

The threat of the ambrosia beetle *Megaplatypus mutatus* (Chapuis) (=*Platypus mutatus* Chapuis) to world poplar resources

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Summary

We describe the life cycle of *Megaplatypus mutatus* (Chapuis) (= *Platypus mutatus*) and the damage it causes to poplar resources in Argentina. This insect, native to the subtropical and tropical areas of South America, has extended its range into temperate regions, reaching as far south as Neuquén in Argentinean Patagonia. The damage is caused by the adult insects, which bore large gallery systems into living poplars (*Populus* spp.), willows (*Salix* spp.) and many other broadleaf species, including important fruit trees species such as apples (*Malus* spp.), walnuts (*Juglans* spp.) and avocados (*Persea* spp.). The galleries degrade the lumber and weaken the tree stems, which often then break during windstorms. A recent introduction of *M. mutatus* to Italy demonstrates that this insect can be transported long distances between countries, and therefore presents a threat worldwide—particularly to poplar cultivation. We review the taxonomic nomenclature for this pest, provide a summary of the life cycle, hosts and damage and summarize actions taken to reduce the risk of introduction of *M. mutatus* to Canada.

Introduction

There is great concern among trading nations vis-a-vis the transportation of invasive alien insects and diseases with trade commodities, as these organisms can affect forests, agriculture, livestock, fresh water and human health (Kliejunas *et al.*, 2006). Most non-native forest insects arrive in new environments as unexpected invaders. In for-

estry, exotic insects, such as the balsam woolly adelgid (*Adelges piceae* (Ratzeburg)) (Johnson and Lyon, 1988), the hemlock woolly adelgid, (*Adelges tsugae* Annand) (Orwig *et al.*, 2002) and the emerald ash borer (*Agrilus planipennis* Fairmaire) (Poland and McCullough, 2006) in North America, have caused severe damage to forest ecosystems and forest products. The impacts of more recently discovered introductions, such as the brown spruce

long-horned beetle (*Tetropium fuscum* (Fabricius)) (Smith and Hurley, 2000), the European woodwasp (*Sirex noctilio* Fabricius) (Hoebeker *et al.*, 2005) and the Asian long-horned beetle (*Anoplophora glabripennis* (Motschulsky)) (Haack *et al.*, 1996) in North America, as well as *A. glabripennis* and the citrus long-horned beetle (*Anoplophora chinensis* (Forster)) (Hérard *et al.*, 2006) in Europe, have yet to be determined. Exotic invaders may cause changes to native forests as new arrivals can interfere with normal ecosystem functions, displace native species and alter ecosystem balances such as predator–prey relations. In addition to such direct losses, established exotic insects increase the costs of commodities because of the phytosanitary measures required by trading partners.

Ambrosia beetles are an important insect group in forest ecosystems. They usually attack mostly felled or weakened trees, where they bore galleries into the wood. The common name, ‘ambrosia beetle’, is derived from the symbiotic fungus which the beetle introduces into its galleries and on which the beetle larvae feed.

Megaplatypus mutatus (= *Platypus mutatus*) (Chapuis, 1865; Coleoptera: Platypodidae, Platypodinae, Platypodini) is native to South America (Wood, 1993). Unlike most ambrosia beetles, it attacks only living standing trees. The beetle is a serious problem in commercial plantations of a number of broadleaf tree species, but is especially damaging to poplars (*Populus deltoides* Bartr. ex Marsh.) in Argentina (Etiennot *et al.*, 2000; Giménez and Etiennot, 2003). The dark staining produced by the ambrosial mycelia that grow on the tunnel walls bored by *M. mutatus* (Bascialli *et al.*, 1996) reduces wood quality, making it unsuitable for certain uses, such as peeling (veneer production) and reducing the wood’s market value.

The beetle’s continuing damage to hybrid poplar plantations in Argentina, its wide distribution in South America (Figure 1) as well as its recent introduction into Italy (Tremblay *et al.*, 2000; Allegro and Della Beffa, 2001) have raised concerns regarding the potential of this South American insect becoming a globally invasive pest of *Populus* species.

Control of exotic invaders is most likely to succeed if detection occurs soon after their arrival into new environments. Emergency eradication measures can then be initiated to eliminate

populations while they are still small and before they spread into new habitats. However, low populations are difficult to detect, and eradication programs are costly, environmentally risky and often encounter public opposition. For these reasons, risk of economic damage caused by introduction of exotic pests into new habitats is most effectively reduced if the introduction is prevented. Prevention of pest movement across regions and borders requires public education. With this in mind, we review here the taxonomic nomenclature of *M. mutatus*, provide a summary of its life cycle, hosts, symptoms and damage and summarize actions being taken to reduce the risk of its introduction into Canada.

Nomenclature of *M. mutatus* (Chapuis, 1865) (Coleoptera: Platypodidae)

Key to effective management of an exotic species is clarification of its taxonomic position. *Megaplatypus mutatus* is often referred to in the literature as *Platypus sulcatus* or *Platypus mutatus*, which has created confusion. Wood (1993) provided the first revision of the genera of Platypodidae, designated nine new genera, provided keys for their recognition and assigned the described species to the new genera. The species of concern, *Platypus mutatus* Chapuis, was assigned to genus *Megaplatypus*. This generic transfer was adopted in the second supplement to the world catalogue of Scolytidae and Platypodidae (Bright and Skidmore, 2002). Thus, the correct designation for this species is currently *Megaplatypus mutatus* (Chapuis).

Wood and Bright (1992) and Bright and Skidmore (1997) summarize the history of the nomenclature of *M. mutatus*. The species was originally described by Chapuis (1865, cited in Wood and Bright, 1992) as *Platypus mutatus* from a specimen collected in Brazil. Two additional species of *Platypus*—*P. sulcatus* Chapuis and *Platypus plicatus* Brethes—have been synonymized with *M. mutatus* (Wood and Bright, 1992). *Platypus sulcatus* Chapuis was placed into synonymy with *P. mutatus* Chapuis in 1865 by Strohmeier (1910, cited in Wood and Bright, 1992), and the synonymy was confirmed by Schedl (1960, cited in Wood and Bright, 1992), whereas



Figure 1. The occurrence by country (denoted in grey; after Wood and Bright, 1992) and generalized distribution in Argentina (cross-hatched) of *Megaplatus mutatus* (Chapuis) (modified from Giménez and Etiennot, 2003).

P. plicatus Brethes, 1909, was synonymized by Bosq (1934, cited in Wood and Bright, 1992).

Megaplatus is a large genus of more than 90 species whose distributions can range from Mexico to Argentina (Wood, 1993; Bright and Skidmore, 2002). *Megaplatus mutatus* is widely distributed in South America: Wood and Bright (1992) note its occurrence in Argentina, Bolivia,

Brazil, French Guiana (as Cayenne), Paraguay, Perú, Uruguay and Venezuela, and Giménez and Etiennot (2003) detail its distribution in Argentina (Figure 1).

Across its native range, *M. mutatus* attacks many species of broadleaf and coniferous hosts included in the genera *Acacia*, *Acer*, *Ailanthus*, *Balfourodendron*, *Callophyllum*, *Casuarina*,

Cedrela, *Citrus*, *Erythrina*, *Eucalyptus*, *Fraxinus*, *Grevillea*, *Laurus*, *Ligustrum*, *Liquidambar*, *Magnolia*, *Malus*, *Melia*, *Persea*, *Pinus*, *Platanus*, *Populus*, *Prunus*, *Pyrus*, *Quercus*, *Robinia*, *Salix*, *Taxodium*, *Tilia* and *Ulmus* (Wood and Bright, 1992; Bright and Skidmore, 2002; Giménez and Etiennot, 2003). *Megaplatypus mutatus*, like other Platypodidae, feeds on wood and fungus. Although single, paired or small clusters of specialized mycetangial pores (specialized cuticular structures associated with secretory glands that are involved in the transfer of ambrosial fungi) are present on the pronota of other *Megaplatypus* species (Wood, 1993), these pore structures are absent in *M. mutatus*, suggesting that other mycangial structures (Nakashima, 1971, 1972) are present in this species. Guerrero (1966) identified the ambrosial fungus of *M. mutatus* in Argentina as *Raffaelea santoroi* Guerrero; phylogenetic analyses by Jones and Blackwell (1998) confirm placement of the associated fungus in the genus *Raffaelea*.

The arrival of *M. mutatus* in Italy

In 2000, *M. mutatus* was discovered to have established in Italy (Tremblay *et al.*, 2000; Allegro and Della Beffa, 2001; Allegro, 2003), causing damage to a poplar plantation in the province of Caserta, near Naples. Its distribution in Italy has increased only moderately since then. Unfortunately, any eradication effort is expected to be difficult on account of the diverse feeding habits of this insect, which is severely affecting many broadleaved trees in the area, including apple (*Malus*), walnut (*Juglans regia* L.), hazel (*Corylus avellana* L.) and poplar (*Populus* × *canadensis* Moench). In Italy, walnut and poplar plantations grown for timber production have sustained the greatest economic damage, as the beetle's extensive galleries within the tree stems significantly decrease wood value (Allegro and Della Beffa, 2001). A valuable apple cultivar, Annurca, which is traditionally grown in the infested area, is also likely to suffer significant economic losses.

How *Megaplatypus* was introduced into Italy cannot be determined with certainty; however, the significant number of phytosanitary interceptions associated with solid wood packaging

(Allen and Humble, 2002, Haack, 2006) suggests that *M. mutatus* likely arrived in untreated wood packaging produced from infested wood from somewhere within its native range. Unless active surveillance is undertaken and appropriate phytosanitary measures implemented, this insect may possibly spread to other countries of the European Community. The countries of the Mediterranean temperate belt (Spain, France, Greece, Turkey and others), where poplar plantations and fruit crops are widely spread, are at risk. One positive step that has been taken is the listing of *M. mutatus* on the European and Mediterranean Plant Protection Organization's (EPPO) Alert List of Quarantine Pests.

The distribution of *M. mutatus* in Italy in 2007 still appears to be limited. However, considering the potential spread of this pest in coming years and the possible severity of its impact, establishment of an effective control strategy is recommended. This strategy must consider both human and environmental safety (cultivated plains in Italy are densely populated), as well as the need to maintain economic benefits from poplar cultivation.

Biology, symptoms and damage

Santoro (1957, 1963, 1965) described the characteristics of this insect and its biology. *Megaplatypus mutatus* is small—measuring 7–8 mm in length (Figure 2)—brown to black in colour and has a head as long as its pronotum and short antennae. The female is easily differentiated from the male: the elytral declivity is rounded, whereas that of the male is slanted. *Megaplatypus mutatus* attacks the stems of live trees, boring large internal tunnels in the xylem, which weaken the stems causing them to break under extreme wind stress (Figure 3).

Megaplatypus mutatus does not mass attack host trees. Attacks occur primarily in late spring (September to November in the southern hemisphere), with males usually initiating attack. Coarse boring dust can be observed on newly attacked trees (Figure 4), which usually exude sap through the entrance holes (Figure 5). Females join the males soon after successful attack, and construct most of the galleries as they lay eggs. This parental gallery system is constructed exclusively in the transversal plane of xylem, extensive



Figure 2. Adult *Megaplatypus mutatus*.

and spiral in shape (Figure 6). Larval galleries are short and are oriented vertical to the parental galleries. The walls of adult and larval galleries are covered with the mycelia of *Raphaelea santoroi*. In the Delta region of the province of Buenos Aires, Argentina, new adults emerge between November and January.

The threat to world poplar resources

When assessing the potential threat of an exotic insect, it is customary to compare the climate and hosts in the area of origin and in the threatened areas, and to assess the likelihood of the pest being transported out of its place of origin. The following check list led us to conclude that this



Figure 3. Damage to a poplar plantation, Bragado, Argentina, 2004.

insect poses a high risk to the economy of many regions of the world:

- 1 The broad geographic distribution of *M. mutatus* in its continent of origin indicates that this insect is able to thrive in habitats ranging from tropical to cool temperate.
- 2 The temperature regimes at the southern edge of its current South American distribution (Figure 7) suggest that the beetle could survive in north temperate regions of Eurasia and North America.
- 3 The extensive host range includes many species common to all temperate regions of the world.
- 4 Its distribution throughout South America provides many source populations for potential global transportation.
- 5 The insect's establishment in Italy demonstrates that *M. mutatus* can be transported with trade to other parts of the world.



Figure 4. Entrance hole of *Megaplatypus mutatus*.



Figure 5. Exudation of sap by attacked poplar tree.

We conclude that *M. mutatus* is a threat to the fruit tree industries and forest resources in many areas of the world. In North America, this insect is of particular concern to California, Oregon and Washington, and to the west coast of British Columbia, where significant plantations of hybrid poplars and a large fruit industry occur and temperature regimes are favourable for this pest.



Figure 6. Gallery system of *Megaplatypus mutatus*.

Proactive management of the *Megaplatypus* threat

Rarely do we have the luxury of anticipating which pests pose a serious threat to our forests. *Megaplatypus mutatus* is one such pest. We are actively working on reducing the likelihood of this insect entering Canada and have taken the following steps to limit its introduction:

In-house training

We are preparing pest advisory notes to help train customs and other shipping inspectors on what to watch for with regard to *M. mutatus*, and are also working to increase awareness of the threat among the public at large so as to help reduce the chance of people inadvertently transporting these organisms and to allow them to distinguish damage symptoms caused by this pest from that caused by native species.

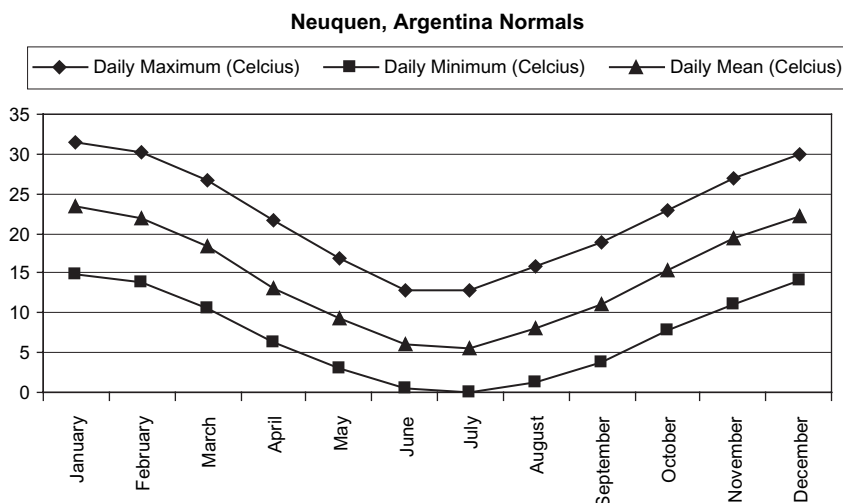


Figure 7. Temperature normals ($^{\circ}\text{C}$) for the city of Neuquén (Latitude $38^{\circ} 56' \text{S}$; Longitude $68^{\circ} 1' \text{W}$), in Argentinean Patagonia, at the southernmost range of *Megaplatus mutatus*. Source: *Climatological Normals of Neuquen* 2003, Government of the Hong Kong Special Administrative Region, Hong Kong Observatory, viewed 17 May 2007, http://www.hko.gov.hk/wxinfo/climat/world/eng/s_america/ar_ch/neuquen_e.htm.

Training at the source

Building capacity in the countries of origin, sharing information and providing training to develop population reduction methods and contamination avoidance measures will reduce the likelihood of *M. mutatus* being transported out of the South American region.

With financing from Argentina, the World Bank and Canada, a cooperative project between the Canadian Forest Service, the Argentinean Ministry of Agriculture, University of La Plata and Centro de Investigaciones de Plagas e Insecticidas (CITEFA) of Argentina was launched in 2001 to prepare a work plan for that country (Alfaro, 2003). This plan included recommendations for a range of measures that would increase the understanding of the biological cycle of *M. mutatus*, the threat (pathways of movement) of this insect to other parts of the world and the potential damage to forests and agriculture it could cause. The plan also recommended the development of effective survey systems to detect the insect.

Critical for detecting the movement of this insect is the availability of an effective pheromone that could be used for surveying and population control. Pheromones are the main tool and first line of detection against invasive

insects. Pheromones for other Canadian ambrosia beetles have been successfully employed for population control in western US and Canadian sawmills and log-sorting areas for more than 20 years (Borden and McLean, 1979). No such readily available pheromone for *M. mutatus* currently exists, and the work plan recommends that efforts be concentrated in this area. Accordingly, efforts have focused on building capacity within Argentina for the identification of pheromones of this insect and for the development of a system for detection.

In 2002, 2003 and 2004, potential pheromones and trap systems were sent from Canada to Argentina, and experiments were carried out in the Delta region of the Rio de la Plata and Neuquén (Patagonia). In 2002, in collaboration with the Istituto di Sperimentazione per la Pioppicoltura Casale Monferrato, Italy, the experiments were replicated in Italy.

Results from these experiments indicated that one of the components of the *M. mutatus* pheromone was Sulcatol (Gonzalez *et al.*, 2005), which is also a component of pheromones of some North American ambrosia beetles (Borden and McLean, 1979). However, the low degree of attraction to Sulcatol by *M. mutatus* indicated that other

components were missing. Electro-antennogram studies coupled with gas chromatography analyses and olfactometric studies concluded that female *M. mutatus* are also responsive to Sulcatone (Gonzalez *et al.*, 2005).

Informing the international community

This synthesis publication, combined with presentations on the subject in other venues, represents our efforts to inform the international community of the potential threat of this destructive insect.

International regulatory efforts

Although the pathway for introduction of *M. mutatus* into Italy is unknown, its establishment could only have resulted through the transport of the insect in some of its life stages in association with untreated wood or wood products. Because *M. mutatus* has a relatively short peak flight period (November to January in the southern hemisphere), and spends ~9 months of its life within its host tree in its various life stages, the most plausible pathway is via the transportation of callow adults or larvae either in untreated roundwood or in wood packaging cut from infested trees. The latter pathway has been recognized globally as significant in the movement of invasive bark- and wood-boring pests between countries. In 2002, the International Plant Protection Convention adopted international guidelines recommending treatment of all wood used to package commodities for international trade (FAO, 2002) in order to prevent introductions of invasive pests in association with wood packaging. The adoption and implementation of this standard, ISPM #15, will greatly enhance the protection of all forests from invasive wood-boring pests, including *M. mutatus*.

Conclusion

The proactive risk reduction model—which includes building capacity in Canada and in the country of origin, informing the international community and supporting and implementing international regulatory efforts—being put in place

by Canada and other countries will help to reduce the likelihood of this insect's introduction into Canada. The descriptions of the insect, its symptoms and damage are part of that model; it will serve as a guide to field technicians and public at large, and will be useful in helping to reduce chances of further dispersion of *M. mutatus*.

Conflict of Interest Statement

None declared.

References

- Alfaro, R.I. 2003 [The large poplar borer, *Platypus mutatus*: an important pest of Argentinean poplars: an action plan]. *SAGPyA Forestal*. 28, 11–18. (in Spanish).
- Allegro, G. 2003 PLATIPO *Platypus mutatus* Chapuis (Coleoptera, Platypodidae). Istituto di Sperimentazione per la Pioppicoltura, Casale Monferrato (AL). 2 pp. <http://www.populus.it/platipo.pdf> (accessed 29 June 2004).
- Allegro, G. and Della Beffa, G. 2001 Un nuovo problema entomologico per la pioppicoltura Italiana: *Platypus mutatus* Chapuis (Coleoptera, Platypodidae). *Sherwood Foreste ed alberi oggi*. 66, 31–34.
- Allen, E.A. and Humble, L.M. 2002 Non-indigenous species introductions: a threat to Canada's forests and forest economy. *Can. J. Plant Pathol.* 24, 103–110.
- Bascialli, M.E., Jiménez, R.A., Etiennot, A.E. and Toscani, H. 1996 Manejo de la población de *Platypus sulcatus* Chapuis, durante tres años en la región del Delta del Río Paraná mediante control químico. *Invest. Agr. Sist. Recur. For.* 5, 129–140.
- Borden, J.H. and McLean, J.A. 1979 Secondary attraction in *Gnathotricus retusus* and cross attraction of *G. sulcatus* (Coleoptera: Scolytidae). *J. Chem. Ecol.*, 5, 79–88.
- Bright, D.E. and Skidmore, R.E. 1997 A Catalog of Scolytidae and Platypodidae (Coleoptera) Supplement 1 (1990–1994). National Research Council Press, Ottawa, Ontario, 368 pp.
- Bright, D.E. and Skidmore, R.E. 2002 A Catalog of Scolytidae and Platypodidae (Coleoptera) Supplement 1 (1995–1999). National Research Council Press, Ottawa, Ontario, 523 pp.
- Etiennot, A., Giménez, R., Mareggiani, G., Moya, M. and Verdejo, J. 2000 *Manejo integrado de salicáceas*.

- Fac de Agronomia, Universidad de Buenos Aires, Buenos Aires, Argentina, 68 pp.
- FAO 2002 International Standards for Phytosanitary Measures No. 15: Guidelines for Regulating Wood Packaging Material in International Trade. Secretariat of the International Plant Protection Convention, Food and Agriculture Organization of the United Nations, Rome, 15 pp.
- Giménez, R.A. and Etiennot, A.E. 2003 Host range of *Platypus mutatus* (Chapuis, 1865) (Coleoptera: Platypodidae). *Entomotropica*. 18, 89–94.
- Gonzalez, P., Villaverde, R., Alfaro, R. and Zerba, E. 2005 Identification of volatile emissions from *Platypus mutatus*. (= *sulcatus*) (Coleoptera: Platypodidae) and their behavioral activity. *J. Econ. Entomol.* 98, 1506–1509.
- Guerrero, R.T. 1966 Una nueva especie de hongo imperfecto asociado con el coleoptero *Platypus sulcatus* Chapuis. *Rev. Invest. Agropecu. Ser. 5*, 3, 97–103.
- Haack, R.A. 2006 Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Can. J. For. Res.* 36, 269–288.
- Haack, R.A., Cavey, J.F., Hoebeke, E.R. and Law, K. 1996 *Anoplophora glabripennis*: a new tree-infesting exotic cerambycid invades New York. *Newsl. Mich. Entomol. Soc.* 41 (2–3), 1–3.
- Hérard, F., Ciampitti, M., Maspero, M., Krehan, H., Benker, U. and Boegel, C. 2006 *Anoplophora* species in Europe: infestations and management processes. *EPPO/OEPP Bull.* 36, 470–474.
- Hoebeke, E.R., Haugen, D.A. and Haack, R.A. 2005 Sirex noctilo: Discovery of a Palearctic Siricid Woodwasp in New York. *Newsl. Mich. Entomol. Soc.* 50 (1–2), 24–25.
- Johnson, W.T. and Lyon, H.H. 1988 *Insects That Feed on Trees and Shrubs*. Cornell University Press, Ithaca, NY, 556 pp.
- Jones, K.G. and Blackwell, M. 1998 Phylogenetic analysis of ambrosial species in the genus *Raffaelea* based on 18S rDNA sequences. *Mycol. Res.* 102, 661–665.
- Kliejunas, J.T., Burdsall, H.H., DeNitto, G.A., Eglitis, A., Haugen, D.A. Haverty, M.I. and Micales-Glaeser, J.A. 2006 Pest Risk Assessment of the Importation into the United States of Unprocessed *Pinus* Logs and Chips from Australia. USDA Forest Service, Forest Health Protection, FHTET (Series) 2006–06. Washington, D.C. 159 pp.
- Nakashima, T. 1971 Notes on the associated fungi and the mycetangia of the ambrosia beetle, *Crossotarsus niponicus* Blandford (Coleoptera: Platypodidae). *Appl. Entomol. Zool.*, 6, 131–137.
- Nakashima, T. 1972 Notes on the mycetangia of the ambrosia beetles, *Platypus severini* Blandford and *P. calamus* Blandford (Coleoptera: Platypodidae). *Appl. Entomol. Zool.* 7, 217–225.
- Orwig, D.A., Foster, D.R. and Mausel, D.L. 2002 Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *J. Biogeogr.* 29, 1475–1487.
- Poland, T.M. and McCullough, D.M. 2006 Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *J. For.*, 104, 118–124.
- Santoro, F.H. 1957 Contribucion al conocimiento de la biologia de *Platypus sulcatus* Chapuis (Taladro del Alamo Mussolini y de otras especies forestales). *Rev. Invest. Forest.* 1, 7–24.
- Santoro, F.H. 1963 Bioecologia de *Platypus sulcatus* Chapuis (Coleoptera: Platypodidae). *Rev. Invest. Forest.* 4, 7–24.
- Santoro, F.H. 1965 Descripcion de cinco estadios larvales y de la pupa de *Platypus sulcatus* Chapuis. *IDIA.* 16, 49–58.
- Smith, G. and Hurley, J.E. 2000 First North American record of the Palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *Coleopt. Bull.* 54, 540.
- Tremblay, E., Espinosa, B., Mancini, D. and Caprio, G. 2000 Un coleottero proveniente dal Sudamerica minaccia i pioppi. *Inf. Agr.* 56 (48), 89–90.
- Wood, S.L. 1993 Revision of the genera of Platypodidae (Coleoptera). *Great Basin Nat.* 53, 259–281.
- Wood, S.L. and Bright, D.E. 1992 A catalog of Scolytidae and Platypodidae (Coleoptera), part 2: taxonomic index. *Great Basin Nat. Mem.* 13, 1–1553.