

A NEW PREVIOUSLY PREDICTED LARVAL HOST FOR THE ASIAN SEED BEETLE *MEGABRUCHIDIUS TONKINEUS* (PIC, 1904), AND THE INCORPORATION OF *M. DORSALIS* (FÄHRAEUS, 1839) TO THE ARGENTINIAN FAUNA OF BRUCHINAE (COLEOPTERA: CHRYSOMELIDAE)

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Abstract. The Asian seed beetle *Megabruchidius tonkineus* (Coleoptera: Chrysomelidae: Bruchinae), erroneously identified as *Bruchidius endotubercularis*, was accidentally introduced in Argentina after 1993, discovered in 2002 in seeds of the exotic North American *Gleditsia triacanthos* (Caesalpiniaceae). At the same time, it was predicted that *Gleditsia amorphoides* (Caesalpiniaceae), a native plant from northern Argentina, would be adopted as a new larval host. The finding of *M. tonkineus* in seeds of *G. amorphoides* from north Argentina is confirmed here for the first time. New locality records, number of infested and reinfested pods, and viable seeds consumed by two generations of the Asian seed beetle in *G. amorphoides* are given. This native plant may be negatively affected by *M. tonkineus* due to the small size of its pods and the few number of seeds per pod. The incorporation of *Megabruchidius dorsalis* to the Argentinian fauna of Bruchinae in seeds of *G. triacanthos* is accomplished here also for the first time.

Key words: exotic Asian seed beetles, honey locust, South America.

Un nuevo hospedador larval anteriormente predicho para el escarabajo asiático de las semillas *Megabruchidius tonkineus* (Pic, 1904), y la incorporación de *M. dorsalis* (Fähræus, 1839) a la fauna argentina de Bruchinae (Coleoptera: Chrysomelidae)

Resumen. El escarabajo asiático de las semillas *Megabruchidius tonkineus* (Coleoptera: Chrysomelidae: Bruchinae), erróneamente identificado como *Bruchidius endotubercularis*, fue introducido accidentalmente en la Argentina después de 1993, y descubierto en 2002 en las semillas de la exótica *Gleditsia triacanthos* (Caesalpiniaceae) de América del Norte. Al mismo tiempo, se predijo que *Gleditsia amorphoides* (Caesalpiniaceae), una planta nativa del norte de la Argentina, sería adoptada como un nuevo hospedador. Se confirma aquí el hallazgo de *M. tonkineus* en semillas de *G. amorphoides* por primera vez y además se dan nuevos registros de localidades, la cantidad de legumbres infestadas y reinfestadas, y las semillas viables consumidas por dos generaciones del escarabajo asiático de las semillas en *G. amorphoides*. Esta planta nativa puede ser afectada negativamente por *M. tonkineus* debido al tamaño pequeño de sus legumbres y al bajo número de semillas por legumbre. Se establece también por primera vez la incorporación de *Megabruchidius dorsalis* a la fauna argentina de Bruchinae en semillas de *G. triacanthos*.

Palabras clave: escarabajos asiáticos de las semillas, América del Sur.

Introduction

Megabruchidius tonkineus (Pic, 1904) and *M. dorsalis* (Fähræus, 1839) (Coleoptera: Chrysomelidae: Bruchinae) are well established in several European countries, where they adopted the cultivated North American *Gleditsia triacanthos* L. (Caesalpiniaceae) and other cultivated exotic species of *Gleditsia* as new hosts (Table I). In its original ranges, they are specialized in seeds of related species of *Gleditsia* (fig. 1), except one Japanese species in a phylogenetically basal Fabaceae (Table I).

In his revision of the genus *Megabruchidius* in Europe, Yus Ramos (2009) established that *M. tonkineus* was the species present in South America, based on photographs of Argentinean and Chilean specimens sent by J.E. Barriga (Chile, Curicó). At the same time, *Bruchidius endotubercularis* Arora, 1980 was located in synonymy of *M. dorsalis*, based on a comparison between the original description and figures of Arora (1980) and specimens of *M. dorsalis* from Viet Nam. Later Fritzsche & Delobel (2012) revalidated the name *B. endotubercularis*, giving the differences with *M. dorsalis*, also comparing the original description and figures of Arora (1980) with specimens of *M. dorsalis* from Taiwan.

The specimens obtained by Di Iorio (2005) in Argentina, wrong identified as to *B. endotubercularis*, proved to be

M. tonkineus (see materials and methods). This seed beetle was supposed to be able to adopt a new larval host during its dispersal and expansion in Argentina, in particular the native species *Gleditsia amorphoides* (Griseb.) Taub. (Caesalpiniaceae) in the north of the country, because the pods of this legume were compared in appearance and number of seeds to the pods of *Caesalpinia sappan* L. (Caesalpiniaceae) (Di Iorio, 2005). It is interpreted here that *M. tonkineus* may be the species that was regularly intercepted in United States in seeds of *C. sappan* from Viet Nam, based on a personal communication of John Kingsolver (Di Iorio, 2005), although a re-examination of these specimens are needed, and not that the true *B. endotubercularis* switched to a Caesalpiniaceae host by a third time: first to *C. sappan* in Viet Nam, second to *G. triacanthos* in Argentina, and third to *G. amorphoides* also in Argentina (see in Discussion the “Distribution and host plant of *Bruchidius endotubercularis*”). Thus, *C. sappan* may be a secondary host adopted by *M. tonkineus* in Viet Nam, that develops in seeds of *Gleditsia australis* Hemsl. in the same country (Table I).

The main scope of the present contribution is to communicate that *G. amorphoides* was effectively adopted by *M. tonkineus* as a new larval host in northern Argentina, and to

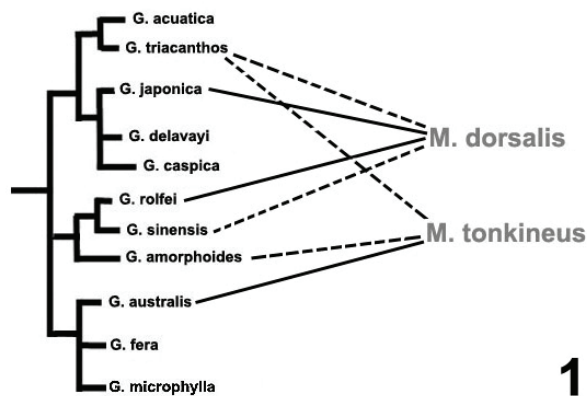


Figure 1. Phylogeny of the species of *Gleditsia* (based on Schnabel & Wendel, 1998), and the known hosts of *M. tonkineus* and *M. dorsalis* (see Table I). Broken lines indicate adopted hosts in countries where the species of *Megabruchidius* were introduced; entire lines indicate hosts in the original ranges of the species of *Megabruchidius* (except perhaps *G. rolfei*, whose country was not stated).

give in knowledge its effects on the seed survival of this plant, together with new locality records. A summary of *M. tonkineus* in South America after 2005 is provided. Also the presence of *M. dorsalis* in Argentina, simultaneously with *M. tonkineus* in the same pods of *G. triacanthos*, is communicated here for the first time.

Materials and methods

A total of 152 mature pods of three cultivated trees of *G. amorphoides* were collected on the trees or recently fallen to the ground in Tucumán, Argentina. An additional seven pods of the same plant were collected in the north of Chaco province (San Martín). The pods were maintained in rearing cages at ambient temperature and humidity at Buenos Aires city. Emergence holes of bruchid beetles per fruit were counted and marked with an indelible pencil before the emergence of the adult beetles of a second generation. After emergences of these last adults, the seeds of each fruit were manually extracted and counted. Three kinds of seeds were found in the pods of *G. amorphoides* from Tucumán: 1) viable seeds: normal size, with the tegument smooth; 2) wrinkled seeds: with the same size as viable seeds, but the integument is wrinkled (it is not known if these seeds are viable or not, but they were not previously seen in populations inside the natural distribution range of the plant); 3) dry seeds: smaller than viable seeds, flattened, with incomplete development, and the integument more strongly wrinkled. For statistic purposes, the wrinkled seeds were initially considered as non viable seeds.

The recognition of the damage to the fruits and seeds, and the characteristic emergence holes of *Lophopoeum timbouvae* Lameere, 1884 (Coleoptera: Cerambycidae), were described by Di Iorio (1995).

Identification of *Megabruchidius* species

The species of *Megabruchidius* were identified by the author with the key, redescrptions and illustrations given by Yus Ramos (2009), and by the differences between *B. endotubercularis* and *Megabruchidius* given by Fritzsche & Delobel (2012). Both species of *Megabruchidius* can be separated

(even at single view) by the hind tibiae with an apical spur slightly longer than half of the first tarsomere in *M. tonkineus*, or this spur is smaller, less than 1/3 of the length of the first tarsomere in *M. dorsalis* (Yus Ramos 2009). All specimens are located in the collection of the author [ODIC].

Abbreviations of the Argentinian provinces used in map

BA, Buenos Aires; **Ca**, Catamarca; **Cb**, Córdoba; **Ch**, Chaco; **CH**, Chubut; **Co**, Corrientes; **ER**, Entre Ríos; **Fo**, Formosa; **Ju**, Jujuy; **LP**, La Pampa; **LR**, La Rioja; **Me**, Mendoza; **Mi**, Misiones; **Ne**, Neuquén; **RN**, Río Negro; **Sa**, Salta; **SC**, Santa Cruz; **SF**, Santa Fe; **SE**, Santiago del Estero; **SL**, San Luis; **SJ**, San Juan; **TF**, Tierra del Fuego; **Tu**, Tucumán.

Results

Megabruchidius dorsalis (Fåhraeus, 1839)

Bruchidius endotubercularis, not Arora, 1980, in part (mixed with specimens of *M. tonkineus*): Di Iorio, 2005: 327-337 (distribution; host); György, 2007: 93 (distribution; host; reference); Tuda, 2008: 454 (reference); Yus Ramos, 2009: 372 (distribution; host; reference): misidentification.

Some specimens obtained before 2005 were believed to be a melanic morph of *B. endotubercularis*, counted together with all specimens emerged from *G. triacanthos* (Di Iorio, 2005). These specimens proved to be *M. dorsalis*, distributed in Argentina in a single locality as follows: ARGENTINA: Buenos Aires: Pereyra, 17-VI-2002, 10 ex., emerged from seeds of *G. triacanthos* (Di Iorio, 2005).

Megabruchidius tonkineus (Pic, 1904)

Bruchidius endotubercularis, not Arora, 1980, in part (mixed with specimens of *M. dorsalis*): Di Iorio, 2005: 327-337 (distribution; host); György, 2007: 93 (distribution; host; reference); Tuda, 2008: 454 (reference); Yus Ramos, 2009: 372 (distribution; host; reference): misidentification.

Bruchidius endotubercularis, not Arora, 1980 (not mixed with specimens of *M. dorsalis*): Turienzo & Di Iorio, 2008: 9 (list), 10 (list), 12, 14 (distribution; shelter); Ferreras & Galetto, 2010: 212 (locality), 214 (host); Marrero, 2013: 15 (locality), 129 (list); Marrero *et al.*, 2014: 2 (locality), 10 (list; adult natural history): misidentification.

Megabruchidius tonkineus: Yus Ramos, 2009: 372 (distribution; host).

Hitherto, the geographical distribution, the date of each locality, and host plants of *M. tonkineus* in South America comprise: CHILE: Metropolitan Region: Santiago city, [year not stated], J.E. Barriga *leg.*, in seeds of *G. triacanthos* (Yus Ramos, 2009); ARGENTINA: Córdoba: La Rancherita (31° 45' 41.2" S, 64° 27' 30.7" W) [southwest from Alta Gracia], 2007, in seeds of *G. triacanthos* (Ferreras & Galetto, 2010); • Entre Ríos: Crespo, 16-VII-2002, emerged from seeds of *G. triacanthos* (Di Iorio, 2005); • Buenos Aires: Río Luján, F.C.G.B.M., 30-VI-2002; Campo de Mayo, 12-VII-2002; San Miguel, 21-VI-2002; Florida, 4-VII-2002; Ezeiza, 7-VII-2002; Pereyra, 17-VI-2002; Chascomús, 20-VII-2002, all emerged from seeds of *G. triacanthos* (Table IV); Magdalena; Mercedes; Mar del Plata [24-IV-2004]; Tres Arroyos [24-VII-2004], emergence holes observed in pods of *G. triacanthos* (Di Iorio, 2005); Campo de Mayo, 17-IV-2005, 1 ex., 9-VII-2005, 2 exx., 6-VIII-2005, 1 ex., sheltered inside stick nests of *Anumbius annumbi* (Vieillot, 1817) [Aves: Furnariidae] (Turienzo & Di Iorio, 2008); Carmen de Areco, 16-VIII-2002, J.E. Barriga *leg.*, in seeds of *G. triacanthos* (Yus Ramos, 2009); Partido de Carlos Casares, Estancia San Claudio

Table I. Species of *Megabruchidius* and their host plants. The asterisks denote exotic hosts in the respective countries where *Megabruchidius* was introduced. Native hosts in the original ranges are remarked in grey color. Host plant families are C, Caesalpinaceae, and F, Fabaceae.

	Host plant	Country	Reference
<i>Megabruchideus dorsalis</i>	C <i>Gleditsia japonica</i>	Japan	Takakura 2002
	C <i>Gleditsia rolfei</i>	Not stated	Tuda & Morimoto 2004
	C * <i>Gleditsia sinensis</i>	Italy	Yus Ramos 2009
	C * <i>Gleditsia triacanthos</i>	Italy	Yus Ramos 2009
	C * <i>Gleditsia triacanthos</i>	Hungary	Yus Ramos 2009
	C * <i>Gleditsia triacanthos</i>	France	Fritzsche & Delobel 2012
	C * <i>Gleditsia triacanthos</i>	Argentina	Present work
<i>Megabruchidius sophorae</i>	F * <i>Styphnolobium japonicum</i>	Japan	Tuda & Morimoto 2004
<i>Megabruchidius tonkineus</i>	C <i>Caesalpinia sappan</i>	Viet Nam	Di Iorio 2005
	C <i>Gleditsia amorphoides</i>	Argentina	Present work
	C <i>Gleditsia australis</i>	Viet Nam	Yus Ramos 2009
	C * <i>Gleditsia triacanthos</i>	Serbia	Gavrilović & Savić 2013
	C * <i>Gleditsia triacanthos</i>	Slovakia	Ferus <i>et al.</i> 2013
	C * <i>Gleditsia triacanthos</i>	Bulgary	Stojanova 2007
	C * <i>Gleditsia triacanthos</i>	Hungary	György 2007
	C * <i>Gleditsia triacanthos</i>	France	Fritzsche & Delobel 2012
	C * <i>Gleditsia triacanthos</i>	Greece	Yus Ramos 2009
	C * <i>Gleditsia triacanthos</i>	Argentina	Di Iorio 2005, Yus Ramos 2009
	C * <i>Gleditsia triacanthos</i>	Chile	Yus Ramos 2009

Table II. Pods of *Gleditsia amorphoides* (n = 152) from Tucumán, Argentina, infested by *Megabruchidius tonkineus* (Mt), *Lophopoeum timbouvae* (Lt), and Lepidoptera: Pyralidae: Phycitinae (Lep).

	n	%	n	%
First generation				
Non infested pods	106	69.73		
Infested pods	46	30.27	infested by Lt	15 9.86
			infested by Mt	28 18.42
			infested by Mt + Lt	2 1.31
			infested by Lep	1 0.65
			Total infested by Mt	30
Total infested by Lt	17	11.18		
Total infested by Lep	1	0.65		
Second generation				
Non infested pods			infested by Mt	83 54.60
			not infested by Mt	38 25.00
Infested pods			re-infested by Mt	23 15.13
			not re-infested by Mt	8 5.26
Total infested by Mt	106	69.74		
Total not infested by Mt	46	30.26		

(Marrero 2013), = 35° 56' S, 61° 11' W, adults on flowers (Marrero *et al.*, 2014); • Buenos Aires city: Palermo, emergence holes observed in pods of *G. triacanthos* (Di Iorio, 2005).

The following new localities, host plants, numbers of collected pods, and situations in which some specimens were found may be add as follows: ARGENTINA: Tucumán: San Miguel de Tucumán, botanical garden of the Fundación e Instituto Miguel Lillo, 16-IX-2005, Di Iorio *leg.*, emerged from seeds of *G. amorphoides* [152 pods on three trees and/or fallen to the ground] (Tables II-III); • Chaco: San Martín, 12-I-2007, already emerged from seeds of *G. amorphoides* [seven pods fallen to the ground]; Resistencia, 15-IV-2015, L. Damer *leg.*, 2 ex., emerged from pods of *G. amorphoides*; • Santa Fe: Rincón Norte, 16-VI-2006, Di Iorio *leg.*, emerged from seeds of *G. triacanthos* [ripen pods on a single tree]; • Buenos Aires: Campo de Mayo, VII-2004, 2 ex., sheltered in vacated larval tunnels of *Achryson foersteri* Bosq, 1958 (Coleoptera: Cerambycidae) in the bole of a dead standing tree of *Celtis ehrenbergiana* (Klotzsch) Liebm [= *Celtis tala* (Gill.) ex Planch., Celtidaceae], 17-IV-2005, Di Iorio *leg.*, 2 ex., feeding pollen on female flowers of *Baccharis salicifolia* (Ruiz & Pav.) Pers. [Asteraceae], 4-IX-2005, V. Trigo *leg.*, 2 ex., emerged from naked seeds of *G. triacanthos* in the rumen extracted from a

dead cow; Bahía Blanca, 24-V-2006, emergence holes observed in pods of *G. triacanthos* [pods fallen to the ground]; • Río Negro: Viedma, 2009, H. Iuri *leg.*, 1 ex.

Infested pods and consumed seeds of *Gleditsia amorphoides* in Argentina

• San Miguel de Tucumán (Tucumán)

In this sample, only 30.27% of the pods were infested by the first generation of *M. tonkineus*. The second generation infested 78.30% of the previous not infested pods, and re-infested the 50.00% of the previous infested pods (Table II). From a total of 38 pods that remained uninfested after the second generation, 26 of them have all seeds dry, but probably these pods were oviposited but no one larva survived.

A total of 769 seeds were counted: 248 were viable, and the remaining 521 were not viable (wrinkled + dry seeds). A total of 30 (12.09% of the viable seeds, and 28.12 % of all seeds) were consumed by the first generation of *M. tonkineus*, from which four seeds had two emergence holes. The second generation of *M. tonkineus* eliminated 88.89% of the remaining viable seeds, leaving only 3.37% of viable seeds (Table III). Also wrinkled seeds of *G. amorphoides* were used for larval development but in a minor proportion than viable seeds (Table III).

Table III. Seeds in pods of *Gleditsia amorphoides* from Tucumán, Argentina, consumed by *Megabruchidius tonkineus* (Mt) and *Lophopoeum timbouvae* (Lt). Mean (X), standard deviation (SD) and range were calculated in seeds per pod. Isolated and single values in the range are given between parentheses.

			X	SD	n pods	Range	Seeds	%
First generation								
Viable seeds	Eaten by Lt		-	-	-	-	2	0.26
	Eaten by Mt	with one emergence hole	1.36	0.59	19	1-3	26	3.38
		with two emergence holes	-	-	4	-	4	0.52
	Not eaten		2.18	1.45	99	1-6 (9)	216	28.12
Wrinkled seeds	Eaten by Lt		1.40	0.63	15	1-3	21	2.73
	Eaten by Mt	with one emergence hole	1.20	0.42	10	1-2	12	1.56
		with two emergence holes	-	-	2	-	2	0.26
	Not eaten		1.32	1.00	37	1-4 (6)	49	6.37
Second generation								
Viable seeds	Eaten by Mt	with one emergence hole	1.66	1.04	57	1-5	95	12.35
		with two emergence holes	1.68	1.02	57	1-5	96	12.48
		with three emergence holes	-	-	1	-	1	0.13
	Not eaten		1.14	0.47	21	1-3	24	3.12
Wrinkled seeds	Eaten by Mt	with one emergence hole	1.25	0.91	32	1-2 (6)	40	5.20
		with two emergence holes	1.50	1.22	6	1 (4)	9	1.17
Dry seeds per pod			2.87	1.62	37	1-7 (8)	437	56.82
Total seeds per pod			5.05	1.63	152	1-9	769	100
Total viable seeds per pod [Note 1]			2.34	1.54	106	1-9	248	32.24
Total non viable seeds per pod [Note 2]			3.42	1.60	152	0-8	521	67.75
Total viable seeds eaten by Be			2.31	1.46	96	1-6 (9)	222	28.87

Note 1: = Eaten by Lt + Eaten by Mt + Not eaten by Be

Note 2: = Wrinkled seeds eaten by Lt + wrinkled seeds eaten by Mt + dry seeds

The number of viable seeds with two emergence holes increased from four to 57 between both generations of *M. tonkineus* (Table III). In the second generation, the numbers of viable seeds with one or two emergence holes were practically equal (in equal number of pods), and an exceptional seed with three emergence holes was produced (Table III).

Seeds consumed by the larvae of *L. timbouvae* were 21 wrinkled seeds in 15 pods, two viable seeds in another pod (Table III), and four pods were infested but no seeds were consumed. From these 15 infested pods, four adults emerged 28-X-05 (winter generation), and other six adults emerged in January and February (summer generation). At the time of dissecting pods (April 2006), small larvae of *L. timbouvae* were present (second winter generation), originated from oviposition by the adults previously emerged (summer generation).

• San Martín (Chaco)

A total of seven pods of *G. amorphoides* was infested by *M. tonkineus* as follows: one pod with one emergence hole; three with two emergence holes; one with three emergence holes; one with five emergence holes, and one pod was not infested. Two of these pods were infested with one larva of *L. timbouvae* each. This longhorned beetle was previously reared on *G. amorphoides* only from Chaco National Park, Chaco (Di Iorio, 1995, 2004).

Discussion

• Distribution and host plant of *Bruchidius endotuberculosis*

Tuda (2008) included *B. endotuberculosis* in a Group 5 of Asian and African species of *Bruchidius* that develops on *Acacia* Mill. and *Albizia* Durazz. (Mimosaceae) seeds. This species was also erroneously included among the “few exceptional species utilizing or host-switched to Caesalpinioideae”, based on the previous record of Di Iorio (2005). In view of the new data, the true *B. endotuberculosis* may be excluded from the species of *Bruchidius* that switched to Caesalpinace-

ae (Tuda, 2008), remaining restricted to its original host (*Albizia* sp.) in India (Arora, 1980).

• Current distribution of *M. tonkineus* in Argentina

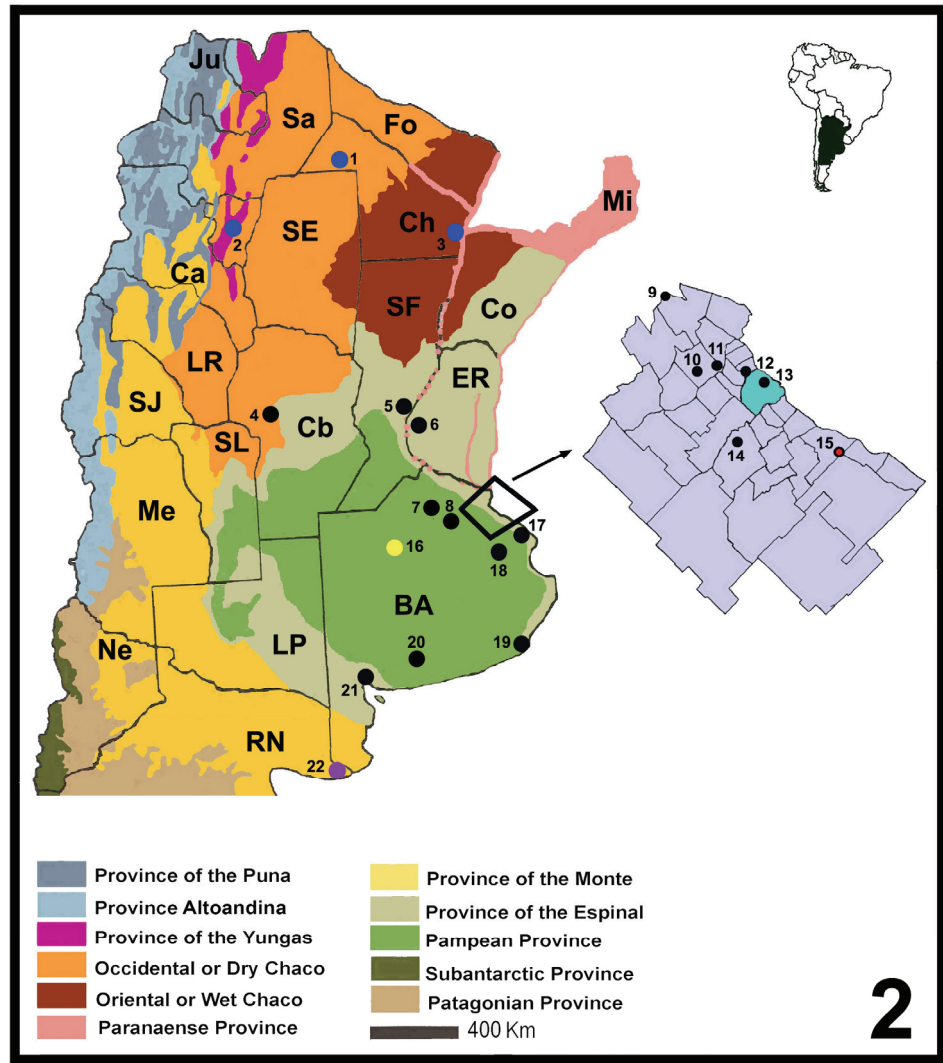
The wide distribution of *M. tonkineus* in Argentina is actually comprised in the Yungas (Tucumán), the Dry Chaco (Chaco; Córdoba), the Wet Chaco (Chaco), the Espinal (Santa Fe; Entre Ríos; Buenos Aires), the Pampean (Buenos Aires), and the Monte (Rio Negro) biogeographic provinces (fig. 2). *G. amorphoides* is naturally distributed in Bolivia, Brazil, Paraguay, Uruguay and Argentina: Jujuy; Salta; Formosa; Chaco; Santa Fe; Misiones; Corrientes; Entre Ríos (Zuloaga & Morrone, 2001). Thus *M. tonkineus* can be expected on this plant in some of these provinces and/or adjacent countries, but also on *G. triacanthos* in cultivated or naturalized trees.

From the previous data presented by Di Iorio (2005), it was supposed that the entry point of *M. tonkineus* in the country was the city of Buenos Aires, then widespread in a radiated pattern (fig. 1). The collections made now at very distant localities, such as San Martín (Chaco), San Miguel de Tucumán (Tucumán), Bahía Blanca (Buenos Aires), and Viedma (Rio Negro) (fig. 2) probably indicate that the dispersal of *M. tonkineus* was very fast because these localities were reached in less than 14 years (after 1993 through 2005-2007). The northern (San Martín) and southern (Viedma) distribution points are separated by 1640 km (fig. 2).

This fast dispersion of *M. tonkineus* in Argentina was probably facilitated by three concurrent situations: 1) *G. triacanthos* has a wide distribution comprising naturalized populations and cultivated trees; 2) the bruchids are capable to find a shelter during unfavorable weather conditions (Turienzo & Di Iorio, 2008; material examined); and 3) they feed on pollen of flowers (Marrero *et al.* 2014; material examined). The last two situations undoubtedly increased its adult survival and dispersal capacity.

Considering hypothetically that *M. tonkineus* was introduced at Buenos Aires city in 1995 (Di Iorio, 2005), the spread ratios to some distant points of its current distribution (fig. 2) will be as follows:

Figure 2. Current distribution of *Megabrucidius tonkineus* in Argentina: black circles, in *Gleditsia triacanthos*; blue circles, in *Gleditsia amorphoides*; yellow circles, adults visiting flowers; violet circle, without host date; small red circle inside black circle, the locality where *M. dorsalis* was reared from the same pods of *G. triacanthos* together with *M. tonkineus*. Localities: 1, San Martín; 2, San Miguel de Tucumán; 3, Resistencia; 4, La Rancherita; 5, Rincón Norte; 6, Crespo; 7, Mercedes; 8, Carmen de Areco; 9, Río Luján; 10, San Miguel; 11, Campo de Mayo; 12, Florida; 13, Palermo; 14, Ezeiza; 15, Pereyra; 16, Carlos Casares; 17, Magdalena; 18, Chascomús; 19, Mar del Plata; 20, Tres Arroyos; 21, Bahía Blanca; 22, Viedma.



- Buenos Aires (1995) to San Miguel de Tucumán (2005): 1070 km in 10 years = 107.0 km/year
- Buenos Aires (1995) to Bahía Blanca (2006): 570 km in 11 years = 51.8 km/year
- Buenos Aires (1995) to La Rancherita (2007): 720 km in 12 years = 60.0 km/year
- Buenos Aires (1995) to San Martín (2007): 1060 km in 12 years = 88.3 km/year
- Buenos Aires (1995) to Viedma (2009): 800 km in 14 years = 57.1 km/year

According to Zimmermann *et al.* (2000), the spread rate of a phytophagous insect may depend on host plant availability and abundance. Individual females of the cactus moth *Cactoblastis cactorum* (Berg, 1885) (Lepidoptera: Pyralidae) were recorded as flying as far as 24 km to oviposit. In Australia, the cactus moth spread unaided for about 16-24 km in 2.5 years in dense *Opuntia* infestations (Cactaceae). In South Africa, the unaided rate of spread was about 3-6 km in 2.5 years, but in Florida (United States), the moth had dispersed 576 km northwards from 1989 to 1991, giving a spread ratio of 256 km/year, decreasing to 40 km per year thereafter. Perhaps the lower densities of hosts in Florida northwards induced a more rapid and widespread natural dispersal of the cactus moth than was the case in Australia and South Africa, where they were very high host-plant densities.

Another seed beetle, *Merobruchus bicolor* (Pic, 1927), specific of *Enterolobium contortisiliquum* (Vell.) Morong (Mimosaceae), also followed a long dispersal pattern from north to south Argentina (Di Iorio 1995), reaching the city of Buenos Aires even on cultivated trees in squares [see other examples of long dispersal of native longhorned beetles on cultivated host plants in Argentina in Di Iorio, 1993, 1995, and Di Iorio & Farina, 2009].

A similar situation probably occurred with the distribution of *G. triacanthos* and the dispersal of *M. tonkineus* in some parts of Argentina. In the Espinal and Pampean regions, there are the biggest naturalized populations of *G. triacanthos* along water courses and lowlands (north of Buenos Aires, south of Santa Fe and south of Córdoba) (fig. 2), but in the northern half of Córdoba, where the Dry Chaco begins towards the north in Tucumán, Santiago del Estero, and western Chaco provinces (fig. 2), *G. triacanthos* is cultivated in squares and gardens of innumerable towns separated by several km where this plant is absent (Di Iorio, pers. obs.). The adoption of *Gleditsia* and the extensive distribution of *M. tonkineus* in Argentina (fig. 2) is similar to the current situation in Europe (Table I).

• Host plants of *M. tonkineus* in Argentina

Both legume plants adopted by *M. tonkineus* in Argentina were not previously occupied by other native bruchid species.

The native *G. amorphoides* has no previous native seed beetle associated (Di Iorio, 1995; Kingsolver & Muruaga de L'Argentier, 2004), probably due to the chemical defenses in its seeds (Evans & Bell, 1878). Nevertheless, these chemical defenses are the same that are also present in Asian species of *Gleditsia* and in the North American *G. triacanthos*, but not in *C. sappan* (Evans & Bell, 1878). As the Asian species of *Megabruchidius* seems to be adapted to these chemical defenses, there were not impediment for the adoption of *G. amorphoides* as a further host (it is well known that some chemical defenses in plants can act as attractants for specialized insects).

By the other side, *G. triacanthos* in Argentina have also no bruchid species associated before 1993 (Di Iorio, 1995), but in its natural range it is infested by *Amblycerus robiniae* (Fabricius, 1781) (Chrysomelidae: Bruchinae) (György, 2007). The native species of *Amblycerus* from Argentina develops in legume plants of the genera *Cassia* L., *Senna* Mill., *Geoffroea* Jacq. (Caesalpinaceae), *Phaseolus* L. (Fabaceae), and *Cordia* L. (Boraginaceae) (Kingsolver & Muruaga de L'Argentier, 2004), but no native species of *Amblycerus* were able to infest *G. triacanthos* since its introduction in the country at the beginning of XIX century (Kingsolver & Muruaga de L'Argentier, 2004; Di Iorio, 2005). A revision of mature pods of *Styphnolobium japonicum* (L.) Schott. (Fabaceae) from Buenos Aires (Ciudad Universitaria, 15-IV-2015), cited as a host of one *Megabruchidius* species in Japan (Table I), gave a negative result for bruchid beetles.

A culture in laboratory of *M. tonkineus* from Argentina was considered for the biological control of *G. triacanthos* in South Africa (S. Nesser, pers. com.). In view of the host specificity of *Megabruchidius* to species in the genus *Gleditsia* (Table I), *M. tonkineus* may be a suitable candidate for biological control of *Gleditsia triacanthos*, but other Caesalpinaceae need to be tested, because *M. tonkineus* may has also *C. sappan* as a host (Table I). According to its natural history observed in Argentina (Di Iorio, 2005) and Hungary (György, 2007), *M. tonkineus* may be included in the Guild A of bruchids that oviposit in pods on the plant (Johnson & Romero, 2004).

At difference with the pods infested by native species of bruchids in Argentina, no native parasitic Hymenoptera emerged yet from pods of *Gleditsia* species infested by *M. tonkineus*. The same situation was observed in Hungary by György (2007).

• Consumption of viable seeds by *Megabruchidius* in Argentina

In Argentina, the viable seeds of *G. triacanthos* consumed by *M. tonkineus* in 2002 ranged between 38.33% and 78.59%, except by a low value in Chascomús (5.88%), and the remaining viable seeds after both generations ranged from 21.40% to 68.95%, except 94.12% in Chascomús (Table IV). These percentages of viable seeds consumed by *M. tonkineus* are considerably higher than the percentages of seeds of *G. triacanthos* consumed in Slovakia, that range from 0.0% in one locality to 2.61, 2.71, 4.05, 4.54, 7.69, and 9.15% in other localities (Ferus *et al.*, 2013). In contrast, *G. amorphoides* has the highest percentage of viable seeds consumed by *M. tonkineus*, and only 10.48% of the total viable seeds survived after the second generation of *M. tonkineus* (Tables III-IV).

Regretably, the seeds consumed by *M. tonkineus* in Argentina were not tested for germination, an issue that will

deserves a further research, but no germination was observed in infested seeds of *G. triacanthos* in Slovakia (Ferus *et al.*, 2013). Takakura (2002) found that one specialist species of seed beetle in the genus *Bruchidius* in Japan plays a crucial role in the seed germination of *Gleditsia japonica*. Other less extreme examples of low germination percentages in seeds that were infested by bruchids but the embryos were not consumed were given in literature.

• Number of generations per year

Two generations per year of *M. tonkineus* were recorded in Argentina (Di Iorio, 2005), as well as in Serbia (Gavrilović & Savić, 2013), and Hungary (György, 2007). It can be remembered here that the adults of *M. tonkineus* from the winter generation in Argentina emerged from middle winter to the beginning of spring, an unusual time compared with the native species of seed beetles (Di Iorio, 2005). This could explain its necessity for find shelters during unfavorable weather conditions (Turienzo & Di Iorio, 2008; present work).

• Number of emerged adults

In general, each seed corresponds to one emerged adult beetle, but at least in *M. tonkineus*, more than one beetle can emerge from each seed. The second emergence holes were always smaller than the first, and the adults produced were \approx 50% smaller or less than the normal size of the species. György (2007) also mentioned two emergence holes per seed of *G. triacanthos* in Hungary, with these second small individuals able to mate and produce viable offspring.

A remarkable point found here in Argentina is the difference in the number of seeds with two emergence holes between the exotic *G. triacanthos* and the naïve *G. amorphoides*. In the first plant, a total of 16 seeds with two emergence holes was observed among 5359 viable seeds examined from three localities (Table IV). In *G. amorphoides*, the number of viable seeds with two emergence holes gave a total of 61 (Tables III-IV). Probably, this difference in the number of seeds with two emergence holes be due to the also different number of seeds per pod in both *Gleditsia* species. While *Gleditsia amorphoides* has 6.39 ± 1.56 seeds per pod ($n = 100$ pods) in its original range (Di Iorio, 1995), or 5.05 ± 1.63 seeds per pod ($n = 152$ pods) in the small cultivated population of Tucumán, these numbers are considerably smaller than the $15.16-26.96 \pm 3.17-6.36$ seeds per pod in *G. triacanthos* (Di Iorio, 2005). As an additional information, the number of non viable seeds in Tucumán (including here the number of wrinkled seeds) was considerably higher than in the original range (Di Iorio, 1995), probably as a consequence of inbreeding, thus decreasing the number of viable seeds for the bruchids. Therefore, the same viable seeds in the small cultivated population of Tucumán may be infested or re-infested by more than one larva due to the pressure suffered by the bruchid beetles in pods with less viable seeds.

In contrast to *M. tonkineus*, the few specimens (except one) of *M. dorsalis* in Argentina were of a normal size for the species, an indication that a nearly equal number of seeds were used for development, and that they developed in seeds not previously infested by *M. tonkineus* (except perhaps by the single smaller specimen). Yus Ramos (2009) obtained three specimens of *M. dorsalis* and 49 of *M. tonkineus* from the same pods of *G. triacanthos* from Hungary, and Fritzsche & Delobel (2012) obtained only 2 males and 3 females of *M. dorsalis* among 1000 specimens of *M. tonkineus* from the

Table IV. Viable seeds of *Gleditsia triacanthos* (Gt) and *Gleditsia amorphoides* (Ga) consumed by *Megabruchidius tonkineus* (Mt) and *M. dorsalis* (Md) in Argentina. Percentages of total viable seeds are respect to the total seeds per locality; percentages of viable seeds eaten by *Megabruchidius*, viable seeds remaining, and seeds with two holes are respect to the total viable seeds. The data on *G. triacanthos* were condensed and/or modified from Di Iorio (2005).

Locality	Year	Total pods (# of trees)	Total seeds	Total viable seeds	Viable seeds eaten by M	Viable seeds remaining	Seeds with two holes	Adults Mt	Adults Md
Gt	Crespo 2002	65 (one tree)	1753	1514 (86.36%)	1190 (78.59%)	324 (21.40%)	-	1190	-
Gt	C. de Mayo 2002	112 (two trees)	2607	2254 (86.45%)	864 (38.33%)	1390 (61.67%)	6 (0.47%)	870	-
Gt	San Miguel 2002	85 (one tree)	1422	1348 (94.79%)	542 (40.20%)	806 (59.79%)	-	542	-
Gt	Florida 2002	150 (one tree)	3305	3063 (92.67%)	951 (31.04%)	2112 (68.95%)	-	951	-
Gt	Ezeiza 2002	100 (three trees)	2024	1761 (87.00%)	780 (44.29%)	981 (55.71%)	-	780	-
Gt	Pereyra 2002	150 (two trees)	3361	2901 (86.31%)	2076 (71.56%)	825 (28.43%)	9 (0.31%)	2075	10
Gt	Chascomús 2002	12 (one tree)	229	204 (89.08%)	12 (5.88%)	192 (94.12%)	1 (0.49%)	13	-
Ga	Tucumán 2005	152 (three trees)	769	248 (32.24%)	222 (89.52%)	26 (10.48%)	61 (24.59%)	283	-

same pods of *G. triacanthos* in France. In Argentina, the proportion of *M. tonkineus* / *M. dorsalis* was 2075 specimens of *M. tonkineus* and 10 adults of *M. dorsalis* only from Pereyra (Table IV), that is similar to the proportion of Fritzsche & Delobel (2012) in France, i.e. ≈ 5 *M. dorsalis* by each 1000 *M. tonkineus*.

• Final remarks

According to the new data discussed here, there are no other further predictable hosts for *M. tonkineus* in the country. The native *G. amorphoides* may be negatively impacted by *M. tonkineus* due to the small size of its pods and the low number of seeds per pod (Di Iorio, 1995; Table III). Another issues that will deserve a further research in Argentina are: 1) if *M. tonkineus* actually consumes more viable seeds of *G. triacanthos* than in 2002 (Table IV), resulting in a more effective biological control of this invasive plant, 2) to know in which degree the viable seed survival of *Gleditsia amorphoides* in its native distribution is affected, and 3) the further distribution and hosts of *M. dorsalis* in the country.

According to the phylogeny of the species of *Gleditsia* (fig. 1), new hosts are expected in those countries where both *Megabruchidius* were introduced, and where other species of *Gleditsia* are cultivated (Table I).

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