959), Sinadsky (1963, 1968) and Khamraev (2003) to probably refer primarily to *D. carinulata* rather than *D. carinata* (Map 5). Consequently, we consider the following four unconfirmed distribution records of *D. elongata* as uncertain records of *D. carinulata* (Map 5):

UZBEKISTAN: Chertombayskoy Forest dachau [geocoordinates not locatable], Amu Darya Valley, heavy defoliation on *Tamarix*, VIII-1954; Nazarkhan [42.3333°N, 59.9833°E]; Nukus [42.8333°N, 59.4833°E]; Turtkul [41.5544°N, 61.0111°E] (Sinadsky 1963, 1968).

Discussion. Taxonomy. *Galeruca carinulata* (Desbrochers 1870) was described from Sarepta, Russia and incorrectly synonymized under *D. elongata* var. *carinata* by Weise (1893). Berti and Rapilly (1973) removed *D. carinulata* from synonymy with both *D. elongata* and *D. carinata* based on their investigation of the endophallus. However, as discussed under *D. carinata* (above), only Warchalowski (2003) has accepted this taxonomic change.

We dissected a single male topotype specimen (DEI 2003-07) from the type locality of *D. carinulata* in Sarepta, Russia, with endophalli matching that of Berti and Rapilly's (1973) illustration of the endophallus of the holotype. This evidently old specimen (possibly from the late 1800's) bore the following hand written label data: "Sarepta"; "*G. carinulata* Desbrochers". A total of five males dissected from Astrakhan and Ikryanoye, Russia, ca. 365 km southeast of Sarepta (Map 5), also bore endophalli matching that of the description by Berti and Rapilly (1973), and three specimens of *D. carinulata* (of DEI) from Astrakhan also bore identification labels of *G. carinulata* Desbrochers. Three key characters of the endophallus of *D. carinulata* that distinguish it from other members of the *D. elongata* group can be seen in the illustrations of the endophallus of the holotype (Fig. 19b–c of Berti and Rapilly 1973) and our figures (Figs. 17, 22, 27, 32): (1) the acutely rounded distal margin of the palmate endophallic sclerite; (2) elongate endophallic sclerite with blade extending for less than 2/3 the length of the sclerite; and (3) lack of hooked apex of the elongate sclerite. Desbrocher's (1870) holotype male for *G. carinulata* was 5.5 mm in length, below that usually found for *D. carinata* (mean male length is 6.29 mm, minimum male size is 5.12 mm, Table 2) but well within the size range of the 6 males we dissected from Sarepta, Astrakhan, and Ikryanoye (4.98–5.85 mm). We are confident that these specimens form a single species conspecific with *D. carinulata*. We find additional distinguishing characters in the endophallic sclerites and female genitalia (vaginal palpi and internal sternite VIII) of *D. carinulata* from the vicinity of the type locality in southern Russia and throughout its range to western China that distinguish it from *D. elongata*, *D. carinata* and other members of the *D. elongata* group (see **Male-Genitalia** and **Female-Genitalia** above; Figs. 17, 22, 27, 32, 37, 42; Map 5). The distinctive genitalic characters of *D. carinulata* are maintained in the same areas where *D. carinata* and *D. elongata* occur and near its abutting range boundary with *D. meridionalis*, and this is strong evidence for reproductive isolation

between these species (see **Biogeography** below; Map 1, Table 8). Although *D. sublineata* is allopatric with *D. carinulata*, their status as reproductively isolated is supported by the number of diagnostic genitalic characters separating *D. sublineata* from *D. carinulata* (6 characters) being greater than the number of characters separating the moderately sympatric *D. carinata* from *D. carinulata* (5 characters) (Table 5). Therefore, we firmly support Berti and Rapilly (1973) in restoring *D. carinulata* to species status, removing it from synonymy with both *D. elongata* and *D. carinata*. Habitus drawings of “*D. elongata*” adults from southern Russia (Fig. 30 of Ogloblin 1936) and Eastern Europe (Fig. 50 of Bieńkowski 2004) are probably *D. carinulata*. Drawings of “*D. elongata*” larval structures from southern Russia (Fig. 31 of Ogloblin 1936; Fig. 41.7 of Ogloblin and Medvedev 1971) probably also belong to *D. carinulata*.

Chen (1961) described *D. e. deserticola* from the Taklamakan Desert region of Xinjiang Autonomous Region, China. The type locality of *D. e. deserticola* is Yuli (= Wei-li) (Map 5) and 8 additional localities are listed for paratypes. Yu *et al.* (1996) elevated *D. e. deserticola* to species status as *D. deserticola* without comment, and this change is mostly overlooked in recent biological literature (e.g., Li *et al.* 2000; DeLoach *et al.* 2003b; Lewis *et al.* 2003a, 2003b; Cossé *et al.* 2005; Milbrath and DeLoach 2006a), except by Meng *et al.* (2005) and Zhang and Baoping (2006). Lopatin *et al.* (2004) extended the range of *D. e. deserticola* to eastern Kazakhstan. We dissected two male and two female paratypes of *D. e. deserticola* collected from the type locality of Wei-lei, Xinjiang, China (Figs. 22, 27, 32 —Wei Lei Ta) and all belong to *D. carinulata* NEW SYNONYMY. We identified as *D. carinulata* all specimens dissected from Chen’s original given distribution of *D. e. deserticola*, China and Mongolia (Map 5).

Chen’s description of *D. e. deserticola* gives ranges in body length of 5–6 mm for males and 5.5–7 mm for females, which is close to our observed size ranges of 4.6–6.1 mm for males and 5–7 mm for females (Table 2). Lewis *et al.* (2003b) gives mean lengths for males (5.6 ± 0.2 mm) and females (5.9 ± 0.2 mm) that are slightly larger than we observed in specimens collected over the entire range of *D. carinulata* (Table 2). The size range of 4.5–8 mm given for adult *D. carinulata* in regional keys of Mongolia (as *D. e. ab. sublineata*; Medvedev and Voronova 1977b, Medvedev 1982) and China (as *D. e. sublineata*; Gressitt and Kimoto 1963a) erroneously includes the larger size of other sibling species that can exceed 7 mm in length (Table 2), such as *D. carinata*, but which we have not found in these areas (Map1). An excellent habitus drawing of *D. carinulata* (as *D. deserticola*) from China is provided in Fig. 4-14 of Yu *et al.* (1996).

Laboissière (1935) described *D. koltzei* ab. *basicornis* Laboissière from Khotan (=Hotan), Turkestan (now in Xinjiang Uygur Zizhiqu, China) from a single female. Wilcox (1971) listed *D. k. ab. basicornis* as a synonym of *D. koltzei*. However, Ogloblin (1936) had earlier synonymized *D. koltzei* under *D. rybakowi* and ranked it as the aberration *D. rybakowi* ab. *koltzei*. We dissected the genitalia of Laboissière’s (1935) female type specimen (from ZMAN) and identified it as *D. carinulata*. We also studied 9 syntypes of *D. koltzei* (from DEI; label data: Ili [Ili Kazakh Autonomous Prefecture, Xinjiang Uygur Zizhiqu, China] [18]’97; Weise; Coll. Koltze; Syntype) and 7 identified specimens of *D. rybakowi* (6 from USNM and 1 from DEI), and we concur that *D. koltzei* is conspecific with *D. rybakowi* which is very distinct from *D. carinulata*. Therefore, we conclude that *D. k. ab. basicornis* is conspecific with *D. carinulata* NEW SYNONYMY.

The external characters provided by Berti and Rapilly (1973) to separate *D. carinulata* and *D. carinata* involve mainly the posterior angles of the pronotum and number of elytral carinae, and these characters are considered by Warchalowski (2003) as separating *D. carinulata* from *D. elongata*. However, we find these characters to be interspecifically variable and of no use in species diagnosis (see **Discussion-Taxonomy** under *D. carinata*). Chen (1961) noted that the ventral tarsal pubescence was medially absent, leaving a glabrous median line under the tarsi; in *D. carinulata* (as *D. e. deserticola*), but that the ventral tarsal pubescence is generally distributed in *D. sublineata* (as *D. e. ab. sublineata*) from North Africa. We examined dissected specimens of *D. sublineata* from North Africa with the same pattern of ventral tarsal pubescence as Chen described for *D. e. deserticola*, making this character too variable for use in species separation. We have dissected specimens of *D. carinulata* that were misidentified by taxonomists using external diagnostic characters as *D. elongata* from six countries and as *D. e. sublineata* or *D. e. var. sublineata* from Mongolia (see **Material examined**).

Common Name. The vernacular name “striped tamarisk leaf beetle” has been applied to *D. carinulata* in Kazakhstan (as *D. rybakowi*; Mityaev 1958, Mityaev and Jashenko 2007) and China (as *D. e. deserticola*; Tian *et al.* 1988, Bao 1989, Sha and Yibulayin 1993). Because stripes can also be prominent in several other species of the *D. elongata* group (especially *D. sublineata*), we have dropped the term “striped” from the name and adopt the name “northern tamarisk beetle”, referring to its northernmost range of all tamarisk beetles (Fig. 51B, Map 1).

Biology. *Host Plants.* Sha and Yibulayin (1993) listed the following hosts of *D. carinulata* (as *D. e. deserticola*) in order of preference based on numbers collected from the Turpan Eremophyte Botanical Garden in China: *Tamarix laxa* (Wildenow), *T. elongata* (Ledebour), *T. kansuensis* Zhang, *T. gracilis* Wildenow, *T. androssowii* Litvinov, *T. arceuthoides*, *T. hispida*, *T. smyrnensis* (as *T. hohenackeri*), and *T. chinensis* (Table 1). Mityaev and Jashenko (1998, 2007) reported *T. leptostachya* as a new host record from Kazakhstan among five other *Tamarix* spp. (see Table 1). The host range of *D. carinulata* (as *D. e. deserticola*) was reviewed by DeLoach *et al.* (2003b) who reported *T. hispida* var. *karelinii* (Bunge) Baum as a new host. DeLoach *et al.* (2003b) found the highest field populations on *T. ramosissima* among a total of seven *Tamarix* spp. on which it was collected in western China (including *T. leptostachya*, which was omitted from DeLoach *et al.* 2003b) (Table 1). Our collaborators R. Jashenko, I. Mityaev, and C. J. DeLoach collected *D. carinulata* from *T. ramosissima* at six locations and *Tamarix* sp. at three locations in Kazakhstan. *Tamarix aralensis* is a new host record for *D. carinulata* collected from Dry Sport Lake, Ashgabat, Turkmenistan by S. Myartseva (GSWRL collection). In addition to *Tamarix* spp., *D. carinulata* feeds upon *Myricaria alopecuroides* Schrenk (Tamaricales: Tamaricaceae) in Mongolia (as *D. elongata*; Medvedev and Voronova 1979) and on one occasion was found to completely defoliate a few shrubs of *Myricaria* sp. by the Shelek River in southeastern Kazakhstan (as *D. e. deserticola*; Mityaev and Jashenko 1997, 2007). Sinadsky (1968) reported what is probably *D. carinulata* (as *D. elongata*, see above discussion) producing heavy defoliation on *T. ramosissima* compared to light damage on *T. hispida* along the Amu Darya in Karakalpakia [Qoraqalpogʻiston Respublikasi], northern Uzbekistan. *Tamarix kotschyi* Bunge (as *T. leptopetela* Bunge) was recorded among the vegetation sampled at Abareq, Iran (Hoberlandt 1981) in the collection of at least 142 specimens of *D. carinulata* that we examined. Later detailed vegetation surveys in this area map *T. kotschyi* as the only *Tamarix* species in the vicinity of Abareq (Baum 1983), and we consider *T. kotschyi* a possible host for *D. carinulata*. Although *T. aphylla* is not a recorded host of *D. carinulata*, *T. aphylla* is common in the Registan-North Pakistan Sandy Desert in eastern Iran (Browicz 1991), an area from which we dissected *D. carinulata* from two locations (Map 6). Populations of *D. carinulata* established in North America are vigorously defoliating *T. ramosissima* in Nevada, Utah, Wyoming and Colorado and *T. chinensis* in Colorado (DeLoach *et al.* 2004). Large populations in western Nevada have fed upon cultivated *T. parviflora*, although this host is less preferred than *T. ramosissima* (Dudley *et al.* 2006, Dudley *et al.* in prep.) as Dalin *et al.* (in press) also observed in multiple-choice field cage studies in California. *Tamarix parviflora* is a new host record and novel host association in that it is not native where *D. carinulata* occurs in Asia. Attack on *T. parviflora* by *D. carinulata* is predictable from field cage studies in which *T. parviflora* did not significantly differ from most accessions of *T. ramosissima*/*T. chinensis* in terms of either suitability for larval survival or preference for adult oviposition (Milbrath and DeLoach 2006a).

DeLoach *et al.* (2003b) found that *D. carinulata* (as *D. e. deserticola*) larvae from Turpan and Fukang, China and Shelek, Kazakhstan had highest survival on *Tamarix* followed by *Myricaria* and *Frankenia*. Adults oviposited less on bouquets of *T. aphylla* compared to *T. ramosissima* in the laboratory. Lewis *et al.* (2003a) found larval survival in the laboratory and adult oviposition in both laboratory and field cages on three North American *Frankenia* spp. (*F. salina*, *F. johnstonii*, and *F. jamesii*) generally were significantly lower than that on species of invasive North American *Tamarix*. But Milbrath and DeLoach (2006a) found that survival of larvae from Turpan was not different among the three North American *Frankenia* spp. and five invasive *Tamarix* spp. However, they confirmed previous results that adult oviposition was insignificant on the three *Frankenia* spp. in a combination of choice and no-choice field cage studies. Dudley and Kazmer (2005) planted alkali heath, *Frankenia salina*, at a site with large populations of *D. carinulata* defoliating tamarisk

near Lovelock, Nevada. In this open field test, *D. carinulata* did not lay eggs on the *Frankenia* and larvae crawling from defoliated tamarisk trees produced <4% leaf damage to *Frankenia*. In field cage tests, *D. carinulata* oviposited significantly less on *T. aphylla* compared to other invasive North American tamarisks, including *T. ramosissima*, *T. chinensis*, *T. canariensis*/*T. gallica* (Lewis *et al.* 2003a, Milbrath and DeLoach 2006a). *Tamarix aphylla* is at moderate risk of damage by *D. carinulata* in the field (DeLoach *et al.* 2003b), but the degree of damage that *D. carinulata* might cause to *T. aphylla*, especially in the absence of other *Tamarix* spp, is difficult to predict. *Frankenia* is at very low risk of damage from *D. carinulata* (Lewis *et al.* 2003a, Milbrath and DeLoach 2006a). Risk of damage to both *T. aphylla* and *Frankenia* by *D. carinulata* is probably much lower when these plants are not in the proximity of preferred *Tamarix* spp. (e.g., Blossey *et al.* 2001).

Ecology. *Diorhabda carinulata* (as *D. e. deserticola*) is probably the most damaging specialized herbivore of tamarisk in Asia as a result of its abilities to: (1) defoliate large acreages of tamarisk, (2) reach high population densities, (3) produce several overlapping generations per season, (4) aggregate in large numbers, and (5) disperse widely from 2–6 km per day (Ding 2004). Sporadic outbreaks of *D. carinulata* (as *D. e. deserticola* or *D. elongata*) can defoliate 90% or more of the tamarisk over wide areas in Kazakhstan (DeLoach *et al.* 2003b), Uzbekistan (Sinadsky 1968), and China, where the beetles are controlled in order to protect tamarisk stands used in soil stabilization (Bao 1989, Tian *et al.* 1988, Sha and Yibulayin 1993, Chen *et al.* 2000, Ding 2004, Peng *et al.* 2005, Li and Wang 2006). In contrast, *D. carinulata* (as *D. elongata*) have been reported at population levels too low to damage tamarisk in the northern part of its range (ca. 45°N) in Mongolia (Medvedev and Voronova 1977b). Bao (1989) reported 66,666 ha of tamarisk colonized by *D. carinulata* (as *D. e. deserticola*), along the Dongge He River (Ping Bao, Alashan Range Extension Station, Nei Mongol Zizhiqu, China, pers. comm.) of Erjina County, Inner Mongolia, China (Map 5). Of the 66,666 ha of colonized tamarisk, Bao reported 40,000 ha, or 60%, was defoliated by *D. carinulata* in this area (a region known for extensive stands of *T. ramosissima*; Kurschner 2004). Factors favoring periodic outbreaks of *D. carinulata* in Anxi County, Gansu Sheng, China, where up to 20,850 ha of tamarisk have been defoliated in a year, include (1) poor regulation from natural enemies, (2) mild winter temperatures increasing adult overwintering survival, (3) low precipitation during times of summer and fall pupation, reducing drowning of pupae on the ground, and (4) low water tables reducing mortality of ground dwelling pupae and overwintering adults (Ding 2004). *Diorhabda carinulata* extensively defoliated tamarisk stands in a 26,300 ha area over a 259 km stretch of the Humboldt River basin by late 2005 near Lovelock, Nevada, where it was introduced in 2001 (Carruthers *et al.* 2006, 2008). Large areas of tamarisk also have been defoliated near Lovell, Wyoming (D. Kazmer, pers. comm.), on the Colorado, Green, and Sevier rivers in Utah, and on the Dolores River in Colorado (D. Bean, pers. comm.). Smaller areas of tamarisk have been defoliated near Pueblo, Colorado (Map 7).

Tamarisk defoliation by *D. carinulata* in Kazakhstan is primarily from feeding of first generation larvae in early summer (Mityaev and Jashenko 1999, 2007). Third instar larvae consume much more tamarisk than earlier stages in Ningxia Province, China (Tian *et al.* 1988). In Inner Mongolia, entire tamarisk trees are wilted from desiccation caused by larval feeding upon foliage and bark of tender branches, and tops of trees are discolored and wilted from aggregated feeding by adults (Chen *et al.* 2000). Densities per tamarisk bush reached over 10,000 larvae, and averaged 1,000 adults (maximum 4,000) in Inner Mongolia (Bao 1989). Near Turpan, China, average densities from 100 sampled tamarisk branches can reach 70 adults and 210 larvae per meter (Sha and Yibulayin 1993). Densities reach 270 adults and 534 larvae per meter of branch, and more than 7,000 larvae per individual tamarisk tree in Anxi County (Ding 2004). Densities of 173 to 247 larvae per meter of branch result in near defoliation of tamarisk near Sarytogay, Kazakhstan (Mityaev and Jashenko 1999, 2007). In northern Uzbekistan, larvae crawl from defoliated trees over ground to seek other tamarisk (Sinadsky 1968), a phenomenon that R. Carruthers and C.J. DeLoach also observed at Lovelock and at Schurz, Nevada, in 2004. Localized migrations of adult *D. carinulata* occur following emergence from overwintering, during mating of each generation, and prior to overwintering (Mityaev and Jashenko 1998, 2007).

Diorhabda carinulata (as *D. elongata*) damages tamarisk over wide areas in all types of situations, including sand stabilization plantations and in the understory of turanga poplar (*Populus euphratica* Olivier), in northern Uzbekistan (Sinadsky 1968). *Diorhabda carinulata* more heavily damages the succulent tamarisk of riparian areas compared to that of drier upland areas in China (Bao 1989) and Kazakhstan (Mityaev and Jashenko 1998, 1999, 2007). Tamarisks growing in dense monoculture are attacked at a higher incidence compared to those in stands mixed with other shrubs such as *Calligonum* (Polygonaceae) and *Haloxylon* (Chenopodiaceae) near Turpan (Sha and Yibulayin 1993). *Diorhabda carinulata* defoliates tamarisk in the understory of plains cottonwood (*Populus deltoides* subsp. *monilifera*) at Pueblo, CO, and in extensive tamarisk monocultures at Lovelock, NV (C. Jack DeLoach, USDA/ARS, Temple, TX, pers. comm.).

Tamarisk severely defoliated by *D. carinulata* completely resprouts in a short time in Kazakhstan (Mityaev and Jashenko 1998, 2007; see DeLoach *et al.* 2003b, Fig. 2). In tamarisk defoliated in the Chertombayskoy area of the Amu Darya, Uzbekistan, bud break is delayed by about 15 days the following spring and some of these bushes exhibit die back in the tops (Sinadsky 1968). Near Lovelock, Nevada regrowth also followed defoliation by *D. carinulata*, but it is usually accompanied by severe dieback and tree death is becoming more widespread in trees defoliated for several successive years (Carruthers *et al.* 2006, 2008). Tamarisk dieback and death at this site is probably related to observed significant reductions in nonstructural carbohydrates in tamarisk root crowns following one to four years of defoliation by *D. carinulata* (as *D. e. deserticola*) (Hudgeons *et al.* 2007b).

Adult *D. carinulata* tend to aggregate in the field, and over 1000 adults were counted in a 2 x 2 m area in Inner Mongolia (Bao 1989). Near Chilik Kazakhstan, newly emerged first generation beetles aggregate on certain bushes just prior to mating (Mityaev and Jashenko 1999, 2007). In populations originating from Fukang, China, a male produced aggregation pheromone was identified consisting of two components: (2*E*,4*Z*)-2,4-heptadienal and (2*E*,4*Z*)-2,4-heptadien-1-ol (Cossé *et al.* 2005). This pheromone is being used to monitor populations near Lovelock, Nevada. A blend of green leaf volatiles is attractive for *D. carinulata* in the field, and the attraction is synergized when pheromone is added with the green leaf volatiles (Cossé *et al.* 2006). Additional observations on biology, including mating behavior, are noted by Tian *et al.* (1988), Bao (1989), Mityaev and Jashenko (1998, 1999, 2007), Zhang (2002), and Zhang and Baoping (2006) in central Asia.

Phenology. *Diorhabda carinulata* has four generations from mid-April to mid-September at Turpan, China (Sha and Yibulayin 1993); three generations from April to October in northern Uzbekistan (Sinadsky 1968); three generations in Fukang (Li *et al.* 2000) and Ningxia province (Tian *et al.* 1988), China; two to three generations in Inner Mongolia Province, China (Bao 1989, Chen *et al.* 2000); and two generations in southern Kazakhstan (Mityaev and Jashenko 1998, 2007) and north of 38° in North America (DeLoach and Carruthers 2004b). Adults enter diapause from mid-August to September in China (Bao 1989, Tian *et al.* 1988, Sha and Yibulayin 1993). In southeastern Kazakhstan, adults begin overwintering in mid-September, but, if moisture is favorable and saltcedar has new growth, larvae still can be seen feeding on plants into September and adults are found into early October (Mityaev and Jashenko 1998, 2007). The typical hibernaculum of second generation adults overwintering in Kazakhstan is the boundary layer between the soil and detritus under saltcedar trees (Mityaev and Jashenko 1998, 2007). In Ningxia Province, China, adults overwinter under dead leaves or soil in areas facing the sun and protected from wind (Tian *et al.* 1988). At Lovelock, NV overwintering adults were found on the soil beneath the saltcedar litter during the fall and winter. Overwintered adults emerge in April in Ningxia Province (Tian *et al.* 1988) and in late April when temperatures rise over 13°C in Inner Mongolia (Bao 1989) and in May in southern Kazakhstan (Mityaev and Jashenko 1998, 2007).

The Fukang, China *D. carinulata* climatype did not initially establish at several sites in North America south of 38°N latitude, probably due to asynchrony of the critical photoperiod inducing diapause with the onset of cooler temperatures in these areas (Bean *et al.* 2007a). In the south, these populations diapause prematurely in the summer, rather than the fall, leaving them inadequate food reserves for overwintering (Lewis *et al.* 2003b).

Development and Reproduction. *Diorhabda carinulata* has three larval instars and a development time of 34 days from egg to adult at 24.1°C. Fecundity at 28.6°C on *T. ramosissima* averaged 194 eggs (range 78 to 550 eggs) with a population doubling time of 6.2 days. Fecundity on *T. aphylla* was lower than that found on *T. ramosissima*, *T. canariensis* and *T. parviflora* (Lewis *et al.* 2003b). Herrera *et al.* (2005) found 30–35°C is optimal among six constant temperatures from 15–40°C for highest survival and developmental rates for all life stages of *D. carinulata*. Both Zhang (2002) and Herrera *et al.* (2005) report temperature developmental thresholds and degree-days for development for various stages of *D. carinulata*.

Milbrath *et al.* (2007) found that, at 28°C, *D. carinulata* (as *D. elongata* from Turpan and Fukang, China) had a development time of 18.5–20.4 days from egg to adult (with 74–78% survival), a fecundity of 272–283 eggs, and a population doubling time of 5.2–6.1 days. These values were all very similar to those found for *D. elongata* (Crete), *D. carinata* (Uzbekistan), and *D. sublineata* (Tunisia) (all as *D. elongata*).

Natural Enemies. The parasitoid tachinid fly, *Erynniopsis antennata*, attacks larvae and emerges from adult *D. carinulata* from Fukang and Wujiaqu, Xinjiang Uygur Zizhiqu, China (Zhang 2002). At quarantine in Temple, Texas, we commonly encountered the parasitoid *E. antennata* emerging from the bloated abdomens of killed overwintered adult *D. carinulata* that were originally collected alive in April at Fukang, China. *Diorhabda carinulata* from Fukang, represents both a new host and locality record for *E. antennata*. Unidentified mymarid egg parasitoids attack as much as 24% or more of *D. carinulata* eggs in the field near Fukang and Wujiaqu, China (Zhang 2002, Zhang and Baoping 2006). An unidentified 1mm-long "fly", possibly an eulophid parasitoid hymenopteran, parasitized ca. 14.5–32.5% of the *D. carinulata* pupae in Inner Mongolia (Bao 1989). The ubiquitous fungal pathogen *Beauveria bassiana* (Balsamo) was found infecting adult *D. carinulata* originating from the following locations (all identified by T. Poprawski): Fukang, China (shipment GSWRL(CJD)-1996-27); near Urumqi, China (shipment GSWRL-1998-12); and near Shelek, Kazakhstan (shipment GSWRL-2000-9).

At Turpan, China, the chief predators of *D. carinulata* are reduviids and mantids (Sha and Yibulayin 1993). Ants and coccinellids prey upon eggs and larvae of *D. carinulata* in Inner Mongolia (Bao 1989). In southeastern Kazakhstan, nymphs and adults of the pentatomid *Arma custos* Fabricius, feed on larvae of *D. carinulata* (Mityaev and Jashenko 2000, 2007). Seven species of birds have been reported to feed upon adult *D. carinulata*. In Inner Mongolia, tree sparrows, *Passer montanus* (Linnaeus), and common pheasants, *Phasianus colchicus* (Linnaeus), were observed eating adult beetles, and the crop of one common pheasant hunted in late winter contained over 200 overwintering adults along with a few wheat seeds (Bao 1989). Chen *et al.* (2000) also noted the crested lark, *Galerida cristata* (Linnaeus), as a predator in Inner Mongolia. In Almaty, Kazakhstan, beetle adults were preyed upon by the great tit (*Parus major* Linnaeus), Eurasian blackbird (*Turdus merula* Linnaeus), common myna (*Acridotheres tristis* [Linnaeus]), and house sparrow (*Passer domesticus* [Linnaeus]) (Mityaev and Jashenko 2000, 2007).

Biogeography. *Comparative.* *Diorhabda carinulata* differs from other tamarisk beetles by the following combination of biogeographic characteristics: (1) primarily continental, usually beyond 1,400 km from the ocean at elevations above 400 m; (2) commonly found in temperate cold desert and grassland biomes; and (3) latitudinal range of 29–49°N and most common at 40–44°N. *Diorhabda carinata* and *D. carinulata* are moderately sympatric and syntopic over portions of their western range (see above discussion under *D. carinata*-**Biogeography**) (Map 1, Table 8), and they are the most similar species in the *D. elongata* group in terms of biomes inhabited (Tables 9 and 10, Fig. 53). *Diorhabda carinata* differs from *D. carinulata* in being commonly collected in southern areas from 35–42°N and in preferring temperate grasslands over deserts. *Diorhabda carinulata* is marginally sympatric with *D. elongata* in southern Russia (Dagestan Republic) and allopatric with *D. sublineata* (Map 1; Table 8). *Diorhabda elongata* and *D. sublineata* both differ from *D. carinulata* in being primarily maritime and most common in the Mediterranean biome. *Diorhabda carinulata* is parapatric with *D. meridionalis* in southern Iran. Both *D. carinulata* and *D. meridionalis* have a similar preference for deserts, but *D. meridionalis* differs in being maritime and most common further south at 26–30°N (Maps 1 and 6; Figs. 51–52; Table 8).

Descriptive. *Diorhabda carinulata* occurs over the central portion of the Palearctic realm (Maps 1, 5 and 6). It has been most commonly collected between 40–44°N in the Deserts and Xeric Shrublands and Temperate Grasslands and Shrublands biomes of eastern Central Asia. All reports of damage to tamarisk by *D. carinulata* are from this region of the Palearctic realm from elevations of ca. 30 m (at Turpan, China) to 970 m (Erjina County, Inner Mongolia, China). *Diorhabda carinulata* also occurs in Montane Grasslands and Shrublands biomes in western China around 44°N (from ca. 550–1850 m). From 35–40°N it is usually found in the Deserts and Xeric Shrublands biome from 0–1,400 m elevation. From 36–37°N, *D. carinulata* is occasionally found in the Temperate Conifer Forests biome in Iran (at ca. 1,400 m elevation). From 29–34°N in Iran, collections are from two biomes: Montane Grasslands and Shrublands from ca. 1,625–1,850 m elevation in the Kuh Rud and Eastern Iran Montane Woodlands ecoregion; and the Deserts and Xeric Shrublands biome from ca. 450–700 m elevation in the Registan-North Pakistan Sandy Desert (Map 6). The distribution of *D. carinulata* broadly coincides with that of the common host *T. ramosissima* from Mongolia and China to Iran and southern Russia, but its range appears to fall short of following the western distribution of *T. ramosissima* into Iraq and Turkey (Map 5).

Primary ecoregions for *D. carinulata* in the northern portion of its range (40–46°N) in the Deserts and Xeric Shrublands include the Taklamakan Desert (30–1,600 m), Junggar Basin Semi-Desert (500–1,200 m), and Alashan Plateau Semi-Desert (900–1600 m) in China and Mongolia (Map 5). The primary northern ecoregion of *D. carinulata* in the Temperate Grasslands and Shrublands biome is the Tian Shan Foothill Arid Steppe (500–1,850 m) in southeastern Kazakhstan and northern Tajikistan.

Potential in Tamarisk Biological Control. *Summary.* The northern tamarisk beetle is highly effective in biological control of *T. ramosissima*/*T. chinensis* in temperate cold deserts of the Great Basin Shrub Steppe, Colorado Plateau Shrublands and Wyoming Basin Shrub Steppe (Map 13). *Diorhabda carinulata* may be the most suitable tamarisk beetle for some warm temperate desert areas also, such as western portions of the Mojave Desert, southern portions of the Colorado Plateau Shrublands and Trans-Pecos Chihuahuan Desert (Map 13). Introduction of southern climatotypes of *D. carinulata* from 29–34°N in the Registan North Pakistan Sandy Desert (Map 6) may speed its adaptation to corresponding latitudes in North America.

Discussion. A northern *D. carinulata* climatype from ca. 44°N in China and Kazakhstan has been released and established in North America at several locations north of 37°N (Map 7). *Diorhabda carinulata* from Fukang, China, were introduced into cages in 1999, and released (under permit as *D. elongata*) into the field in 2001 at four sites in Nevada, Colorado, and Wyoming for biological control of *T. ramosissima*/*T. chinensis*. Concurrently, populations from Shelek, and Lavar (10 km west Shelek), and Buryndysu environs (25 km east Shelek), Kazakhstan, were released and established in Utah (DeLoach *et al.* 2004) (Maps 7, 9). In 2005, the USDA-APHIS (2005) began a large-scale introduction program of *D. carinulata* (as *D. e. deserticola*) from Fukang, China into 13 western states north of 38°N latitude. States involved in this program include Colorado, Idaho, Iowa, Kansas, Missouri, Montana, Nebraska, Nevada, North Dakota, Oregon, South Dakota, Washington and Wyoming. By 2005, it had defoliated over 20,000 ha of tamarisk in the Humboldt River basin near Lovelock, Nevada (Map 7). The northern tamarisk beetle has a moderate risk of damaging *T. aphylla* (DeLoach *et al.* 2003b) and a low risk of damaging *Frankenia* (Lewis *et al.* 2003a, Milbrath and DeLoach 2006a), and both these risks are probably much reduced at less proximity to preferred *Tamarix* spp. (e.g., Blossey *et al.* 2001).

The introduced northern *D. carinulata* climatype probably has the greatest potential to defoliate tamarisk in North America in the temperate cold Deserts and Xeric Shrublands and the Temperate Grasslands and Shrublands biomes from 40–44°N (Map 13, see **Biogeography**). Elevations above 1,000 m might extend this defoliation further south in some ecoregions. *Diorhabda carinulata* has already defoliated large acreages of tamarisk at sites in three North American temperate cold desert ecoregions: the Great Basin Shrub Steppe (Lovelock, NV and Delta, UT), the Colorado Plateau Shrublands (Potash, UT), and the Wyoming Basin Shrub Steppe (Lovell, WY) (Map 13). The southern portion of the Snake/Columbia Shrub Steppe is probably also a highly suitable cold desert region (Map 13). The most suitable ecoregions of the Temperate Grasslands and Shrublands biome at 40–44°N probably include the southern portion of the Northwestern Mixed Grasslands

and the northern portions of the Western Short Grasslands (Map 13). *Diorhabda carinulata* has also established well at 38°N at Pueblo, Colorado in the Western Short Grasslands, but *D. carinata* may be better suited to the temperate grassland biome at this latitude (Map 13). The potential spread of the introduced parasitoid tachinid fly *Erynniopsis antennata* from California to Nevada should be monitored as it might severely reduce overwintering survival of northern tamarisk beetles.

The northern climatype of *D. carinulata* from Fukang, China was initially ill-adapted to areas south of 38°N (DeLoach *et al.* 2004) because of premature entry into diapause during short summer daylengths (Lewis *et al.* 2003b; Bean *et al.* 2007a, 2007b). Overwintering of the northern Fukang climatype failed at field cages in Big Pine, California, Artesia, New Mexico, and Seymour, Temple, and Lake Thomas, Texas. The lower elevation *D. carinulata* northern climatype from Turpan, China failed to establish in cages at Lake Thomas, Texas (personal observation), and is establishing poorly at John Martin Reservoir, Colorado (Debra Eberts, USDI/Bureau of Reclamation, Denver, CO, pers. comm.) (Map 7). However, in 2008, populations originating from Delta, Utah, had established south to about 37°N on the Virgin River at Littlefield, Arizona (L.D. Walker, pers. comm.) and in Ute Canyon, Colorado (Dan Bean, pers. comm.). Natural expansion of the population was rapid in 2008, covering over 75 km south of Gateway along the Dolores River (D. Bean, pers. comm.). In 2006, a population of the northern Fukang climatype from Nevada began to increase and defoliated about 0.8 ha of tamarisk in the open field at Artesia, New Mexico (at ca. 33°N), but populations disappeared by 2008 (D. Thompson, pers. comm.). Apparently, the northern Fukang climatype may be gradually adapting further south. Putative climatotypes from the extreme southern range limits of *D. carinulata* occur from 29–34°N in widely varied habitats of southeastern Iran, such as the Registan-North Pakistan Sandy Desert (at ca. 450–700 m elev.) and Kuhrud Mountains (at ca. 1,625–1,850 m elev.) (Map 6). In North America, these southern climatotypes may more quickly adapt to areas in the southern half of the Colorado Plateau Shrublands, western portions of the Mojave Desert, Trans-Pecos Chihuahuan Desert, and southwestern portions of the Western Short Grasslands ecoregions. According to our HSI models, *D. carinulata* will probably not establish further south in subtropical deserts such as the Sonoran, Tamaulipan Mezquital and southern Chihuahuan (Map 13).

Initial attempts at establishing the northern Fukang *D. carinulata* climatype were unsuccessful north of 46°N at Fort Peck, Montana (D. Kazmer, pers. comm.) (Map 7). Putative climatotypes of *D. carinulata* from the extreme northern limits of its native range occur from 46–48°N at low elevations (ca. 0 m) in the Volga Valley of southern Russia and higher elevations (at ca. 1,200 m) of the Junggar Basin Semi-Desert in western Mongolia (Map 5). These extreme northern climatotypes of *D. carinulata* may be better preadapted to Montana.

***Diorhabda meridionalis* Berti & Rapilly, 1973 NEW STATUS**

southern tamarisk beetle

(Figs. 9, 18, 23, 28, 33, 38, 43)

Diorhabda carinulata meridionalis Berti & Rapilly, 1973:881 (Type locality: Minab, Iran); Warchalowski, 2003:328 (catalog of Mediterranean Region, Iran).

Diorhabda elongata: Riley *et al.*, 2003:69,189 (part, catalog of North America [not yet introduced]).

Male. Genitalia. *Diorhabda meridionalis* can be distinguished from all other members of the *D. elongata* group by two unique characteristics of the elongate endophallic sclerite (EES): (1) the presence of a strongly hooked apex (Figs. 18, 28), and (2) the length of the blade of the EES being greater than or equal to 0.67 times the length of the EES (Table 3; Figs. 18, 23, 48). In all other members of the *D. elongata* group, the blade is less than or equal to 0.66 times the length of the EES (Figs. 14–17, 19–22) and the apex of the EES is not hooked (Figs. 24–27). The palmate endophallic sclerite (PES) of *D. meridionalis* is also unique among the *D. elongata* group in that its distal margin is narrowly rounded and generally smooth, with only one or two small subdistal spines, and it has a length to width ratio of 0.35–0.63 (Figs. 18, 33; Table 3). In contrast, the distal margin of the PES is truncate or more broadly rounded with larger distal or subdistal spines in *D. elongata*, *D.*

carinata, and *D. sublineata* (Figs. 14–16, 29–31), and the PES is acutely rounded with a length to width ratio of 0.61–1.02 in *D. carinulata* (Figs. 17, 32).

Measurements. See Tables 2 and 3.

Female. Genitalia. Female *D. meridionalis* can be distinguished from all other members of the *D. elongata* group by the following combination of characters in the vaginal palpi (VP) and internal sternite VIII (IS VIII): (1) the vaginal palpi are broadly rounded and as long as wide or longer with a width to length ratio (LP/WP) of 1.0–1.31 (Fig. 38; Table 4), and (2) the width of the stalk (WST) of IS VIII is 0.22–0.33 mm and this width is 0.33–0.48 times the width of the apical lobe (WAL) (Figs. 38, 43; Table 4). In contrast, the vaginal palpi are wider than long, with a length to width ratio of 0.46–0.94 in *D. elongata*, *D. carinata* and *D. sublineata* (Figs. 34–36). In addition, the vaginal palpi are triangulate in *D. carinata* and *D. sublineata* (Figs. 35–36). In *D. carinulata*, the width of the stalk of IS VIII is 0.36–0.57 mm and this width is from 0.49–0.77 times the width of the apical lobe (Fig. 37, 42). In addition, the width of the widest lobe of the stalk of IS VIII is from 0.04–0.09 mm in *D. meridionalis* (Fig. 38, 43); whereas, in *D. carinulata* the width of the widest lobe of the stalk is usually greater than 0.10 mm (Figs. 37, 42; Table 4).

Measurements. See Tables 2 and 4.

Coloration. Coloration of dead *D. meridionalis* (Fig. 9) is similar to that discussed above for *D. sublineata* and *D. carinulata* (Figs. 5, 7). We have not had the opportunity to examine live material of *D. meridionalis*.

Type material. Berti and Rapilly (1973) deposited the holotype male and allotype female of *D. meridionalis*, both from Minab, Iran, and four paratypes (3♂♂, 1♀) from Minab, Borazjan and Shush (= Susa), Iran at MNHN. As discussed above (see *D. elongata* - **Type Material**), we were unable to obtain type materials from MNHN. We studied the original description by Berti and Rapilly (1973), including their illustrations of the endophallus of the male holotype. We also examined a male specimen from 30 km NNE of Borazjan, a paratype locality, with an identification label as “*D. carinulata meridionalis* Berti & Rapilly det. Berti X-1996” (MBPF 2003-03) and additional material near type and paratype localities.

Material examined. 22♂♂ dissected (diss.), 19♀♀ diss., 13♂♂, 18♀♀, 147 unsexed specimens. **IRAN:** 2♂♂ diss., 3♀♀ diss., 11♂♂, 9♀♀, Bahu–Kalat [25.73330°N, 61.53330°E; 68 km south Rask, Sarbaz River; *T. dioica* and *T. aphylla* present (Hoberlandt 1981)], 3–4-IV-1973, Exp. Nat. Mus. Praha Loc. No. 147, NMPC [2004-48, 2005-16, 17, 18, 19]; 3♂♂ diss., Bilai [26.48333°N, 57.15000°E; coastal savanna; *Tamarix* sp. not recorded (Hoberlandt 1981)], 23–24-V-1973, Exp. Nat. Mus. Praha Loc. No. 209, *Diorhabda elongata* det. I.K. Lopatin 1978 [1♂ diss., USNM], NMPC [2004-57, 2005-22], USNM [2003-11]; 1♂ diss., 2♀♀ diss., 1♀, Borazjan, 20 km northwest [29.38333°N, 51.03333°E; Shabankareh, clay semi-desert; *Tamarix* sp. not recorded (Hoberlandt 1983)], 18-IV-1977, Exp. Nat. Mus. Praha Loc. No. 297, NMPC [2004-05, 42, 43]; 3♂♂ diss., 1♂, 3♀♀, Borazjan, 30 km north northeast [29.53333°N, 51.40000°E; 10 km N Dalaki, Hableh Rud River; *Tamarix* sp. present (Hoberlandt 1983)], 18–19-IV-1977, Exp. Nat. Mus. Praha Loc. No. 298, *D. carinulata meridionalis* Berti & Rapilly det. Berti X-1996 [1♂ diss., MBPF], NMPC [2004-12, 2005-20], MBPF [2003-03]; 2♀♀ diss., Jeugir (33° 27' N, 49° 01' E) [sic; Jolow Gir; 32.96667°N, 47.81611°E; coordinates corrected from relation to Sarab–e Jahangir], 20 km southeast Sarab–e Jahanagir, Lorestan, 8–10-X-1998, Chvojka, *D. elongata* det. A. Warchalowski, NMPC [2005-28, 2006-01]; 1♂ diss., 2♀♀ diss., 1♀, Nikshahr, 13 km south southeast [26.13333°N, 60.18333°E; Rudkhaneh Nikshahr river; *T. dioica* present (Hoberlandt 1981)], 8–9-IV-1973, Exp. Nat. Mus. Praha Loc. No. 152, USNM [2003-05, 2004-05, 06], NMPC; 1♂ diss., 1♂, 3♀♀, Omidiyeh, 34 km southeast [30.55000°N, 49.91667°E; Rud-e Zohreh river; *Tamarix* sp. present (Hoberlandt 1983)], 16–17-IV-1977, Exp. Nat. Mus. Praha Loc. No. 292, NMPC [2004-44]; 8♂♂ diss., 5♀♀ diss., 1♂, 2♀♀, 142 specimens [NMPC], Rask [26.23528°N, 61.40111°E; 3 km N Rask; *T. dioica* present (Hoberlandt 1981)], Sarbaz River valley, 3–4-IV-1973, Exp. Nat. Mus. Praha Loc. No. 146, *D. carinulata meridionalis* det. Lopatin 1984 [1♂, 1♀, NMPC], *D. elongata* det. I.K. Lopatin [2♀♀, USNM], USNM [2003-04, 12, 13, 2004-03; 2008-02, 03, 04, 05, 06], NMPC [2004-58, 2005-21, 2006-8–9]; 1♂ diss., 2♀♀ diss., 1♀, Sabzevaran [Sabzvaran], 33 km south [28.40000°N, 57.83333°E; ruderal plants near plantation; *Tamarix* sp. present (Hoberlandt 1983)], 17-V-1977, Exp. Nat. Mus. Praha Loc. No. 335, NMPC

[2004-27, 2005-23, 24]; 1 ♀ diss., Sekand [26.71667°N, 61.53330°E; oasis of saline marshes; *Tamarix* sp. not recorded, *Frankenia pulverulenta* present (Hoberlandt 1981)], 27 km east northeast Sarbaz, 31-III to 1-IV-1973, Exp. Nat. Mus. Praha Loc. No. 144, USNM [2004-02]; 1 ♀ diss., Shushtar [32.05°N, 48.85°E; river Karun; *Tamarix* sp. present (Hoberlandt 1983)], 13-IV-1977, Exped. Nat. Mus. Praha Loc. No. 287, NMPC [2005-35]; **PAKISTAN**: 1 ♂ diss., 1 ♀ diss., Turbat [26.02780°N, 63.05060°E], west Balochistan, 8–19-IV-1993, S. Becvar, EGRC [2005-01, 04]; **SYRIA**: 1 ♂ diss., Alep[po] [Halab; 36.20278°N, 37.15861°E], Syrie, NHMB [2003-15].

Distribution. *General.* *Diorhabda meridionalis* is primarily known from extreme southern Iran and along the southern portion of Iran's border with Iraq. Its native range is from Syria to western and southern Iran and southern Pakistan (Map 5). Additional surveys should be made for *D. meridionalis* in eastern Iraq and along the western coast of the Persian Gulf in Kuwait, Saudi Arabia, United Arab Emirates, Oman, and east to northern India (following the distribution of a suspected host *T. dioica* Roxburgh ex Roth, see below; Map5).

Confirmed Records. We confirm the presence of *D. meridionalis* in Iran (Berti and Rapilly 1973) (see above **Material examined**) (Maps 5–6). Although *D. meridionalis*, *D. carinulata* and *D. carinata* occur on tamarisk throughout Iran (Map 6), Barkhodari *et al.* (1981) recorded no *Diorhabda* in their detailed survey of the *Tamarix* entomofauna in Iran. This is evidence of a possibly sporadic nature of tamarisk beetle populations in Iran.

New Records. Pakistan and Syria are new distribution records for *D. meridionalis* (Map 5).

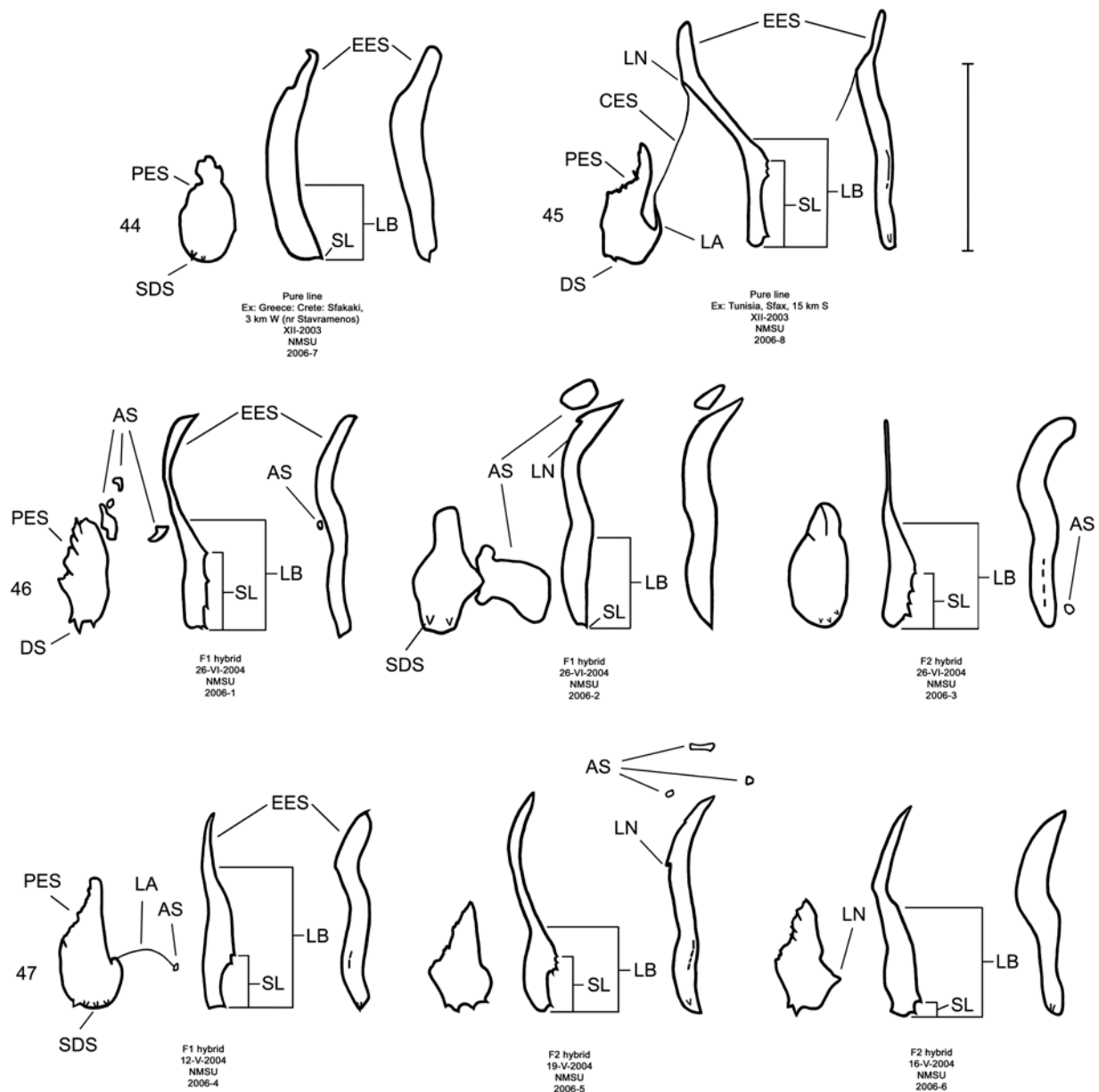
Unconfirmed Records. We find no country distribution records that remain unconfirmed. We have not examined specimens from the following locations of *D. meridionalis* in Iran reported by Berti and Rapilly (1973) (Map 5):

IRAN: 1 ♂, 1 ♀, Borazjan [29.26222°N, 51.20528°E], 24-V-1969, R. Naviaux and M. Rapilly, on *Tamarix* sp., PARATYPE, MNHN; 2 ♂, 1 ♀, Minab [27.14667°N, 57.07361°E], 25-IV-1971, Naviaux and M. Rapilly, on *Tamarix* sp., HOLOTYPE, MNHN; 1 ♂, Susa [Shush; 32.19417°N, 48.24361°E], 1899, Escalera, PARATYPE, MNHN.

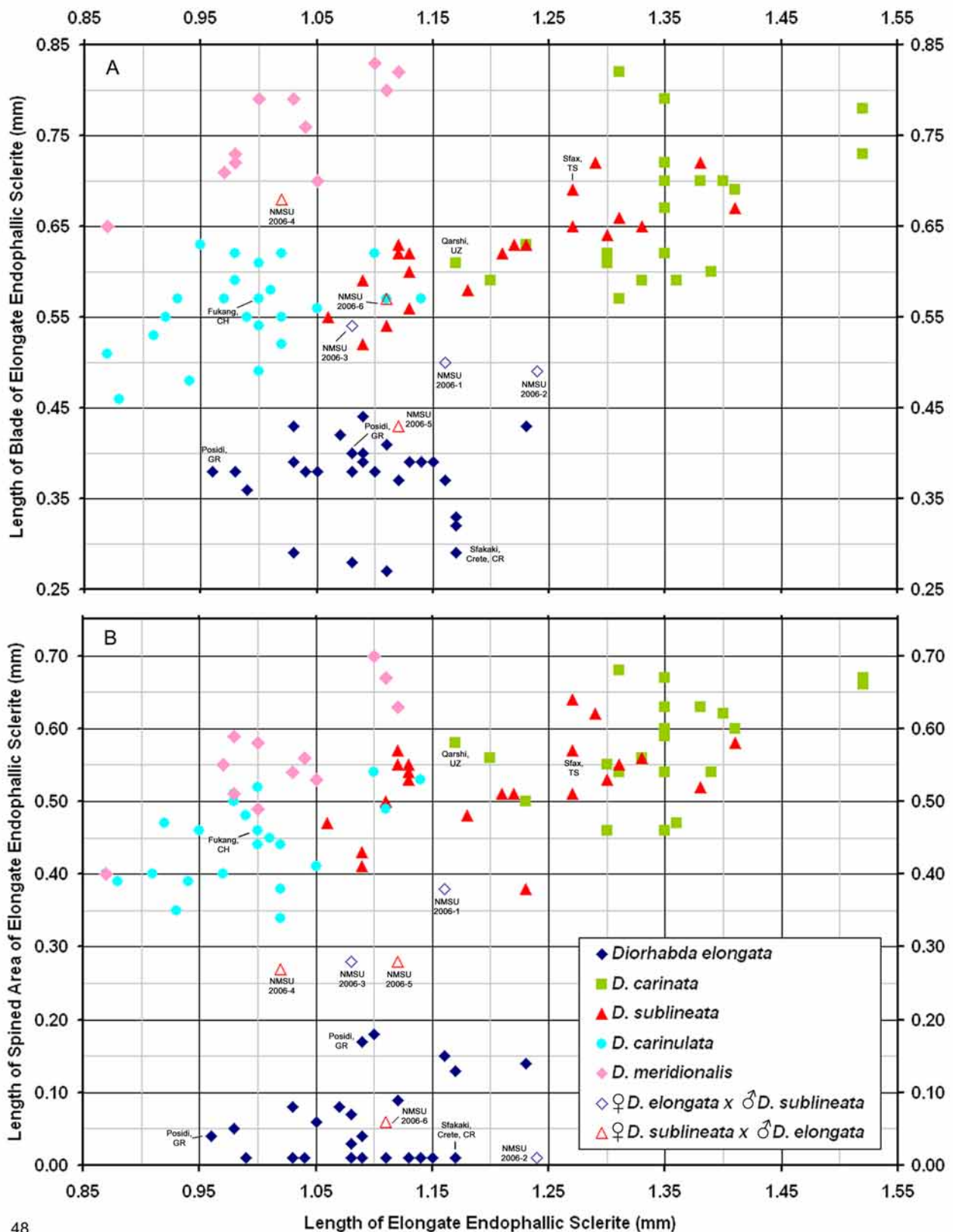
Discussion. *Taxonomy.* *Diorhabda carinulata meridionalis* was described from Minab, Iran with paratype localities in Shush and Borazjan, all along the southwestern border of Iran (Berti and Rapilly 1973). We examined one male specimen from 30 km NNE of Borazjan, a paratype locality, with an identification label as “*D. carinulata meridionalis* Berti & Rapilly det. Berti X-1996” (MBPF 2003-03) with endophalli matching that of the description by Berti and Rapilly (1973). Other males with endophalli matching that of *D. c. meridionalis* were examined from Bilai, 74 km NNW from the type locality of Minab, from 20 km NNW of Borazjan, and from six other locations along the southwestern Iranian border (Map 5). Three key characters of the endophallus of *D. c. meridionalis* that distinguish it from other members of the *D. elongata* group can be seen in the illustrations of the endophallus of the holotype (Fig. 19d–e of Berti and Rapilly 1973) and our figures (Figs. 18, 23, 28, 33): (1) narrowly rounded distal margin of the palmate endophallic sclerite; (2) elongate endophallic sclerite (EES) with blade extending for more than 2/3 the length of the sclerite; and (3) the hooked apex of the EES. We are certain that specimens we studied with endophalli matching that of *D. c. meridionalis* are conspecific. We find additional characters in the endophallic sclerites (Figs. 18, 23, 28, 33) and female genitalia (vaginal palpi and internal sternite VIII; Figs. 38, 43) of *D. c. meridionalis* throughout its range (Map 5) that distinguish it from other members of the *D. elongata* group (see **Male-Genitalia** and **Female-Genitalia** above; Figs. 14–17, 19–22, 24–27, 29–32, 34–37, 39–42). If *D. c. meridionalis* were a subspecies of *D. carinulata*, we would expect intermediate forms to occur in areas where their distributions approach one another in southern Iran. Diagnostic characters of the endophalli and female vaginal palpi of *D. c. meridionalis* are distinct from that of *D. carinulata*, even in the populations at Sabzvaran, Iran, that approach within 102 km of *D. carinulata* at Abaraq, Iran (see **Biogeography** below; Maps 1 and 5, Table 8). The lack of intermediate forms between the two taxa is strong evidence of their reproductive isolation. The distinctive genitalic characters of *D. c. meridionalis* are also maintained in the same areas where *D. carinata* occurs and near the abutting range boundary of *D. c. meridionalis* with *D. elongata*, and this is strong evidence for reproductive isolation between these species. Although *D. c. meridionalis* is allopatric with *D.*

sublineata, their status as reproductively isolated is supported by the number of diagnostic genitalic characters separating *D. c. meridionalis* from *D. sublineata* (8 characters) being greater than the number of characters separating the moderately sympatric *D. carinata* from *D. carinulata* (5 characters) (Table 5). Therefore, we elevate *D. c. meridionalis* to species status as *D. meridionalis* Berti and Rapilly NEW STATUS.

We were unable to fully evert the tip of the endophallus containing the gonopore in *D. meridionalis* without damaging the specimens (Fig. 18), and a more fully everted pointed tip can be seen in the illustration of the holotype endophallus in Fig. 19d–e of Berti and Rapilly (1973). We have examined specimens of *D. meridionalis* that were misidentified by taxonomists as *D. elongata* from Iran (see **Material Examined**).

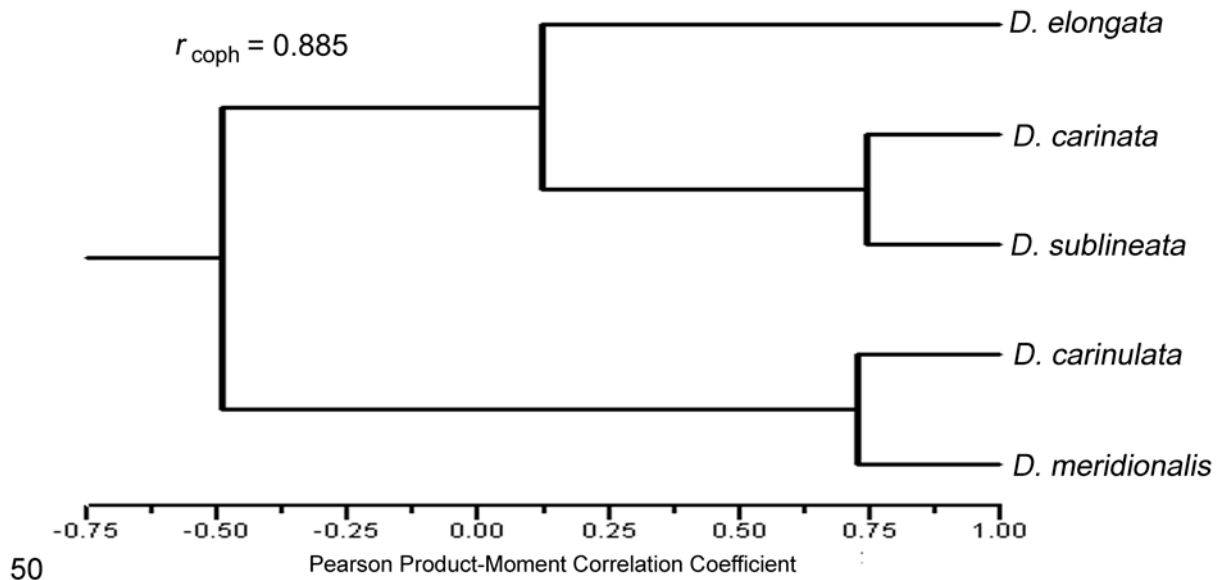
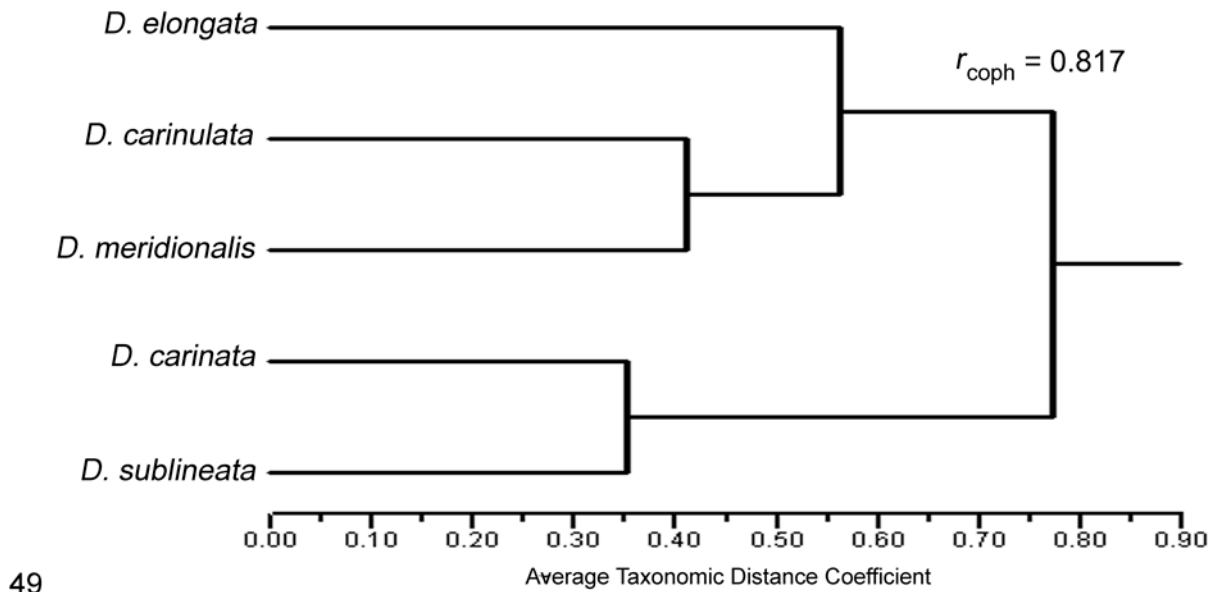


FIGURES 44–47. Palmate, connecting (dorsal views), and elongate (dorsal and lateral views) endophallic sclerites with abnormal sclerites in laboratory pure lines of *Diorhabda elongata* and *D. sublineata* and laboratory produced *D. sublineata* × *D. elongata* hybrids from New Mexico State University (NMSU). 44—♂ *D. elongata* pure line, 45—♂ *D. sublineata* pure line, 46—♀ *D. sublineata* × ♂ *D. elongata* hybrids (F1 and F2), 47—♀ *D. elongata* × ♂ *D. sublineata* hybrids (F1 and F2). AS—abnormal sclerite, CES—connecting endophallic sclerite, DS—distal spines, EES—elongate endophallic sclerite, LA—lateral appendage, LB—length of blade, LN—lateral notch, PES—palmate endophallic sclerite, SDS—subdistal spines, SL—length of spined area of blade. Scale bar 1.0 mm.



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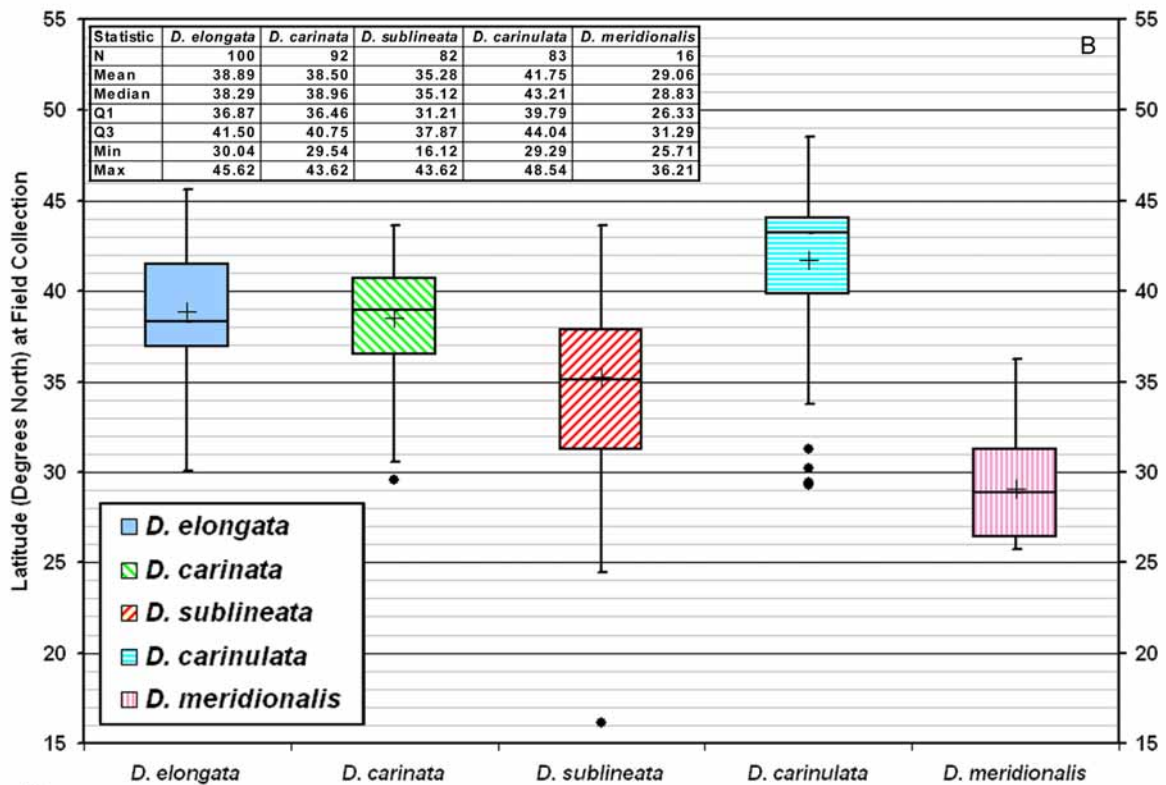
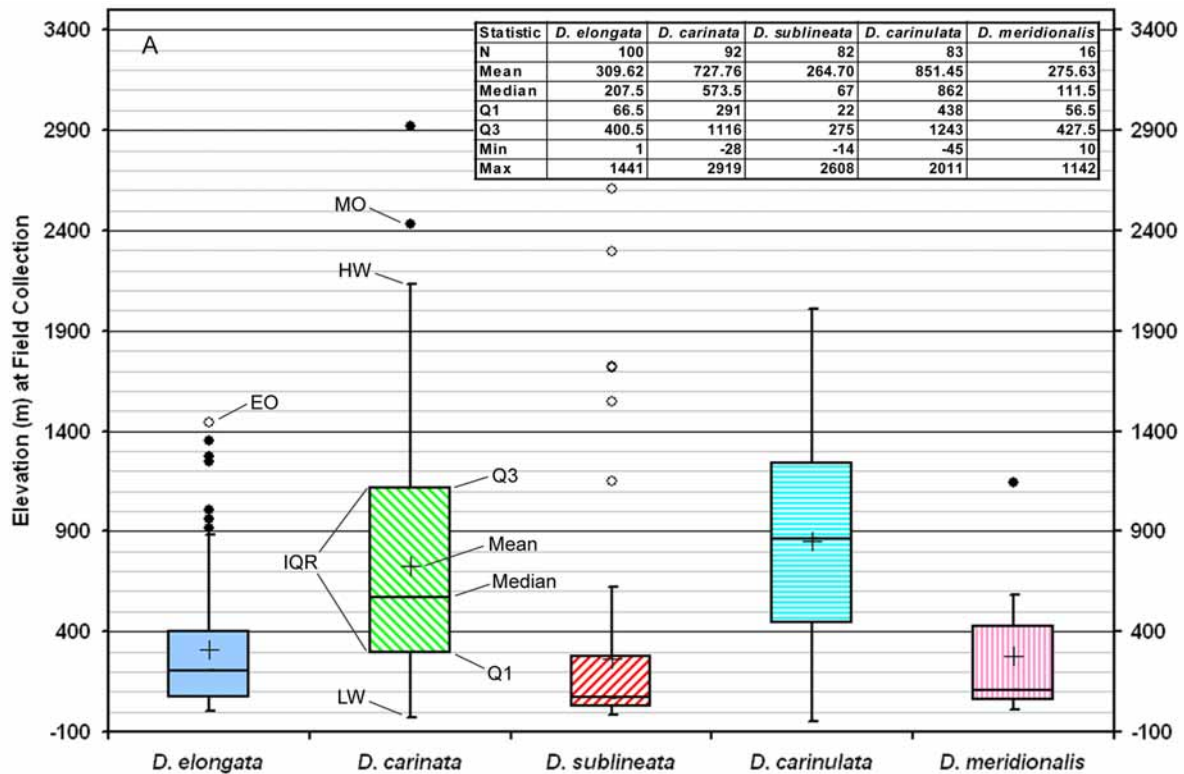
FIGURE 48. Scatter plots of length of blade of elongate endophallic sclerite (A) and length of spined area of elongate endophallic sclerite (B) versus the length of the elongate endophallic sclerite for field collected material of *Diorhabda elongata* species group and laboratory produced F1 and F2 *D. elongata*/*D. sublineata* hybrids (see Figs. 45–47 for illustrations of endophallic sclerites for individual hybrids identified by alphanumeric codes in plots; see Table 3 for sample sizes and statistics for measurements).



FIGURES 49–50. Genitalic phenograms for the *Diorhabda elongata* species group. 49—dissimilarity phenogram based on average taxonomic dissimilarity matrix (Table 5), 50—similarity phenogram based on and Pearson product-moment correlation similarity matrix (Table 6). Phenograms produced with NTSYSpc Tree plot module (Rohlf 2006) from clusters formed with unweighted arithmetic average clustering (UPGMA) (NTSYSpc SAHN module).

Common Name. The vernacular name “southern tamarisk beetle” refers to its Latin name “*meridionalis*” and its southern range in relation to the closely related and parapatric *D. carinulata* (Fig. 51B).

Biology. Host Plants. Berti and Rapilly (1973) report *Tamarix* sp. as a host plant for *D. meridionalis* (as *D. c. meridionalis*) in Iran (Table 1). Records of *Tamarix* identified to species and other plants present were made in conjunction with collections of *D. meridionalis* in southeastern Iran by the second Czechoslovak-Iranian Entomological Expedition in 1973 (Hoberlandt 1981; see above **Material Examined**). We examined *D. meridionalis* from one of two expedition collection sites with both *T. dioica* and *T. aphylla* (Bahu–kalat), two of five sites with *T. dioica* and no *T. aphylla* (Rask and 13 km SSE Nikshahr), and none of eight sites with *T. aphylla* and no *T. dioica*. Based on these records, *T. dioica*, a close relative of *T. aphylla*, is a probable host plant in southeastern Iran. We found no reports of *T. dioica* in western Iran and Syria (Schiman-Czeika 1964,



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FIGURE 51. Schematic box plots for elevations (A) and latitudes (B) from native presence-only field collection data for the *Diorhabda elongata* species group at 5 minute grid resolution. Box plots for each species depict the mean, median, first quartile (Q1), third quartile (Q3), interquartile range (IQR, Q1–Q3), low whisker (LW; lowest point at or above 1.5*IQR lower than Q1), high whisker (HW, highest point at or below 1.5*IQR higher than Q3), mild outliers (MO, points between the low or high whisker and 3*IQR from Q1 and Q3, respectively), and extreme outliers (EO, points below or above 3*IQR from Q1 and Q3, respectively) (Proc Boxplot; SAS Institute 2005). Sample sizes of field localities (N) and a table summary statistics and plotted values are inset in each chart.

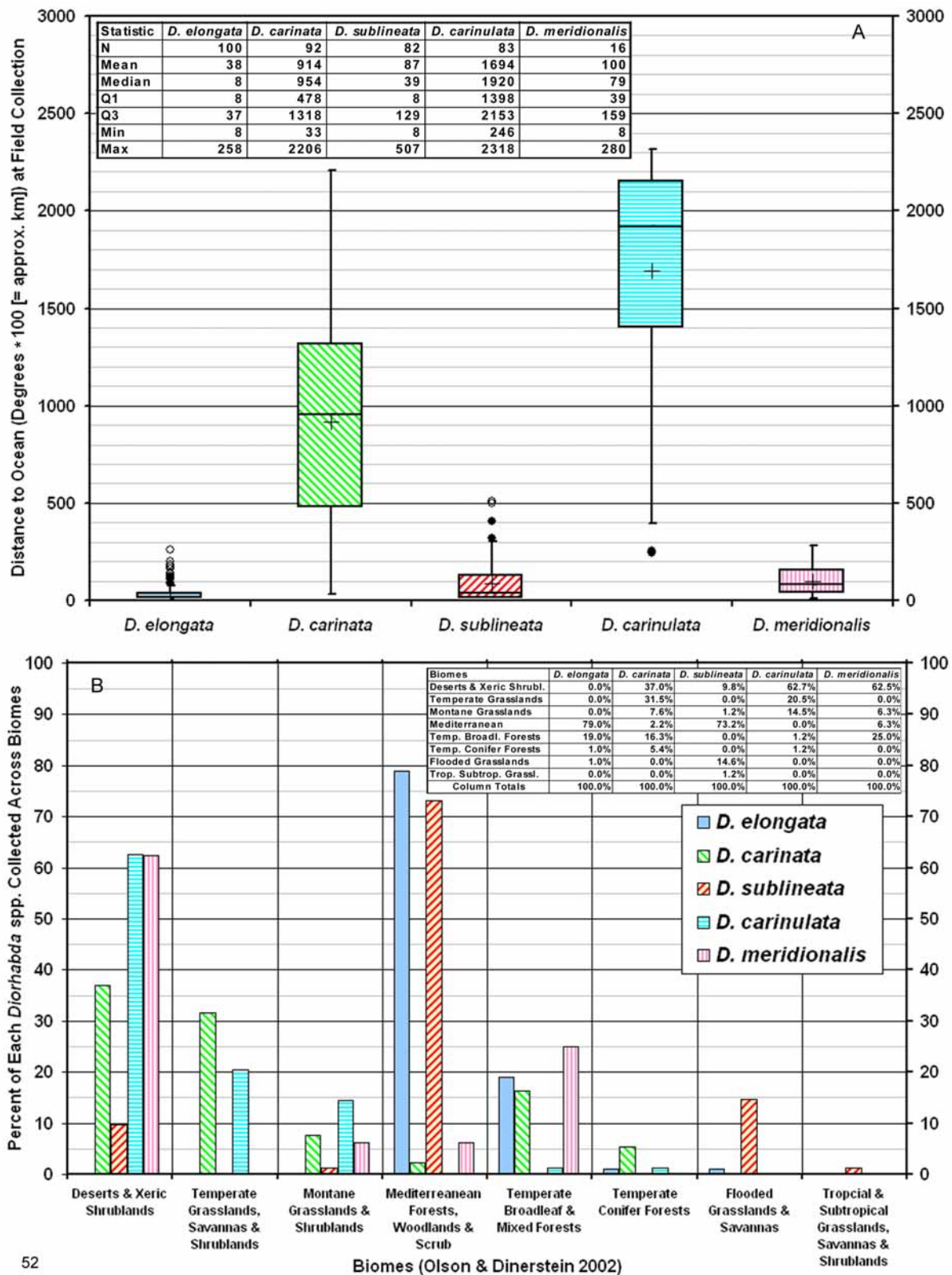
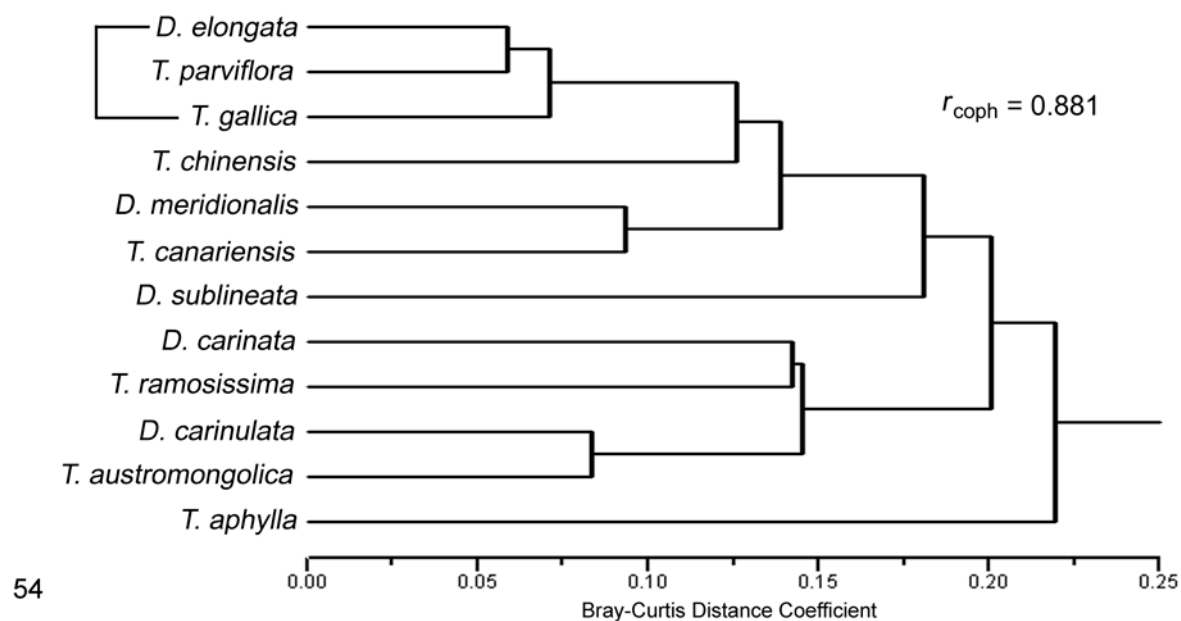
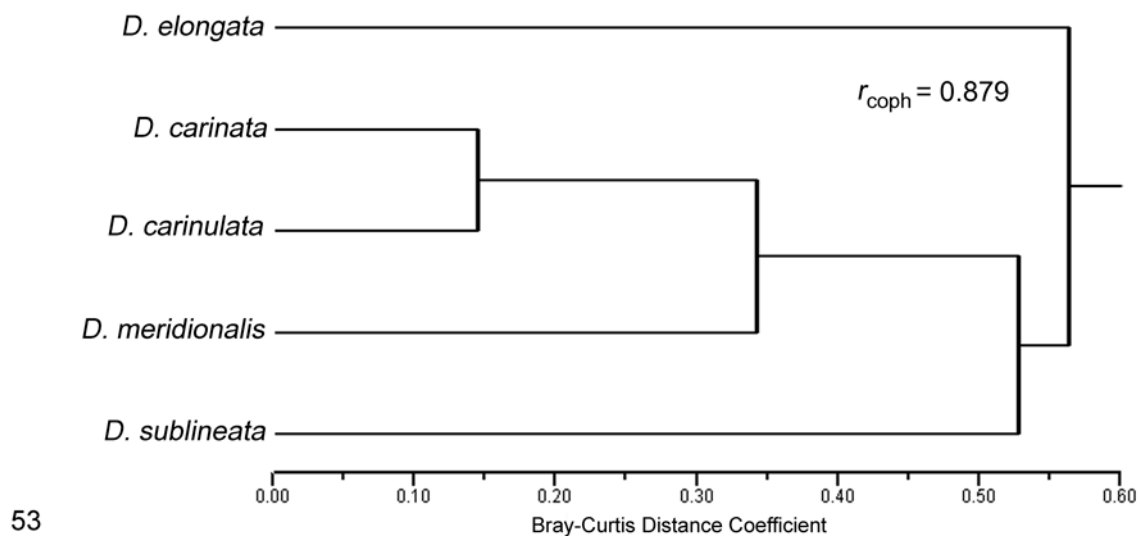


FIGURE 52. Schematic box plots for distances to the ocean (A) (Proc Boxplot [Boxstyle=Schematic]; SAS Institute 2005) and a bar chart of frequency percentages for distribution of each *Diorhabda* species across biomes (B) (Proc Freq; SAS Institute 2005) from native presence-only field collection data for the *Diorhabda elongata* species group at 5 minute grid resolution. Percentage of a species in a biome is number of collections for that species in the biome divided by the number of collections of that species across all biomes. See Figure 51 for explanation of box plots. Sample sizes of field localities (N) and a table summary statistics and plotted values are inset in each chart.



FIGURES 53–54. Biomic dissimilarity dendrograms based on biomic Bray-Curtis dissimilarity matrices. 53—*Diorhabda elongata* species group (from Table 10), 54—both the *D. elongata* group and *Tamarix* species invasive in North America (from Table 12). Dendrograms produced with NTSYSpc Tree plot module (Rohlf 2006) from clusters formed with unweighted arithmetic average clustering (UPGMA) (NTSYSpc SAHN module). Line connecting *D. elongata* and *T. gallica* at left signifies that the positions of these taxa are interchangeable in an alternate dendrogram of equal r_{coph} value.

Baum 1978, Zieliński 1994), and other *Tamarix* spp. probably serve as hosts of *D. meridionalis* in these areas (Maps 5 and 6). *Tamarix aphylla* is common in southern Iran and southern Pakistan (Browicz 1991) where it might serve as a host for *D. meridionalis*.

At the time of collection of *D. meridionalis* in an oasis of small saline marshes at Sekand, Iran, Hoberlandt (1981) recorded as present the annual herb *Frankenia pulverulenta* Linnaeus (of the order Tamaricales with *Tamarix*) but not *Tamarix*. *Frankenia pulverulenta* is indigenous to the southern Palearctic

region and southern Africa (Jäger 1992), and it sometimes grows in association with *Tamarix* in north Africa (Kassas and Imam 1954), southern Europe (Cano *et al.* 2004), and probably also in Iran. It is unlikely that this herbaceous *Frankenia* would serve as a host of *D. meridionalis*, but in future surveys for *D. meridionalis* in the region, *F. pulverulenta* should be surveyed in order to rule it out as a host.

Diorhabda meridionalis and *D. carinata* have been collected together in series from five locations in western Iran and Syria, and they probably share some of the same host *Tamarix* spp. in a manner similar to *D. carinulata* and *D. carinata*.

Ecology and Phenology. Collection dates in Iran and Pakistan for *D. meridionalis* from examined material and collections records of Berti and Rapilly (1973) are from 31 March through 10 October.

Natural Enemies. We found no reports of natural enemies of *D. meridionalis*.

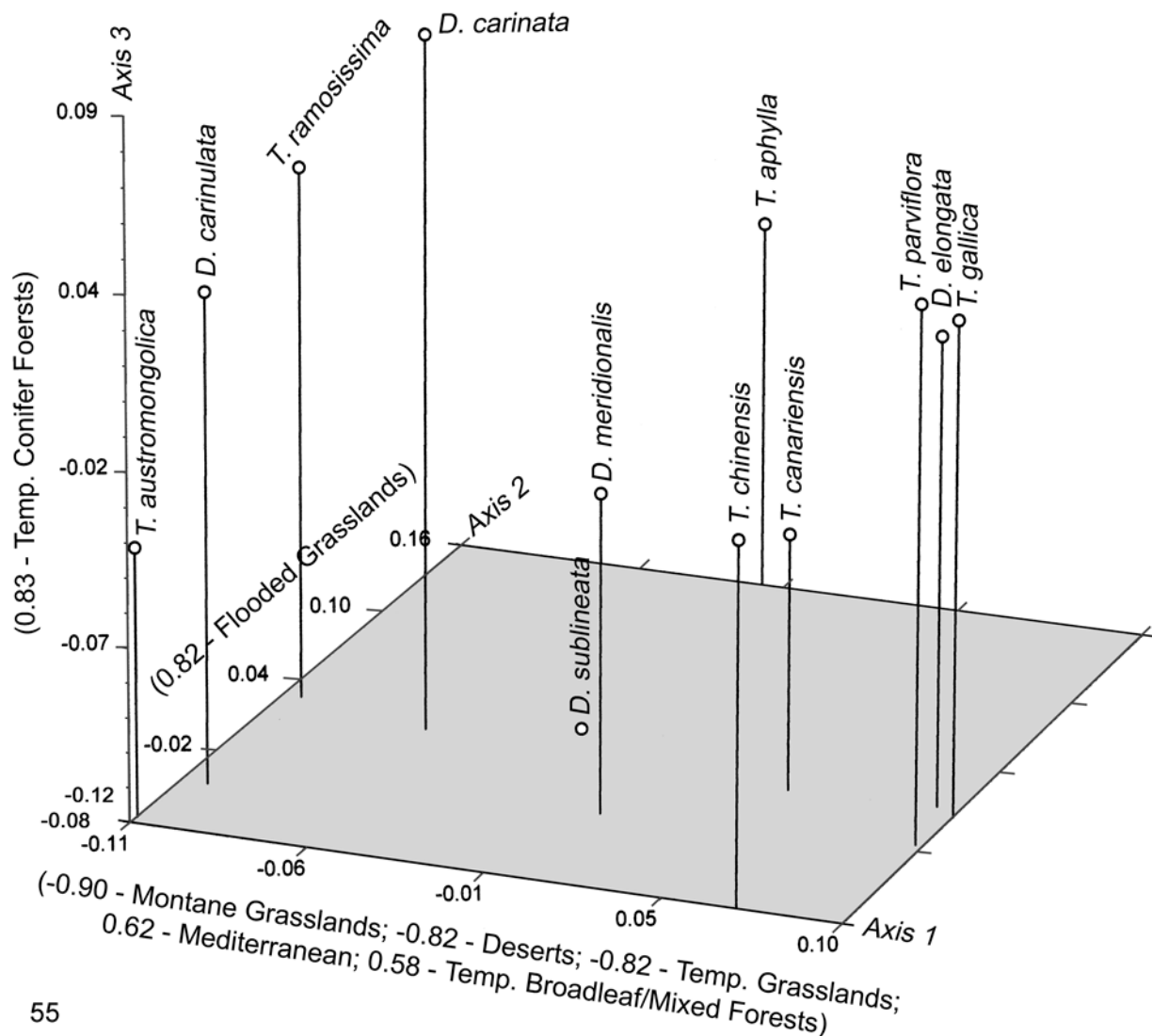
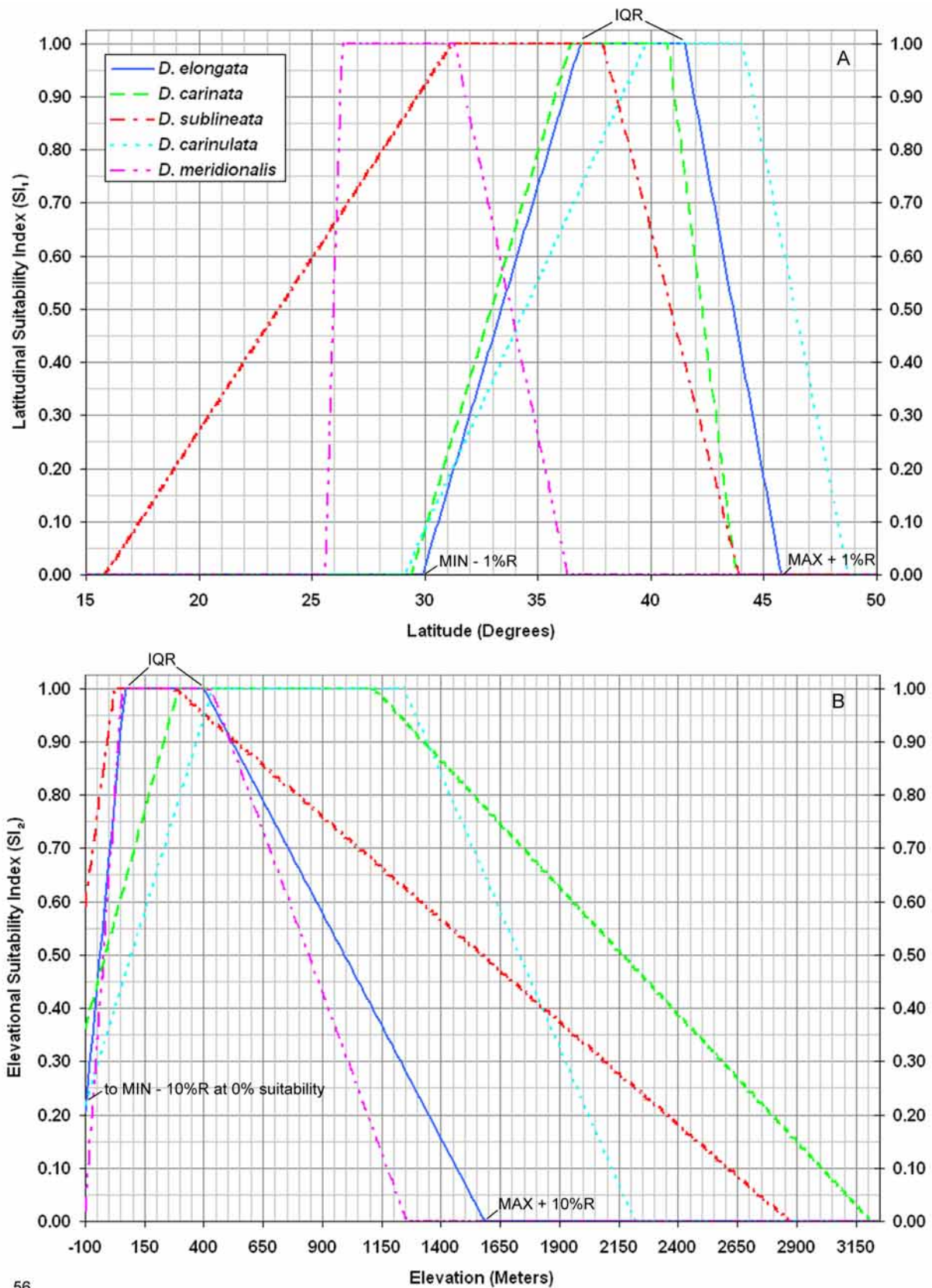
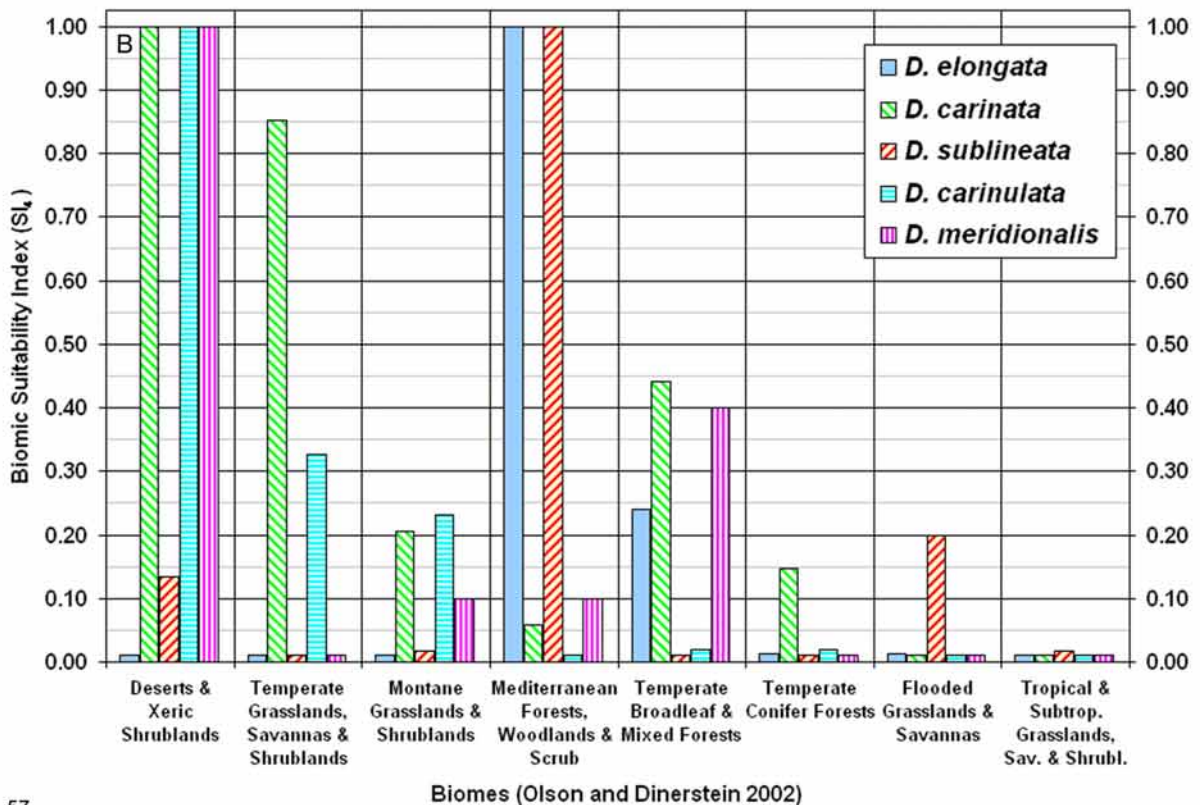
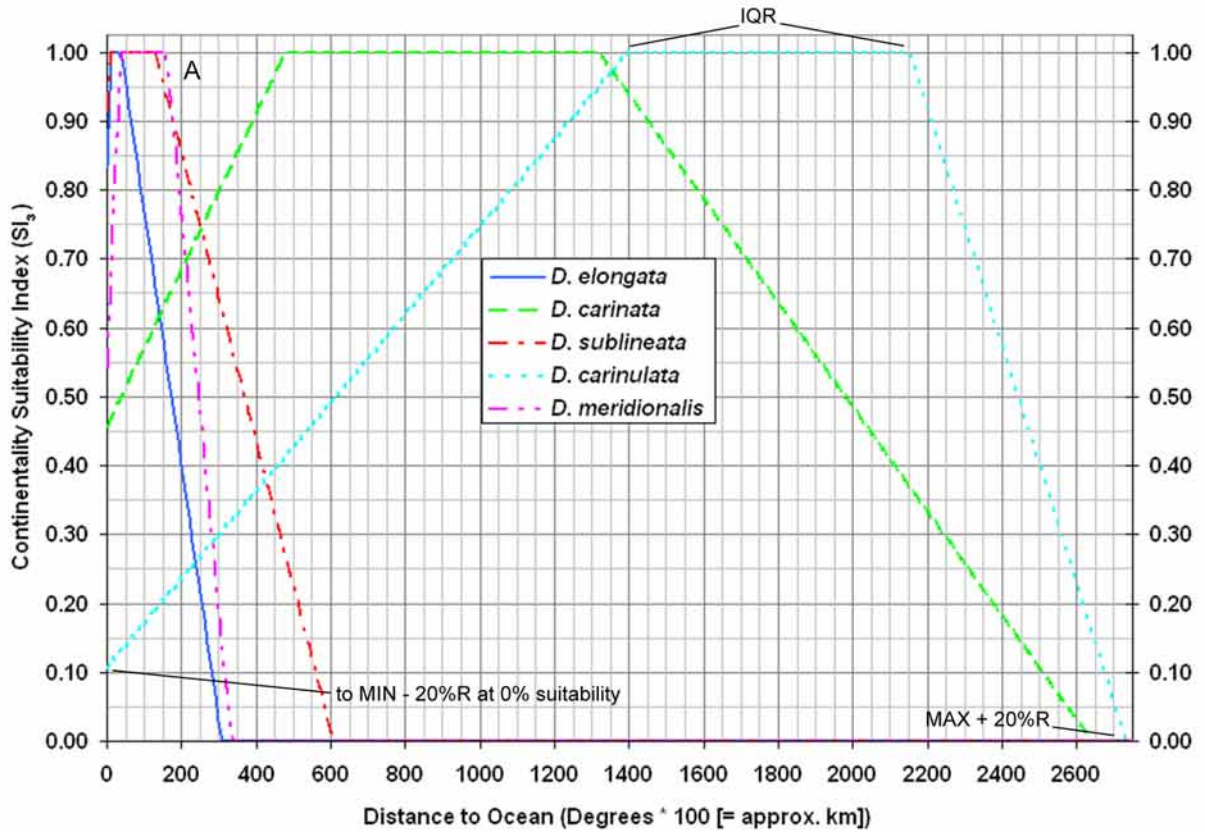


FIGURE 55. Three dimensional biomic principal coordinate analysis (PCoA) scatter plot for the *Diorhabda elongata* species group and *Tamarix* spp. invasive in North America for the first three eigenvectors (cumulative axis loading of 80.92%; Table 13) computed from a biomic Bray-Curtis dissimilarity matrix (Table 12). Biomes in which ranks of species are statistically significantly positively or negatively correlated with ranks of species in each PCoA axis are indicated in parentheses (see Table 13). Plotted with Mod3D module of NTSYSpc (Rohlf 2006).



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FIGURE 56. Linear models for latitudinal (A) and elevational (B) habitat suitability indices for the *Diorhabda elongata* species group. Model parameters calculated from descriptive statistics (Fig. 51), including interquartile range (IQR), minimum (MIN) value minus 1% or 10% of range (R), and maximum value (MAX) plus 1% or 10% of range (labeled for *D. elongata*).



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FIGURE 57. Linear and categorical models for continentality (A) and biomic (B) habitat suitability indices for the *Diorhabda elongata* species group. Model parameters calculated from descriptive statistics (Fig. 52), including interquartile range (IQR), minimum (MIN) value minus 20% of range (R), and maximum value (MAX) plus 20% of range (labeled in A for *D. carinulata*).

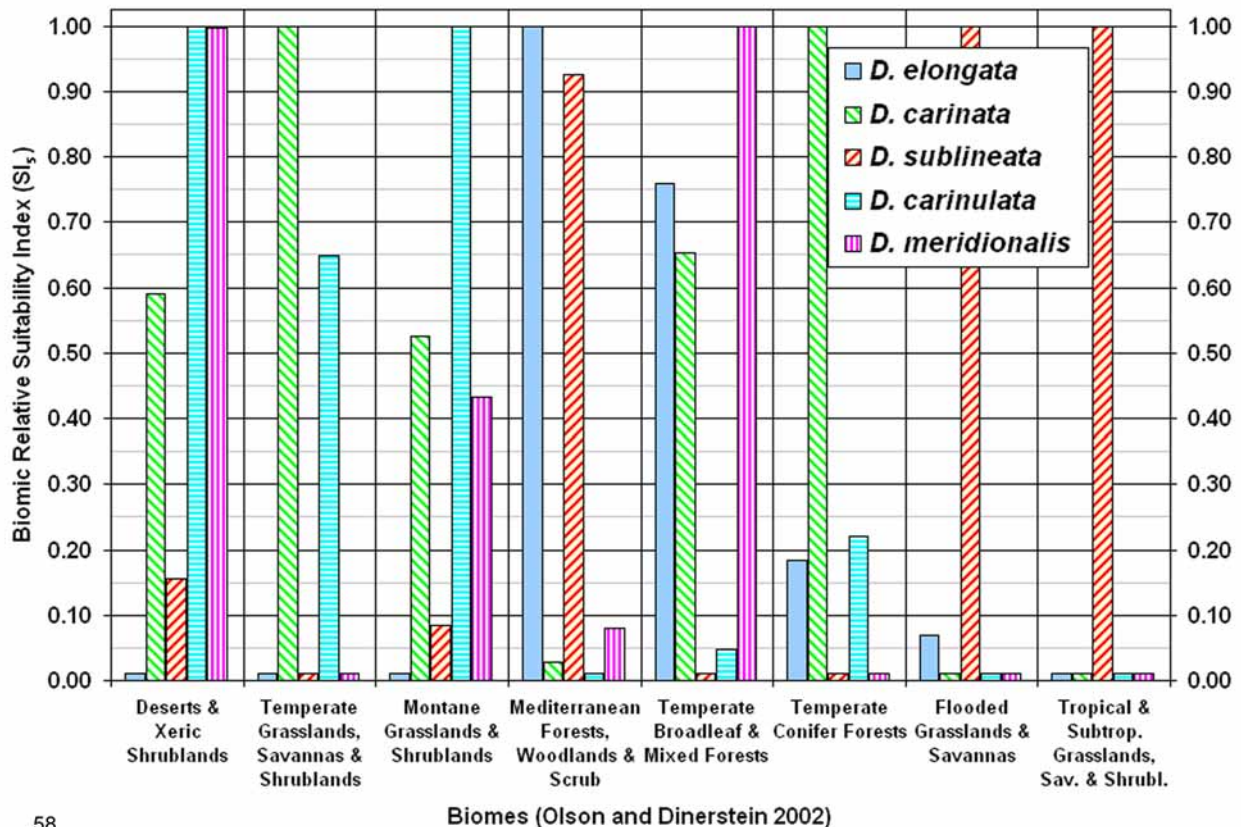
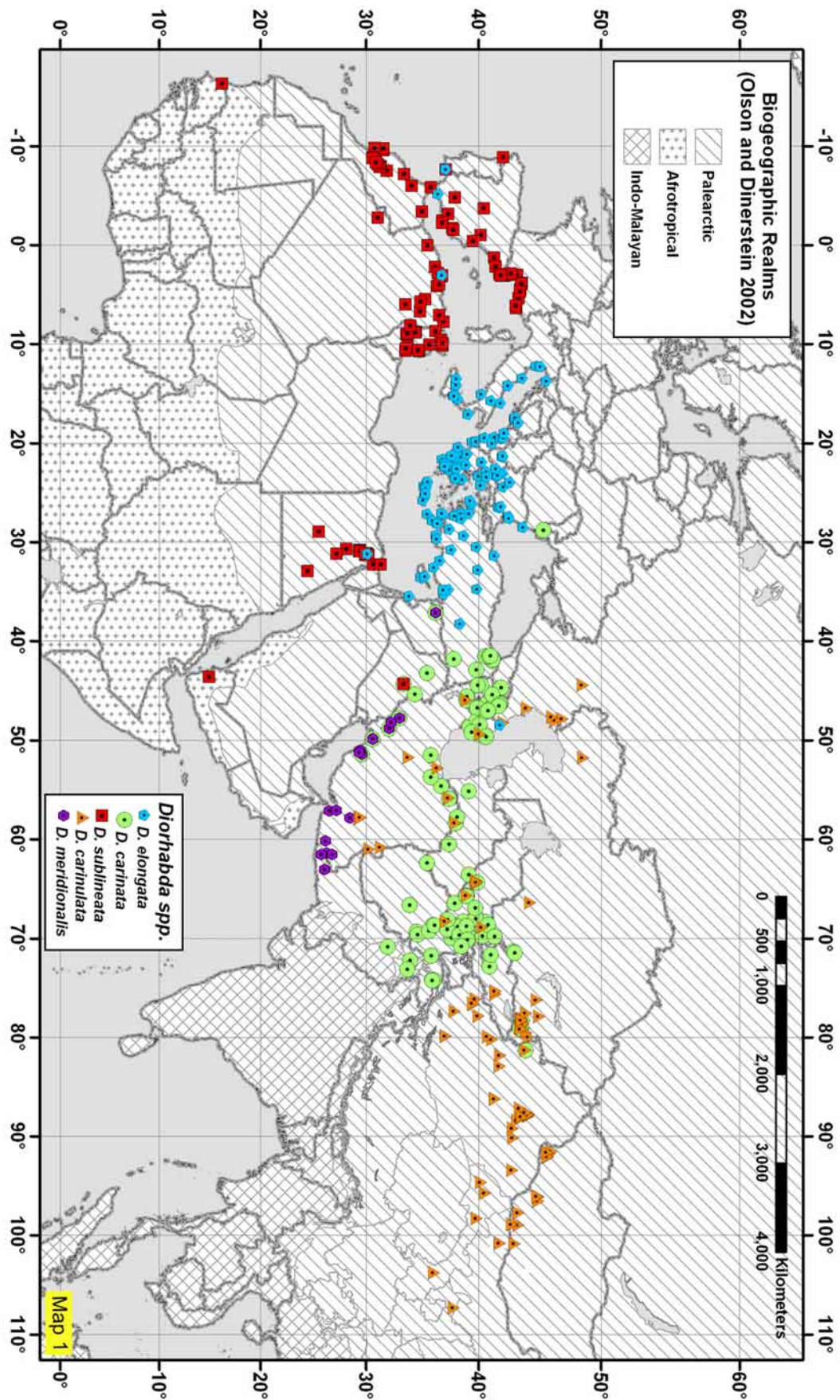


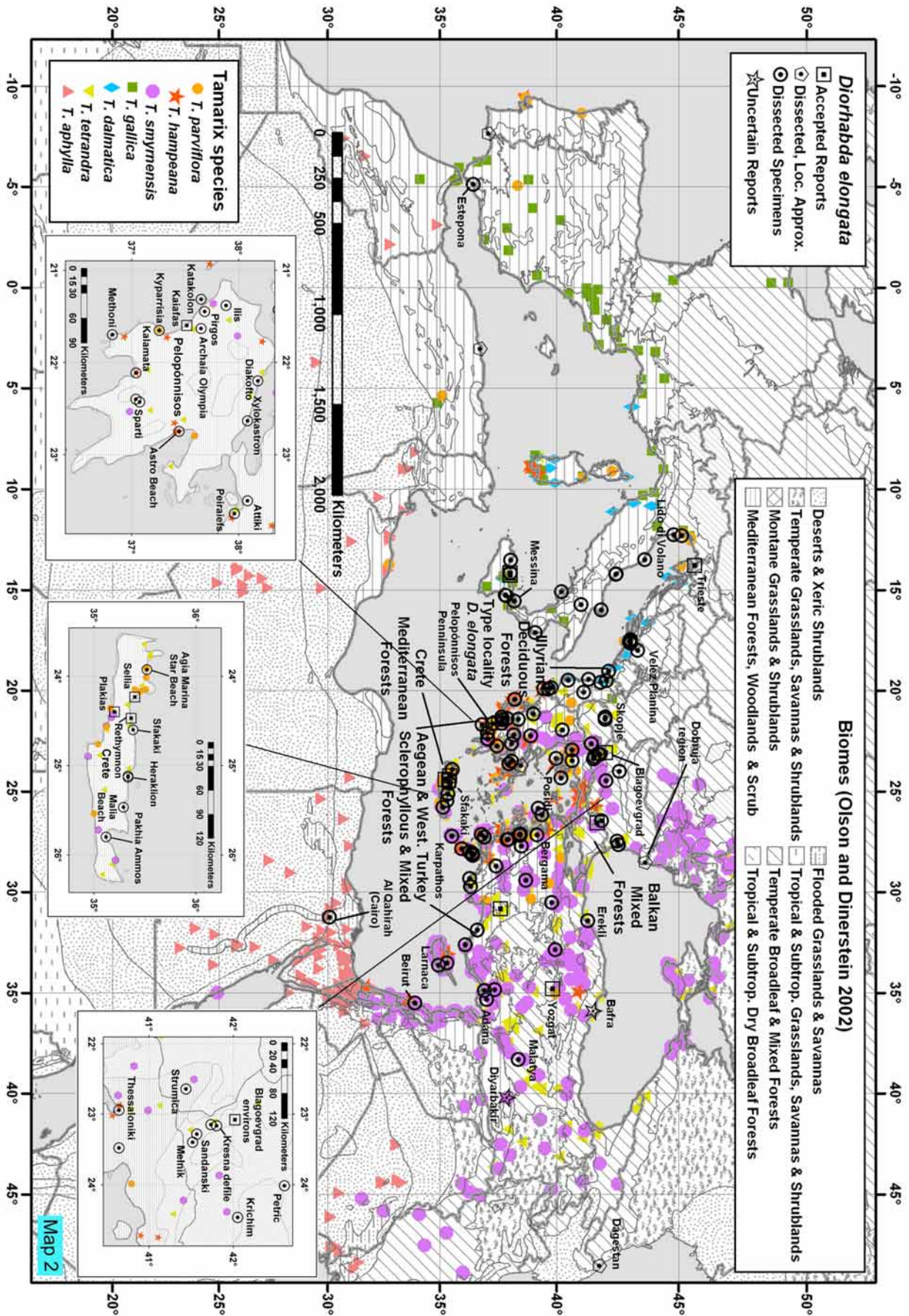
FIGURE 58. Categorical model for biomic relative suitability indices for the *Diorhabda elongata* species group. Model parameters calculated from descriptive statistics (Fig. 52B).

Biogeography. *Comparative.* *Diorhabda meridionalis* differs from other tamarisk beetles by the following combination of biogeographic characteristics: (1) primarily maritime and found within 300 km of the ocean at elevations usually under 600 m (ranges to 1,100 m); (2) usually found in subtropical desert and temperate broadleaf and mixed forest biomes; and (3) latitudinal range of 26–36°N and most common at 26–31°N. *Diorhabda meridionalis* is partially sympatric with *D. carinata*, their ranges overlapping in western Iran and Syria where they appear to be syntopic (see above discussion under *D. carinata*—**Biogeography**) (Maps 1 and 6; Table 8). *Diorhabda meridionalis* is parapatric with *D. carinulata* in southern Iran (Map 6). *Diorhabda meridionalis* is most similar to the species pair *D. carinata*/*D. carinulata* in terms of biomes inhabited (Tables 9 and 10, Fig. 53). Both *D. carinata* and *D. carinulata* differ from *D. meridionalis* in being primarily continental in distribution and more common north of 31°N. *Diorhabda meridionalis* is allopatric with *D. elongata* and *D. sublineata* (Map 1, Table 8). *Diorhabda elongata* and *D. sublineata* differ from *D. meridionalis* in their greater preference of the Mediterranean biome and their commonness north of 31°N. Further collections might reveal that *D. meridionalis* and *D. sublineata* are parapatric or marginally sympatric in the eastern Saudi Arabian peninsula.

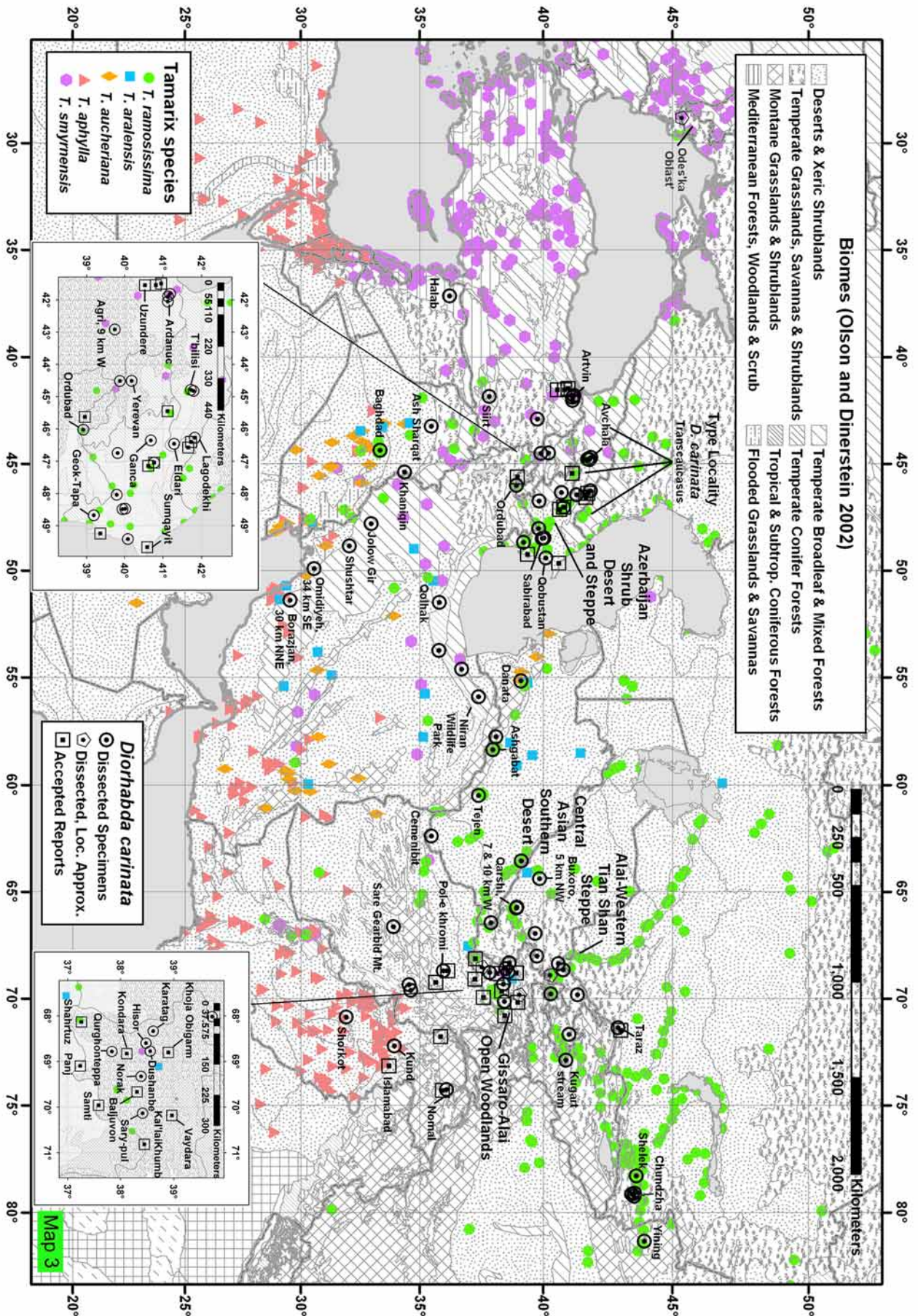
Descriptive. *Diorhabda meridionalis* is a south central Palearctic species that may also occur at the northern tip of the Afrotropical realm in the United Arab Emirates (Map 1). It is most commonly collected from 26–31°N in the Deserts and Xeric Shrublands biome of southern Iran in the South Iran Nubo-Sindian Desert and Semi-Desert ecoregion (20–390 m) (Map 6). According to the biogeographic classification of Morrone (2002), more than half of this ecoregion falls within the northwestern tip of the Oriental region (= Indo-Malayan realm of Olson and Dinerstein [2002]) which is part of the Holotropical kingdom. But we follow Olson and Dinerstein (2002), whose placement of the western border of the Indo-Malayan and Palearctic realms near the border of Pakistan and India (Map 1) is supported by borders of the corresponding



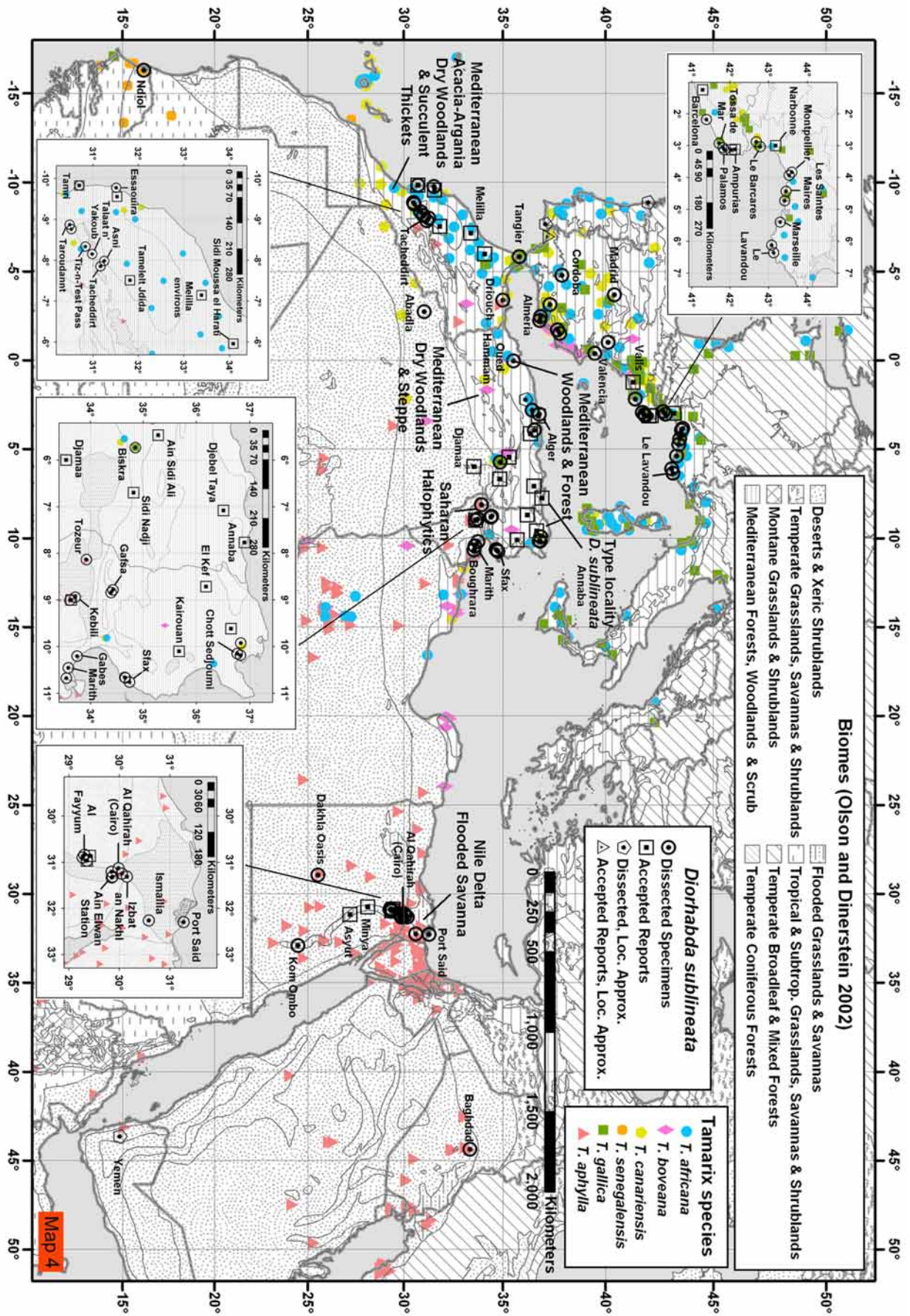
MAP 1. Native distribution of the *Diorhabda elongata* species group. Some symbols for *Diorhabda* spp. overlap and some locations are approximate (see Maps 2–5).



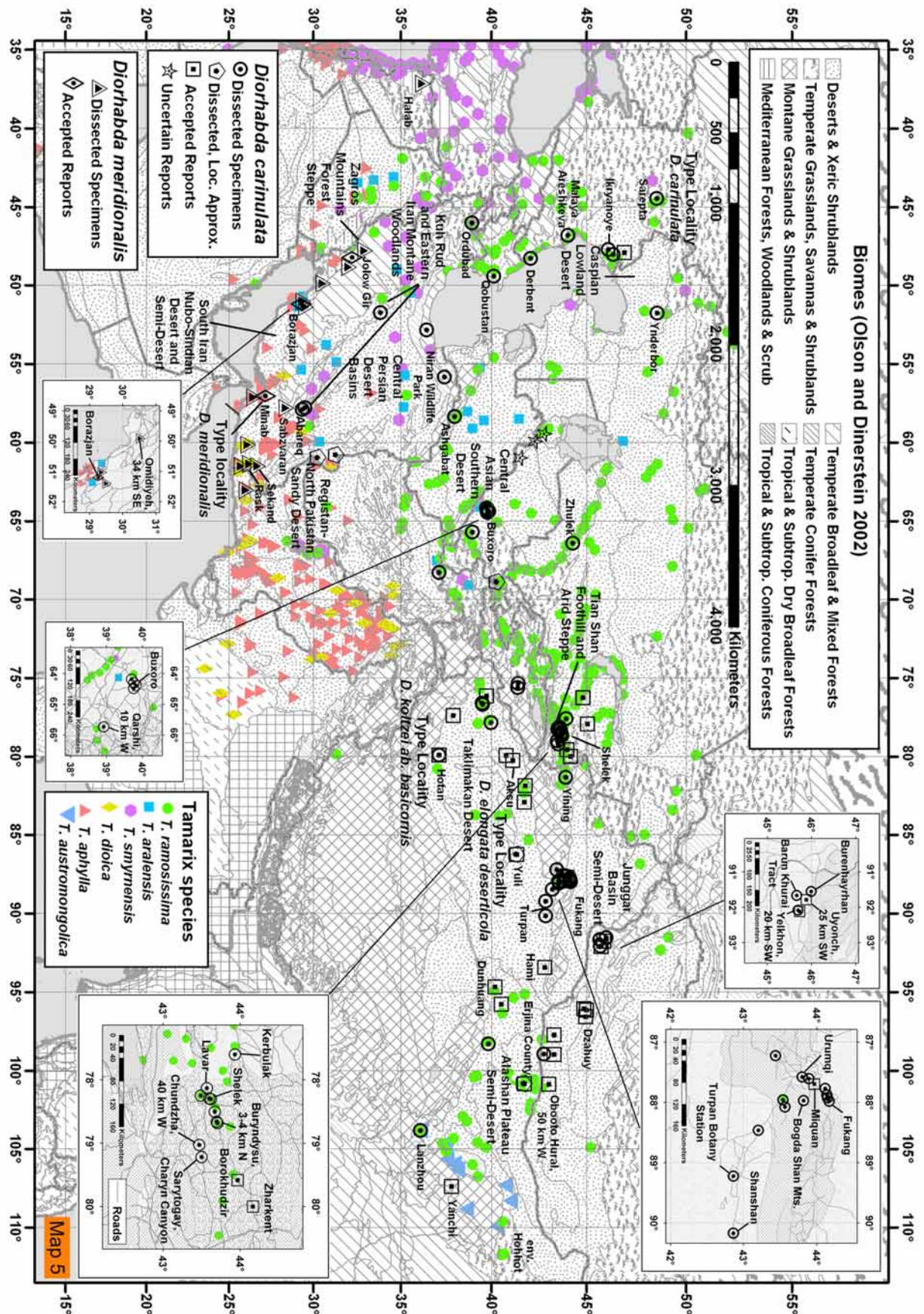
MAP 2. Native distribution of *Diorhabda elongata* with occurrences of selected *Tamarix* spp.



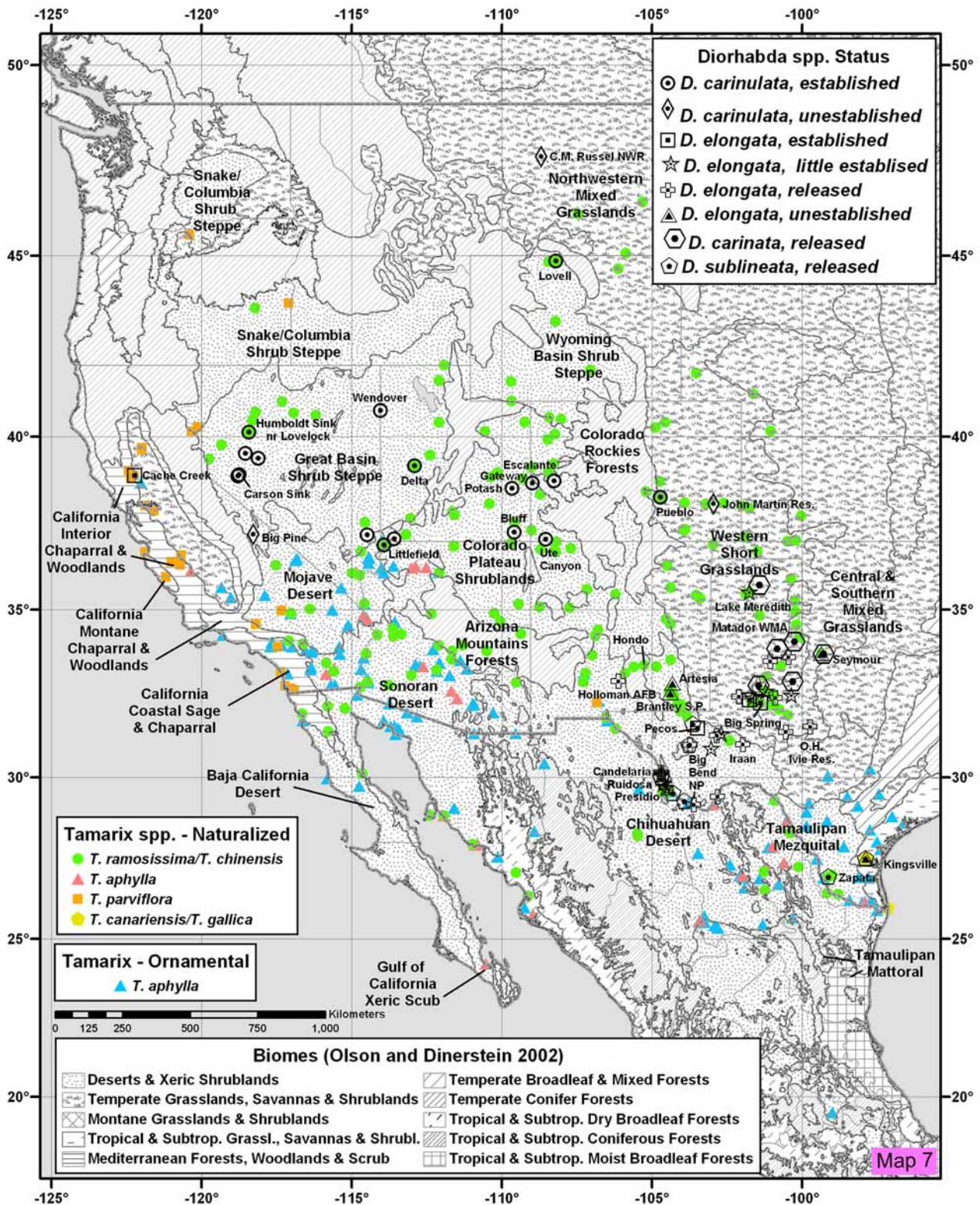
MAP 3. Native distribution of *Diorhabda carinata* with occurrences of selected *Tamarix* spp.



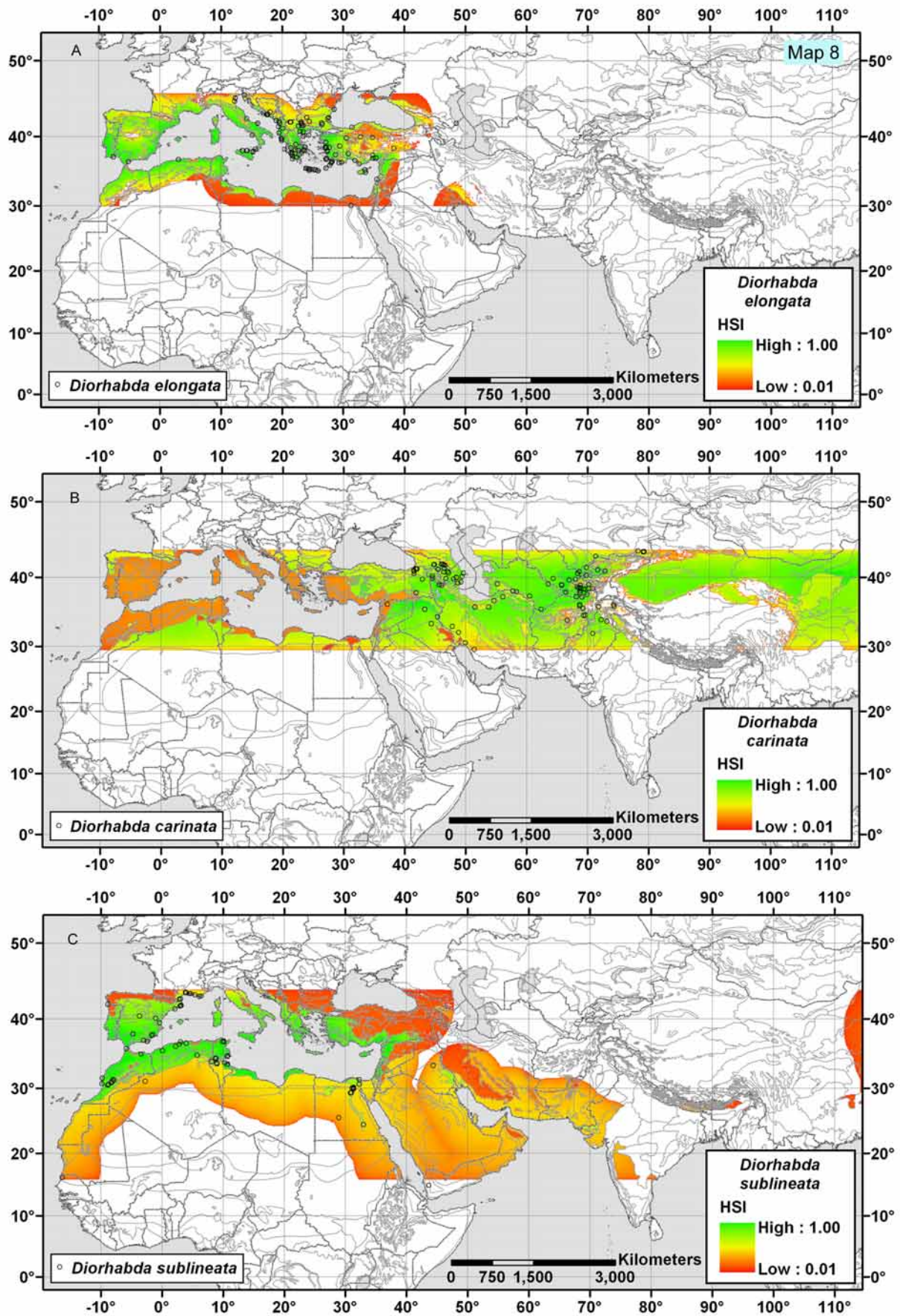
MAP 4. Native distribution of *Diorhabda sublineata* with occurrences of selected *Tamarix* spp.



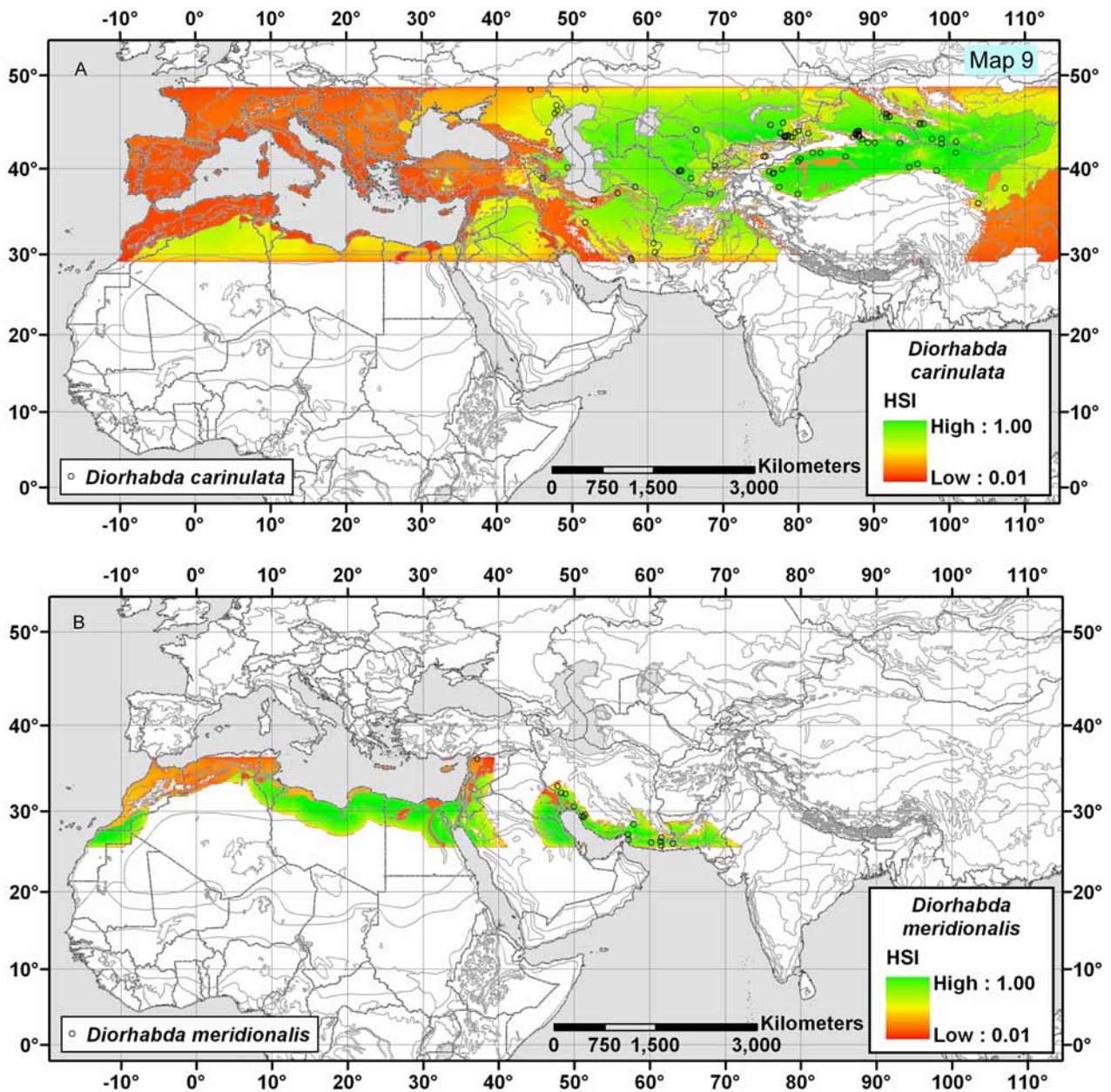
MAP 5. Native distribution of *Diorhabda carinulata* and *D. meridionalis* with occurrences of selected *Tamarix* spp.



MAP 7. Distribution of the *Diorhabda elongata* species group where introduced in North America with occurrences of selected *Tamarix* spp. Some symbols for *Diorhabda* and *Tamarix* spp. overlap.

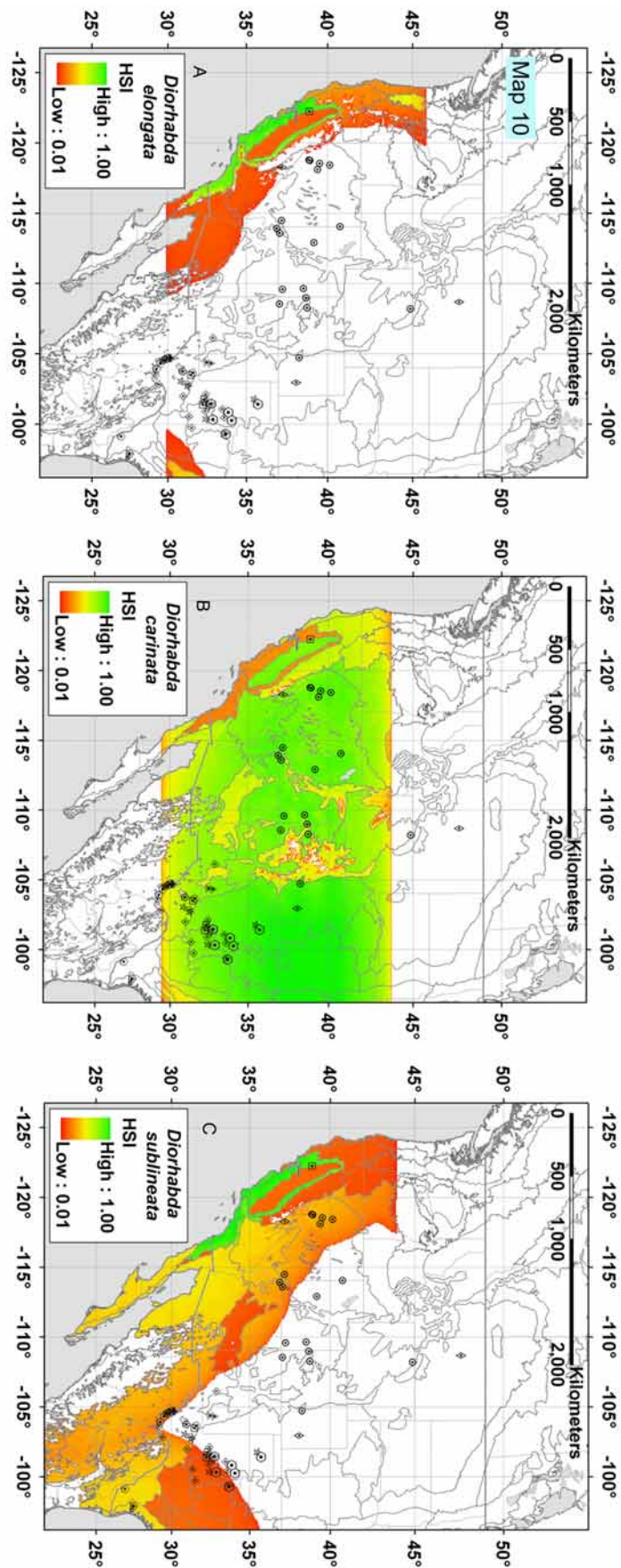


MAP 8. Hand-fitted habitat suitability index (HSI) models for the *Diorhabda elongata* species group over their native distribution: A—*Diorhabda elongata*, B—*D. carinata*, C—*D. sublineata*.

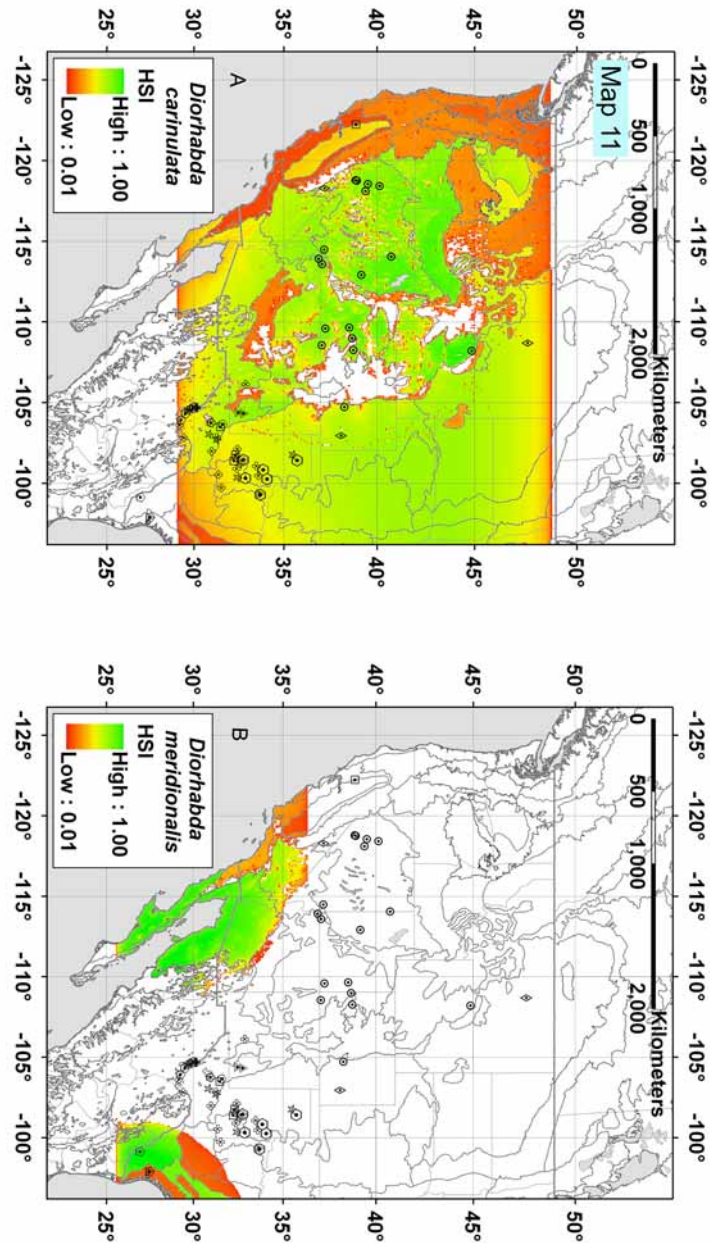


MAP 9. Hand-fitted habitat suitability index (HSI) models for the *Diorhabda elongata* species group over their native distribution: A—*Diorhabda carinulata*, B—*D. meridionalis*.

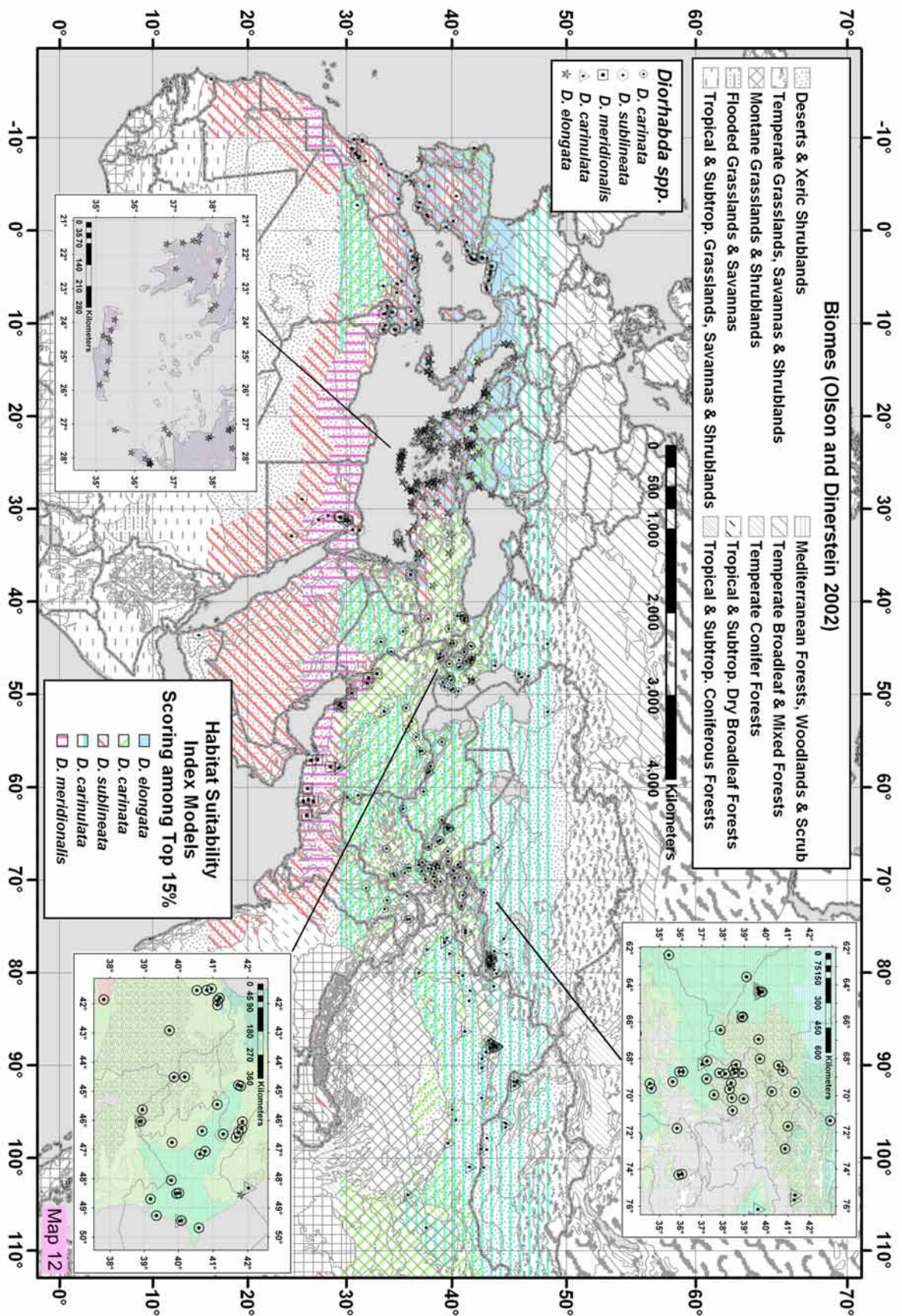
faunistic kingdoms of Bobrov (1997). The distribution of *D. meridionalis* in the South Iran Nubo-Sindian Desert and Semi-Desert ecoregion corresponds to the western distribution of the suspected host *T. dioica*, and further surveys might reveal more overlap between *D. meridionalis* further east and north along the distribution of *T. dioica* in Pakistan and India (Map 5). Habitats of collection sites for *D. meridionalis* in southern Iran are primarily river banks, but also include saline marshes, coastal savannas, clay semi-deserts, and weedy fields (Hoberlandt 1981, 1983). *Diorhabda meridionalis* is also found in the Mediterranean Forests, Woodlands and Scrub biome in Syria (36°N, ca. 380 m), the Temperate Broadleaf and Mixed Forests biome of western Iran (29°N; ca. 60–500 m) and the Montane Grasslands and Shrublands of southern Iran (27°N) to ca. 1,102 m elevation at Sekand (Table 9). Most collection sites are within 100 km of the sea, the maximum distance being 309 km at Jolow Gir, Iran (Table 7; Map 5).



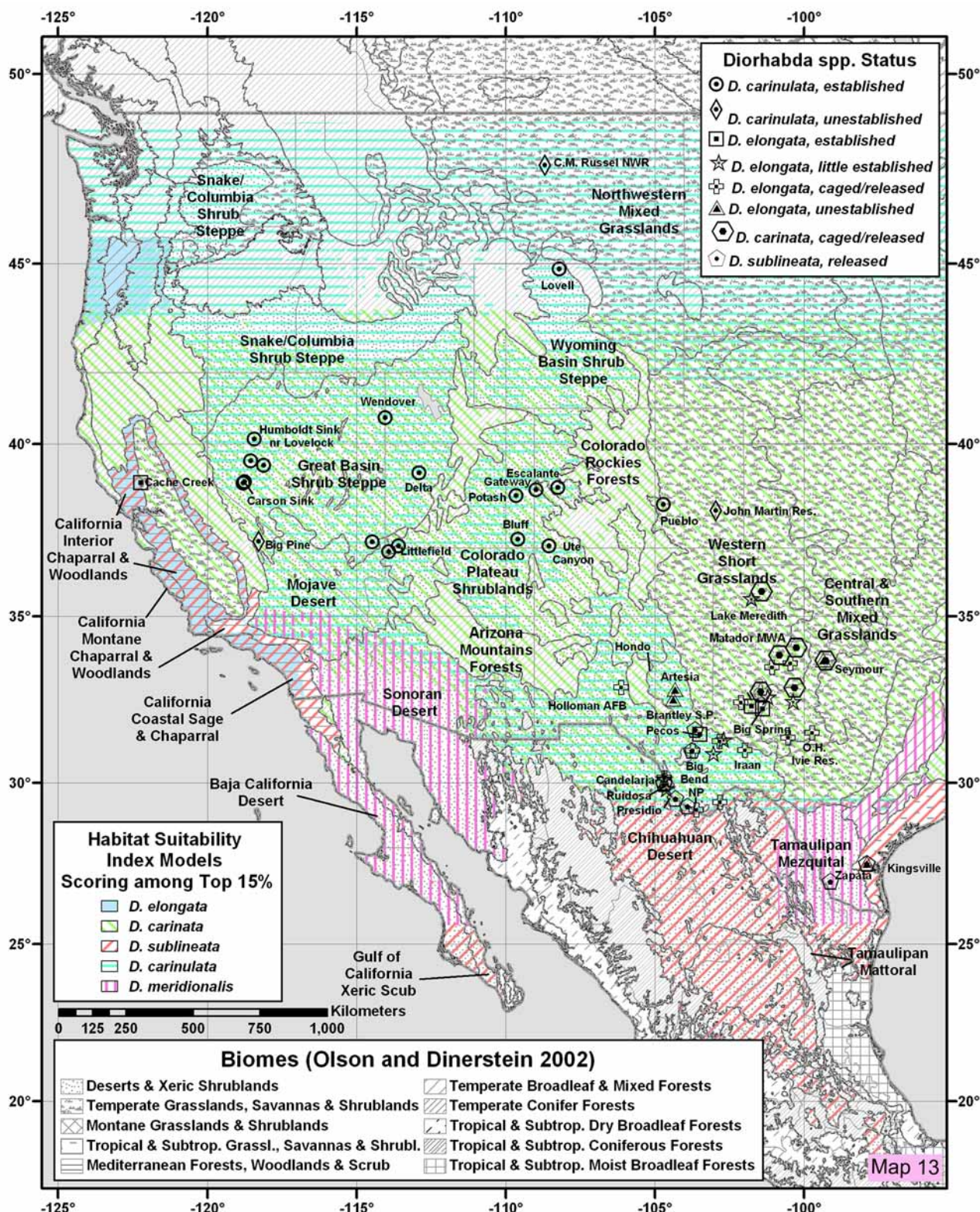
MAP 10. Hand-fitted habitat suitability index (HSI) models for the *Diorhabda elongata* species group over western North America: A—*Diorhabda elongata*, B—*D. carinata*, C—*D. sublineata* (See Maps 7 or 13 for legend of symbols for sites of *Diorhabda* establishment, release, or planned release).



MAP 11. Hand-fitted habitat suitability index (HSI) models for the *Diorhabda elongata* species group over western North America: A—*Diorhabda carinulata*, B—*D. meridionalis* (See Maps 7 or 13 for legend of symbols for sites of *Diorhabda* establishment, release, or planned release).



MAP 12. Composite map of habitat suitability index (HSI) models scoring among the top 15% among the *Diorhabda elongata* species group over their native distribution. The composite map depicts the estimated most suitable *Diorhabda* species or group of species for a given area, not the total potential range for any given species. Some symbols for *Diorhabda* spp. overlap and some locations are approximate (see Maps 2–5).



MAP 13. Composite map of habitat suitability index (HSI) models scoring among the top 15% among the *Diorhabda elongata* species group over North America. The composite maps depict the estimated most suitable *Diorhabda* species or group of species for a given area, not the total potential range for any given species. Some symbols for *Diorhabda* spp. overlap.

Potential in Tamarisk Biological Control. Summary. The southern tamarisk beetle may potentially be the best suited *Diorhabda* species for biological control of tamarisk in portions of maritime subtropical deserts such as the Sonoran Desert and Tamaulipan Mezquital (Map 13). Overseas collections of *D. meridionalis* may

be obtained from the South Iran Nubo-Sindian Desert and Semi-Desert in southern Iran and southwest Pakistan (Map 6). The preference of *D. meridionalis* for *T. ramosissima*/*T. chinensis* versus *T. aphylla* will probably be a critical issue for host range testing. In addition, the potential effects of *D. meridionalis* on *Frankenia* spp. are not known.

Discussion. We find no reports of damage to tamarisk by the southern tamarisk beetle. This species can be abundant in areas such as Rask, Iran from which we examined a large series of at least 159 beetles collected in 1973 by the Czechoslovak-Iranian entomological expedition in an area where Hoberlandt (1981) recorded the presence of *T. dioica*. *Diorhabda meridionalis* probably attacks several *Tamarix* spp., as do other species in the *D. elongata* group, and it may also attack *Tamarix* introduced into North America. Host range studies are needed to verify that *D. meridionalis* is restricted in host range to *Tamarix* spp. and determine its preference for various *Tamarix* spp. introduced into North America. The Palearctic annual herb *Frankenia pulverulenta*, a close relative of *Tamarix* found at a collection site with *D. meridionalis* in Iran (see above), should be included in host range studies. *Frankenia pulverulenta* is naturalized in the U.S. states of Utah and Oregon (Welsh *et al.* 1987, USDA Natural Resources Conservation Service 2008).

Maritime subtropical Deserts and Xeric Shrublands from 26–31°N may be most suitable for *D. meridionalis* in North America (Maps 5–6). Suitable North American ecoregions include the southern Sonoran Desert, the eastern Tamaulipan Mezquital, the Baja California Desert, and the Gulf of California Xeric Scrub (Map 13).

Implications Regarding Biological Control of Tamarisk

Our study illustrates that basic research into the taxonomy and biogeography of potential biological control agents can be essential to timely and effective implementation of weed biological control programs. Below is an outline of our major conclusions as they relate to biological control of tamarisk.

1) Five morphologically diagnosable sibling species of the *Diorhabda elongata* species group are specialized feeders upon *Tamarix*. Four of these species, previously classified as *D. elongata*, have been released into the open field in the United States: *D. carinulata*, *D. elongata*, *D. carinata*, and *D. sublineata*. *Diorhabda carinulata* and *D. elongata* are confirmed as established in the U.S. *Diorhabda meridionalis* has yet to be cultured for study in the U.S.

- a) As distinct species, members of the *D. elongata* group are strongly reproductively isolated and would interbreed rarely, if at all, in the open field whether in the Palearctic or North America.
- b) Laboratory or cage produced interspecific hybrids of these species probably all experience varying degrees of hybrid breakdown which would probably lead to poor persistence in the open field and render them unsuitable in tamarisk biological control, especially in comparison to parental pure lines. However, the degree of breakdown in backcross hybrids may be lower than in hybrid/hybrid crosses and has yet to be studied.

2) Each of the five species of the *D. elongata* group has unique biogeographic characteristics in the Old World, even those species occurring in partial sympatry. These differences are probably related to innate biological characteristics of these species that would probably also lead to unique distributional patterns in the New World.

- a) Each member of the *D. elongata* group is probably uniquely suited to different ecoregions of the North American tamarisk invasion.
- b) *Diorhabda carinulata*, *D. carinata*, *D. sublineata* and *D. meridionalis* all appear to be better suited to differing desert and grassland ecoregions of southwestern North America than is *D. elongata*, primarily a species of the maritime Mediterranean biome. Efforts are needed to establish both *D. carinata* and *D.*

sublineata at various sites in west Texas in order to compare their efficacy in controlling tamarisk with that of *D. elongata*.

3) Previous host range testing demonstrates that *D. carinata* and *D. sublineata* (both recently introduced into the open field in Texas) are just as safe in terms of risks to non-target plants of *Tamarix aphylla* and *Frankenia* species as are the species *D. carinulata* and *D. elongata*.

4) Southern climatotypes of *D. carinata* and *D. carinulata* from southwest Asia may be better pre-adapted to latitudes from ca. 30–34°N in North America than current northern climatotypes of these species in the U.S.

5) Based upon its native distribution, *Diorhabda meridionalis* warrants host-range testing as a potential tamarisk biological control agent that may be the best suited tamarisk beetle to subtropical maritime desert ecoregions of North America.

The morphological and distributional evidence for reproductive isolation between the five species of the *D. elongata* group, including the lack of intermediate hybrid morphologies in nature, has been thoroughly discussed previously in this revision under the species accounts. Our Habitat Suitability Index (HSI) model for the *D. elongata* group in North America depicts how each of the five tamarisk beetles appear to be uniquely suited to different tamarisk infested ecoregions of western North America (Map 13). The HSI model estimates *D. elongata* as best suited to the Mediterranean biome of northern California, and four other *Diorhabda* species as better suited than *D. elongata* to grassland and desert biomes across the southwest (Map 13).

The wide range of geographic areas occupied by the *D. elongata* species group provides great potential not only for interspecific variation in biogeographical traits, but also for intraspecific variability in critical traits such as climatic adaptation and *Tamarix* host preferences (Maps 1 and 8). Intraspecific genetic variants may take the form of climatotypes and *Tamarix* host ecotypes. Climatotypes can differ in synchrony of seasonal changes in physiology and behavior with environmental cues such as daylength and temperature. Geographic (allopatric and parapatric) climatotypes are known among several insect species (Leather *et al.* 1993, Shapiro 1995, Singer *et al.* 1995) and sympatric climatotypes, in the form of voltinism ecotypes, among at least one species (McLeod *et al.* 1979, Coates *et al.* 2004). Bean and Keller (in prep) found evidence for climatotypes in intraspecific populations of *Diorhabda carinulata* (as *D. e. deserticola*) from Fukang and Turpan, China which differ in the critical photoperiod for diapause induction. In chrysomelids, Hsiao (1978) has reported intraspecific geographic host ecotypes and Ikonen *et al.* (2003) has reported sympatric host ecotypes. The value of intraspecific genetic variability found in differing “strains” of biological control agents has been challenged, mainly regarding biological control agents of insects (Clarke and Walter 1995), and more research is needed. But, selection of ecotypes can be critical in successful biological control, because not all populations may carry the genetic variation for desired traits (Zwölfer and Preiss 1983, Zwölfer and Harris 1984, Luck *et al.* 1995, Goolsby *et al.* 2006). Established climatotypes may gradually adapt to wider areas within the biogeographic range of the species as appears to be happening with the northern climatotype of *D. carinulata* which may have potential to establish further south in eastern New Mexico. Tamarisk beetle climatotypes that are mismatched to the area of introduction may establish more slowly, or not at all. A climatic mismatch may have contributed to delayed establishment of *D. elongata* introduced from the warm climates of coastal Crete into northern California. For tamarisk beetle species with native distributions over large latitudinal/climatic gradients, such as *D. carinata* and *D. carinulata*, collecting, host range testing and introducing two or three putative climatotypes from throughout the latitudinal/climatic range of each species might increase or speed establishment success at corresponding tamarisk habitats in North America.

A northern climatotype of *D. carinulata* from northwest China and Kazakhstan has defoliated large acreages of tamarisk and is showing potential for substantial tamarisk suppression in the continental temperate cold deserts of the western U.S. Introduction of a southern climatotype of northern tamarisk beetles

from Iran and Pakistan (Map 6) might facilitate more rapid and complete range expansion into its potential range in the southern half of the Colorado Plateau Shrublands, western portions of the Mojave Desert, the Trans-Pecos Chihuahuan Desert, and southwestern Western Short Grasslands (Map 13).

Diorhabda elongata from Greece shows excellent promise in defoliating *T. chinensis* × *T. canariensis*/*T. gallica* in the Western Short Grasslands of west Texas and *T. parviflora* in the California Interior Chaparral and Woodlands of California. The biomic profile of *D. elongata* best matches *T. parviflora* and *T. gallica* among invasive North American tamarisks. Mediterranean tamarisk beetles may be best suited to maritime temperate warm Mediterranean ecoregions in central and northern California where *T. parviflora* is primarily invasive (Maps 7, 9).

Southern climatypes of *D. carinulata* and *D. carinata* and the species *D. meridionalis* and *D. sublineata* are probably best suited to desert and grassland ecoregions of the southwestern U.S. and could probably replace *D. elongata* where it becomes established in these ecoregions. The biomic profiles of *D. carinulata* and *D. carinata* most closely match that of the target weed *T. ramosissima*. The northern Qarshi climatype of *D. carinata* is probably most suitable to warm temperate grasslands of western Kansas and eastern Colorado. Introduction of a southern climatype of *D. carinata* from Iraq, eastern Iran or central Pakistan (Map 6) might facilitate more rapid and complete range expansion of this species from 31–37°N in deserts and grasslands such as southern portion of the Western Short Grasslands and Central and Southern Mixed Grasslands, the southern portion of the Colorado Plateau Shrublands, the Trans-Pecos Chihuahuan Desert, and northern portions of the Mojave Desert, (Map 13). *Diorhabda sublineata* is probably the best suited tamarisk beetle for several Mediterranean and maritime subtropical desert areas of various ecoregions, including the California Coastal Sage and Chaparral, southern portions of the Chihuahuan, Mojave and Sonoran deserts, and Tamaulipan Mezquital (Map 13). *Diorhabda meridionalis* (not yet cultured) from southwest Asia is a maritime subtropical desert species that may be uniquely adapted to parts of the Sonoran Desert and Tamaulipan Mezquital (Map 13). If *D. sublineata* does not establish well in portions of the Sonoran deserts in extreme southern California and the Tamaulipan Mezquital in south Texas, investigation into the possibility of introducing *D. meridionalis* into these areas might be warranted. Firmly establishing *D. carinata* and *D. sublineata* in the field, and possibly acquiring *D. meridionalis* and southern climatypes of *D. carinulata* and *D. carinata* for testing and introduction, could expand and speed the success of tamarisk biological control across the southwestern U.S.

Interspecific differences in biogeographic preferences of these species are probably not solely the result of variation in synchronization of diapause induction with local photoperiodic and climatic conditions (climatic traits which can also widely vary intraspecifically), but are also likely to be related to differences in adaptation to regional variation in a number of climatic variables, including temperature, relative humidity, and precipitation. Introduction of tamarisk beetle species at North American locations to which they are biogeographically mismatched may result in failed or poor establishment with population crashes or eventual extinction under climatic extremes to which the species are ill-adapted. The poor establishment of *D. elongata* in the northwestern Chihuahuan Desert near Artesia, New Mexico, may be an example of a biogeographic mismatch, as the Mediterranean tamarisk beetle is not known from deserts in its native habitat. Species distribution models (SDMs) can be useful tools in estimating potential ranges of biological control agents of weeds in non-native areas (McFayden 1991). SDMs based on the presence-only locality data from this revision and incorporating a variety of global climatic geographic information system data (e.g., Elith *et al.* 2006) could be used to estimate potential differences in North American distribution of these tamarisk beetles.

Studies in field cages are in progress to evaluate diapause characteristics, voltinism, and overwintering survival across several latitudinal gradients in the western U.S. for populations of *D. elongata* (from Posidi Beach and Sfakaki, Greece), *D. carinulata* (from Fukang and Turpan, China), *D. sublineata* (from near Sfax, Tunisia), and *D. carinata* (from near Qarshi, Uzbekistan) (Peter Dalin and Tom Dudley, University of California, Santa Barbara, CA, pers. comm.). Results from these field studies should be compared to those of species distribution models. At present, laboratory and field studies lack access to populations of *D. meridionalis* and putative southern climatypes of *D. carinulata* and *D. carinata*.

Host range safety testing was conducted for each differing tamarisk beetle population/species prior to release (DeLoach *et al.* 2003b; Lewis *et al.* 2003a; Milbrath and DeLoach 2006a, 2006b; Milbrath *et al.* 2007; Herr *et al.* 2006, in prep.). All four tested tamarisk beetle species (*D. carinulata*, *D. elongata*, *D. carinata* and *D. sublineata*) represent very low risk of damaging North American *Frankenia* spp. (Lewis *et al.* 2003a; Dudley and Kazmer 2005; Milbrath and DeLoach 2006a; Dudley *et al.* 2006; Herr *et al.* 2006, in prep.) and a moderate risk of damaging *T. aphylla* (DeLoach *et al.* 2003b, Milbrath and DeLoach 2006b). Several *Frankenia* species are indigenous throughout the Palearctic (Jäger 1992) and overlap in distribution with the *D. elongata* group where they can also be found together in the same habitat as *Tamarix* (Kassas and Imam 1954). However, no *Frankenia* spp. are recorded hosts of *Diorhabda* in the Palearctic (Table 1). Surveys of *Frankenia* spp. and *Tamarix* spp. in Tunisia by our cooperators R. Sobhian and A. Kirk (USDA-ARS European Biological Control Laboratory [EBCL], Montferrier-sur-Lez, France) revealed *D. sublineata* only on *Tamarix* (DeLoach *et al.* 2003b). *Frankenia* appears only to serve as a factitious, artificial laboratory host, but not a natural host for the four studied species of tamarisk beetles. High populations of tamarisk beetles in the early stages of biological control may pose a transitory risk in damaging leaves of *Frankenia* growing in proximity to tamarisk (see Dudley and Kazmer 2005). The ornamental *T. aphylla* is generally less preferred for oviposition over other *Tamarix* in field cage preference studies of the four species of tamarisk beetles (DeLoach *et al.* 2003b; Milbrath and DeLoach 2006a, 2006b). *Diorhabda elongata* clearly prefers *T. ramosissima*/*T. chinensis* over *T. aphylla* for oviposition in the open field at Big Spring, Texas (Herr *et al.* 2006, Moran *et al.* in press). However, *T. aphylla* is accepted equally well as *T. ramosissima* × *T. chinensis* in no-choice tests of three species of tamarisk beetles (Milbrath and DeLoach 2006b). *Tamarix aphylla* is uncommonly reported as a native host of any tamarisk beetle (Table 1), and we expect that any damage to *T. aphylla* from the four tested tamarisk beetles will be uncommon compared to damage on other tested invasive deciduous *Tamarix* spp. The recent recognition of *T. aphylla* as an invasive tree in part of the southwestern U.S. (Walker *et al.* 2006) should weigh against concerns over possible damage to *T. aphylla* from tamarisk beetles. Only the southern extremes of the indigenous ranges of *D. carinulata* and *D. elongata* overlap with the distribution of *T. aphylla* in the Palearctic realm. We expect that the ranges of *D. elongata* and *D. carinulata* would also rarely come into contact with *T. aphylla* in North America. The benefits of tamarisk biological control with tamarisk beetles outweigh the above described risks to nontarget plants and other environmental risks (DeLoach 1990, DeLoach *et al.* 2000, Dudley *et al.* 2000).

Additional field studies from both native and introduced habitats should provide better understanding of interspecific differences in *Tamarix* host preferences among the *D. elongata* group. Studies across the range of each species of tamarisk beetle also may reveal intraspecific variations in *Tamarix* preferences. *Diorhabda carinulata* is best known in terms of field host preferences. It reportedly prefers *T. ramosissima* over much of its northern and eastern range in Asia, but the *Tamarix* spp. preferred in its southern and western range are unknown. *Diorhabda carinulata* appears to have a fairly broad host range within the genus *Tamarix*, as evidenced by its feeding on a novel host, *T. parviflora*, in Nevada, but *T. ramosissima* is attacked more than *T. parviflora* (Dudley *et al.* 2006). *Diorhabda elongata* is predictably beginning to defoliate one of its natural hosts, *T. parviflora*, in California. *Diorhabda elongata* attacks *T. smyrnensis*, a close relative of *T. ramosissima*, and *T. gallica*, which may account for its successful adaptation to *T. chinensis* × *T. canariensis*/*T. gallica* in west Texas. *Diorhabda carinata* is common on *T. arceuthoides* and *T. hispida* in Tajikistan and it occurs on *T. ramosissima* among several other *Tamarix* spp. in central Asia, but its field host preferences are unknown. Hosts of *D. sublineata* include *T. gallica*, which comprises part of the *T. canariensis*/*T. gallica* complex that commonly hybridizes with *T. ramosissima*/*T. chinensis* in Texas. Very little is known of the *Tamarix* hosts of *D. meridionalis*.

Multiple agents targeting a weed can improve the efficacy of biological control, especially where agents of differing habitat/climatic adaptations are needed and attack of multiple plant parts (e.g., roots and foliage) is achieved. These benefits must be weighed against additional risks to non-target plants (in this case *Frankenia* spp. and *T. aphylla*) and possibly deleterious competitive interactions of the agents (Denoth *et al.* 2002). Potentially counter-productive indirect competition between multiple weed biological control agents

has been observed in several programs, such as between two weevil species used in biological control of the exotic biennial weed musk thistle, *Carduus nutans* Linnaeus (Milbrath and Nechols 2004a, 2004b). On the other hand, many examples are known of multiple agents being successfully used together in biological control over the long term, especially against perennial weeds (Blossey and Hunt-Joshi 2003). Several species of root-mining *Aphthona* spp. flea beetles (Chrysomelidae: Galerucinae) with differing habitat preferences are being successfully used in biological control of exotic leafy spurge, *Euphorbia esula* Linnaeus, in North America (Gassmann *et al.* 1996, Nowierski *et al.* 2002). The syntopic closely related chrysomelids *Galerucella californiensis* (Linnaeus) and *G. pusilla* (Duftschmidt) appear to be equal in their competitiveness and are fully complementary in their biological control of purple loosestrife, *Lythrum salicaria* Linnaeus, in North America (Blossey 1995).

Potential competitive interactions among species of the *D. elongata* group are yet to be studied, but would probably be limited to species occupying similar biogeographic ranges. Biogeographic relationships found among species of tamarisk beetles in their native range (Table 8) would probably also apply to their ranges in North America. The sympatric and syntopic species pairs of *D. carinata*/*D. carinulata* and *D. carinata*/*D. meridionalis* might also be syntopic over partially sympatric ranges in North America. In differing areas of the Old World, one member of these partially sympatric species pairs appears to be generally more abundant than the other. Near Ashgabat, Turkmenistan, *D. carinata* successfully defoliates tamarisk at Dry Sport Lake in the presence of smaller syntopic populations of *D. carinulata*. Likewise, near Shelek, Kazakhstan, *D. carinulata* defoliates tamarisk in the presence of smaller syntopic populations of *D. carinata*. In North America, the efficacy of tamarisk biological control would probably not be reduced where both species of these sympatric/syntopic species pairs are present. *Diorhabda carinulata* and *D. sublineata* are allopatric in their native range and probably would also be allopatric in North America. Species pairs that are parapatric or marginally sympatric in the Old World (Table 8) might compete where their ranges contact in North America, but areas of range contact are likely to be small as a result of interspecific differences in biogeographic traits. Marginally sympatric species pairs in the Palearctic with potential for range contact in North America include *D. elongata*/*D. carinulata*, *D. elongata*/*D. sublineata*, *D. elongata*/*D. carinata*, and *D. sublineata*/*D. carinata*. In the small areas of range contact between these potentially competitive species, one species is likely to predominate with probably no reduction in efficacy for tamarisk biological control. This appears to be the case in the Old World where one of these species is generally dominant in the area of marginal sympatry with another species (Map 1, Table 8). Studies are in progress to evaluate potential competitive interactions between *D. elongata* and *D. carinulata* in field cages in New Mexico (D. C. Thompson, pers. comm.).

Several species of tamarisk beetles hybridize readily in the laboratory, producing hybrids with varying levels of reduced egg viability in their progeny. However, the lack of detected morphological hybrid forms in the Old World provides no evidence that different tamarisk beetles hybridize in nature. Differing mate recognition systems appear to prevent or severely reduce field hybridization of tamarisk beetle species. Uncommon instances of interspecific hybridization with the production of fertile hybrids might occur among different tamarisk beetles in areas of sympatry. Laboratory hybridization of *D. carinulata* and *D. carinata* leads to severely reduced hybrid F1 and F2 egg viabilities and high mortality in copulo for matings of *D. carinata* males and *D. carinulata* females. However, these two species inhabit the same tamarisk trees in parts of central Asia with no apparent interference from hybridization in defoliating tamarisk, either for *D. carinata* in Ashgabat, Turkmenistan, or for *D. carinulata* in Chilik, Kazakhstan. Consequently, these two species should be able to similarly coexist without interference in North America and the same probably applies to all members of the *D. elongata* group. The production of uncommon fertile hybrids in nature is seen in some animal species (Mallet 2005), but Helbig *et al.* (2000) point out the lack of any known cases of complete breakdown in reproductive isolation between any animal species. Recently, evidence of hybrid speciation, a potential means of adaptive radiation when populations invade new environments (Seehausen 2004), has been found among closely related insects (Salazar *et al.* 2005, Schwarz *et al.* 2005, Mavárez *et al.* 2006), but the frequency and occurrence of hybrid speciation among different insects is poorly known.

Differing interspecific biogeographic preferences may be a critical factor in determining where each type of tamarisk beetle can establish in North America. Synchronization of diapause to daylength and temperature in response to variations in latitude and altitude has been a major focus in exploring factors affecting establishment success of *Diorhabda* in North America. However, biogeographic adaptations to variation in bioclimatic conditions across biomes at a given latitude and altitude, such as between desert riparian habitat and Mediterranean riparian habitat, are probably just as important in influencing establishment success. Nowierski *et al.* (2002) found that prior knowledge of the habitat preferences of *Aphthona* spp. flea beetles could have prevented delays in successful biological control of leafy spurge that resulted from trying to establish certain *Aphthona* species in non-suitable habitats in North America. Optimal matching of different tamarisk beetles to North American locations should involve both biogeographic matching at the species level and climatic matching within each species. Within the biogeographic range of each species of tamarisk beetle, intraspecific climatypes are probably adapted to differing daylength/climatic regimes. Introduction of southern climatypes of *D. carinulata* and *D. carinata* from 30–34°N in southwest Asia (Map 6) might speed establishment of these species at corresponding latitudes in biogeographically suitable areas of the southwestern U.S (Map 13). At some sites in southwestern U.S., potentially several species of *Diorhabda* might be able to establish (Map 13), but probably one species is the best biogeographically suited and would establish more vigorously, reach greater population levels over time, and produce more rapid defoliation of tamarisk. For example, the maritime Mediterranean species *D. elongata* is established at several sites in the Trans-Pecos Chihuahuan Desert in west Texas, but our HSI models predict that the desert/grassland species *D. carinata* or *D. carinulata* would perform better at these sites. These HSI models are only a first rough approximation at predicting which species may perform best at any given location and our detailed distribution data should now be used to make further ecogeographic analyses using species distribution models with climatic data. Such models could both speed the process and enhance the prospects of matching appropriate tamarisk beetle species/climatype combinations to specific regions of the North American tamarisk invasion.

Biological control has permanently reduced populations of many target weeds below the economic thresholds justifying use of expensive chemical and mechanical controls (DeLoach 1997, Gould and DeLoach 2002). Biological control ideally should be pursued as the cornerstone of modern integrated pest management programs (IPM) with the aim of reducing the need for chemical controls (O'Neil *et al.* 2003), and not considered primarily as only a follow up treatment to other controls. Integration of biological and chemical controls is appropriate in some weed management situations, but chemical controls can interfere with successful biological control (Ainsworth 2003) while providing less effective control in the long run than would biological control alone (e.g., Larson *et al.* 2007). Chemical control of tamarisk is extensively and aggressively being pursued in the U.S., especially in Texas and New Mexico. In California, Nevada, Utah, Wyoming, Colorado and Texas, tamarisk biological control with *D. carinulata* and *D. elongata* is showing good potential for gradually (over several years) producing sustained reductions in tamarisk stands to levels below the need for chemical control and with no harm to native vegetation. Additional efforts are needed to compare in the field the efficacy of *D. carinata* and *D. sublineata* against *D. elongata* as tamarisk biological control agents in southwestern deserts. More widespread demonstration of the effectiveness, ecological benefits, and low cost of tamarisk biological control in the southwestern U.S. is essential in order for biological control to be recognized as a primary management alternative to chemical control of tamarisk. The geographic extent, rapidity, and effectiveness of tamarisk biological control across the Southwest can potentially benefit from wider utilization of the biogeographic diversity and uniqueness of all five species of tamarisk beetles.

Opportunities for Further Research

Throughout this monograph, we refer to several studies in progress and suggest several areas for further study which we summarize below:

Category	Research Task	Researchers with Potential Interest
Biological Control	Compare efficacy (ease of establishment and rapidity of spread and control of tamarisk) of <i>D. elongata</i> , <i>D. carinata</i> , and <i>D. sublineata</i> in deserts and grasslands of southwestern North America	Mark Muegge, Allen Knutson, Dave Thompson, Tom Dudley
Taxonomy	Search for external diagnostic characters in <i>D. elongata</i> group	Dave Thompson, Jessica Perez, James Tracy
	Analyze external morphometrics of <i>D. elongata</i> group	Joaquin Sanabria, James Tracy
	Characterize three dimensional morphology of inflated endophalli obtained from freshly killed mating pairs in the <i>D. elongata</i> group	
	Search for taxonomically diagnostic characters at both species and genus level in male endophallic sclerites, female vaginal palpi, and interanal sternite VIII among <i>Diorhabda</i> and related genera	
Hybridization	Publish crossing studies of <i>D. elongata</i> group (Thompson <i>et al.</i> in prep.), and cross additional species, especially <i>D. sublineata</i> and <i>D. carinata</i>	Dave Thompson, Dan Bean, Julie Keller, James Tracy, Jack DeLoach
	Publish studies of mitochondrial and nuclear DNA in <i>D. elongata</i> , <i>D. carinata</i> , <i>D. sublineata</i> , and <i>D. carinulata</i> .	Dave Kazmer
	Use genetic and morphological techniques to look for potential hybrids in field population where species potentially interface, such as between <i>D. sublineata</i> and <i>D. elongata</i> in western Italy	
Biogeography	Publish bioclimatic models to species distributions.	James Tracy
	Better determine species distribution of <i>D. elongata</i> group in potential interspecific interface areas such as in western Italy and central Turkey	
Biology	Publish data on critical photoperiod for <i>D. elongata</i> , <i>D. carinata</i> and <i>D. sublineata</i> (Bean and Keller in prep.)	Dan Bean and Ray Carruthers (in prep.)
	Publish field data comparing host suitability (Dalin <i>et al.</i> in press) and site adaptability between <i>D. carinulata</i> , <i>D. elongata</i> , and <i>D. carinata</i>	Peter Dalin, Tom Dudley, Dave Thompson
	Confirm pheromones for <i>D. elongata</i> , <i>D. carinata</i> , and <i>D. sublineata</i> with field testing	Allard Cossé, Tom Dudley
	Publish field data and models for seasonal dispersal and defoliation by <i>D. elongata</i>	Jack DeLoach and Joaquin Sanabria
	Determine native species of <i>Tamarix</i> serving as hosts for <i>D. meridionalis</i>	
	Perform host range testing for <i>D. meridionalis</i>	
	Obtain southern climatotypes of <i>D. carinulata</i> from around 31°N in Pakistan or Iran and compare critical daylength with northern populations	Dan Bean

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