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Synthesis of the interactions between the European species of the genus *Bruchus* (Coleoptera: Chrysomelidae: Bruchinae) and their natural enemies

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Summary. Scientific literature has been studied to determine the known relationships between the European species of the genus *Bruchus* and their natural enemies, restricted to the arthropods. Firstly, an overview of the studies concerning natural enemies of the bruchid beetles is provided. Then, an analysis of the known relationships is given: 48 natural enemy species associated with *Bruchus* are highlighted, with a majority of Hymenoptera parasitoids. Relationships are commented and their validity is assessed. Lastly, a lack of knowledge of most species is indicated by this study.

Résumé. État de l'art sur les interactions entre les espèces européennes du genre *Bruchus* (Coleoptera: Chrysomelidae: Bruchinae) et leurs biorégulateurs. Une synthèse bibliographique des relations connues entre les espèces du genre *Bruchus* citées d'Europe et leurs biorégulateurs, restreints aux arthropodes, est présentée. Dans un premier temps, un bref historique de l'étude des ennemis naturels de bruches est donné. Dans un second temps, les interactions relevées sont analysées. Elles sont commentées et leur validité est discute. Quarante-huit espèces biorégulatrices associées ressortent de cette étude, dont une majorité d'Hyménoptères parasitoïdes. Enfin un manque de connaissances pour la plupart des espèces est mis en évidence.

Keywords: Bruchid beetles; regulation; natural enemies; review

Bruchinae beetles, also called "seed beetles" or "bruchid beetles", include nearly 1650 species globally (Rheinheimer & Hassler 2018). Almost all species feed on seeds at larval stage. Twenty-five *Bruchus* species are recorded in Europe (Anton 2010). Larvae feed on various leguminous plant species, wild or cultivated (Delobel & Delobel 2003). Some *Bruchus* species are pests, the most harmful in Europe being the broad bean weevil *Bruchus rufimanus* Boheman, 1833, the pea weevil *Bruchus pisorum* (Linnaeus, 1758) and the lentil weevil *Bruchus signaticornis* Gyllenhal, 1833 (Chapelin-Viscardi et al. 2019).

Natural enemies are beneficial organisms which are able to control pest populations. They include two groups, predators and parasitoids, which have different trophic interactions. Predators kill their prey to feed themselves or their offspring. They usually kill several prey to ensure their development. Parasitoids develop, at larval stage, in or on a host. Feeding leads to host death. Only one host is usually necessary to achieve their development.

The goal of biological control is to use living organisms, i.e. natural enemies, to control the populations of crop pests (Boyer et al. 2017). Implementing biological control requires extensive understanding of the biology and ecology of both the targeted pests and their natural enemies (Gillespie et al. 2016). The interactions between pests and their natural enemies (pest–natural enemy interactions) may however be quite complex, including many different ecological features, such as for instance gregarious behaviour, host-specificity or hyper parasitism.

Bruchus–natural enemy relations are the subject of several articles, the most recent one being the work of Pérez-Benavides et al. (2019), which is a taxonomic list of the Chalcidoidea associated with Bruchinae at the global scale. The aim of the present paper is to provide an overview of known interactions between natural enemies and European *Bruchus* species, with an analysis of data validity and a brief biologic description of the species involved.

Material and methods

Setting up the natural enemies list

The scope of this literature review includes the natural enemies associated with the genus *Bruchus*, restricted to the species mentioned from Europe in the Catalogue of Palaearctic Coleoptera (Anton 2010), in accordance with the competence field and range of interest of the authors. The geographic area covered includes the European Union member countries, plus Norway, Switzerland, UK, and the Western Balkan countries.

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When only the genus is mentioned in the literature, i.e. the species is not precisely identified, the occurrence is reported as *Bruchus* sp. Studying all *Bruchus* species from Europe allows a better understanding of the natural enemies linked to this genus.

All predatory and parasitoid arthropods quoted in the literature as being associated to a species of the genus *Bruchus* are included in the list, regardless of whether or not they have been mentioned from Europe. This provides an overview of all known natural enemies for each *Bruchus* species, which is interesting in the context of a biological control strategy. The terms "natural enemies" here include the predatory and parasitoid arthropods.

Literature studied

Around 200 scientific publications were consulted for the literature review, of which 100 mention *Bruchus*–natural enemy interactions. The data on the natural enemies of *Bruchus* can be broken down into two groups. The first group includes data from catalogues, lists and specialised databases that cover the natural enemies of Bruchinae. The following were consulted: Parker (1957), Léonide (1960), De Luca (1965), Steffan (1981), Abdul-Rassoul (1990), Balevski (1999), Noyes (2019) and Pérez-Benavides et al. (2019). The second group includes scattered data published in various papers. The most interesting works on the subject, in terms of number of new interactions or reliability, are the works of Curtis (1860), Perris (1873), Menault (1886), Lichtenstein & Picard (1919), Carles (1943), Steffan (1954), De Luca (1962), Bouček (1970), Tobias (1986), Nieves & Askew (1988), Askew & Nieves (2000), Hagstrum & Subramanyam (2009), Fusu (2010), Zerova (2010), Zampetti & Ricci (2012), Baur et al. (2014) and Gibson & Fusu (2016). All publications consulted are quoted in the references.

List layout

All data are gathered in a summary table (Table 1). Each row gives the information on a natural enemy linked to a *Bruchus* species, and corresponds to one citation. For each citation, the given information is presented in seven columns, as follows.

- The column "Reliability" describes how much credit to give to the occurrence. Three values are possible:
  1. Reliable. The occurrence comes from a genuine study of rearing and identification, or (not incompatibly) from various independent publications (meaning it is not the same data transcribed from previous research works).
  2. To be confirmed. Without necessarily being challenged by other authors, the relationship has only been found once in ancient literature (herein refers to papers published before 1950) or was not subject to a well-described rearing.
  3. Unreliable. Several authors contest its reliability in later research works. It mostly concerns information from ancient papers, sometimes altered by nomenclatural changes or due to misidentifications.
- "Natural enemy" gives the Latin name of the natural enemy species, spelled according to Universal Chalcidoidea Database (Noyes 2019) for the Chalcidoidea and to INPN (Muséum national d'Histoire naturelle 2003) for other superfamilies. Regarding species not found in both of these references, the most up-to-date literature has been followed.
- "Natural enemy family" gives the family of the natural enemy species, following the same references as for "Natural enemy".
- The column "Trophic category" indicates whether the natural enemy species is a predator (PR) or a parasitoid (A).
- The column "Natural enemy distribution" indicates in which biogeographic realm the natural enemy species occurs.
- The column "*Bruchus* species" gives the Latin name of the seed beetle, according to the Catalogue of Palaearctic Coleoptera (Anton 2010).
- Lastly, "Original data" gives the reference(s) in which the *Bruchus*–natural enemy interaction is described. When the original data has not been consulted, the oldest list in which the interaction is cited is given in italic type.

Representation of the interactions

The interactions are presented in Figure 1. The figure was produced using RStudio software and the "bipartite" package (Dormann et al. 2008; R Core Team 2019). The function "plotweb" is used, with the parameter "method = normal", resulting in a graphic display of Table 1.

Results and discussion

The list of *Bruchus* – natural enemy interactions resulting from the literature review is given in Table 1.

Figure 1 summarises the known relationships between parasitoids and the European *Bruchus* species. Predators are excluded as there are few *Bruchus*–predator interactions given in the literature, and only interactions considered as "Reliable" or "To be confirmed" are represented. Figure 1 complements Table 1 as it gives a visual representation of the species involved and the number of interactions each one has. To precisely identify the two species involved in an interaction, please refer to Table 1.

Chronology of the studies of Bruchus*–natural enemy interactions*

The literature analysis indicates that the oldest mentions of *Bruchus*–natural enemy connections date back to the second half of the nineteenth century. Seed beetles and natural enemy species were often separately described before this period, and the relationships between them remained unknown.

In 1860, J. Curtis described the association between some seed beetles and their host plant (Curtis 1860) and quoted three species of Hymenoptera parasitoids: *Sigalphus pallipes* Nees, 1816, *Sigalphus caudatus* Nees, 1816 and *Hormius rubiginosus* Nees, 1816. In 1873, E. Perris quoted the species *Bruchus signaticornis* Gyllenhal, 1833, *B. nubilus* Boheman, 1833, *B. pallidicornis* Boheman, 1833 and *B. granarius* Linnaeus, 1767 as being parasitised by *Sigalphus striatulus* Nees, 1816

Table 1. List of the natural enemies associated with the European *Bruchus* species. In the column "Trophic category", "A" stands for "parasitoid" and "PR" for predator. In the column "Original data", a reference in italic type is an article in which the relation between the natural enemy and the *Bruchus* species is cited, and not the original work in which the information was revealed (work not consulted by the authors). More details are given in the paragraph "List Layout" of the Material and methods section.

Reliability	Natural enemy	Natural enemy family	Trophic category	Natural enemy distribution	*Bruchus* species	Original data
1	*Anisopteromalus calandrae* (Howard, 1881)	Pteromalidae	A	Cosmopolitan	*Bruchus brachialis* Fahraeus, 1839	*De Luca 1965*
					Bruchus pisorum (Linnaeus, 1758)	*De Luca 1965*
					Bruchus rufimanus Boheman, 1833	Ahmed 1996
					Bruchus sp.	*Pérez-Benavides et al. 2019*
3	*Aprostocetus aethiops* (Zetterstedt, 1838)	Eulophidae	A	Palearctic	*Bruchus pisorum* (Linnaeus, 1758)	Leonardi 1928
3	*Aprostocetus claviger* (Thomson, 1878)	Eulophidae	A	Palearctic	*Bruchus pisorum* (Linnaeus, 1758)	Leonardi 1928
1	*Atomus* sp.	Acarien	PR	Nearctic	*Bruchus pisorum* (Linnaeus, 1758)	Larson et al. 1938
1	*Baryscapus bruchivorus* (Gahan, 1942)	Eulophidae	A	Holarctic	*Bruchus brachialis* Fahraeus, 1839	Domenichini 1951; Leong & Dickanson 1975
					Bruchus lentis Frölich, 1799	*Pérez-Benavides et al. 2019*
					Bruchus luteicornis Illiger, 1794	Parker 1957
					Bruchus rufipes Herbst, 1783	Parker 1957
					Bruchus ulicis Mulsant & Rey, 1858	Parker 1957
1	*Baryscapus protasis* (Graham, 1991)	Eulophidae	A	Palearctic	*Bruchus* sp.	Graham 1991
3	*Bracon hylobii* Ratzeburg, 1848	Braconidae	A	Palearctic	*Bruchus pisorum* (Linnaeus, 1758)	De Luca 1970
3	*Bracon praecox* (Wesmael, 1838)	Braconidae	A	Palearctic	*Bruchus atomarius* (Linnaeus, 1761)	De Gaulle 1908
					Bruchus lentis Frölich, 1799	*Hagstrum & Subramanyam 2009*
					Bruchus viciae Olivier, 1795	De Gaulle 1908; Leonardi 1928
3	*Bracon variator* Nees, 1811	Braconidae	A	Palearctic	*Bruchus laticollis* Boheman, 1833	De Luca 1965
3	*Cecidostiba fungosa* (Geoffroy, 1785)	Pteromalidae	A	Palearctic	*Bruchus atomarius* (Linnaeus, 1761)	*De Luca 1965*
					Bruchus rufipes Herbst, 1783	*De Luca 1965*
					Bruchus signaticornis Gyllenhal, 1833	*De Luca 1965*
					Bruchus sp.	Perris 1873
					Bruchus viciae Olivier, 1795	*De Luca 1965*
1	*Cerceris labiata* (Olivier, 1792)	Crabronidae	PR	Palearctic	*Bruchus rufipes* Herbst, 1783	*Hagstrum & Subramanyam 2009*
					Bruchus viciae Olivier, 1795	*Zampetti & Ricci 2012*
1	*Cerceris rubida* (Jurine, 1807)	Crabronidae	PR	Palearctic	*Bruchus atomarius* (Linnaeus, 1761)	De Gaulle 1908
					Bruchus rufipes Herbst, 1783	De Gaulle 1908
3	*Chremylus elaphus* Haliday, 1833	Braconidae	A	Cosmopolitan	*Bruchus atomarius* (Linnaeus, 1761)	Leonardi 1928
					Bruchus lentis Frölich, 1799	*Hagstrum & Subramanyam 2009*
					Bruchus rufimanus Boheman, 1833	De Gaulle 1908; Leonardi 1928
3	*Chrysocharis pentheus* (Walker, 1939)	Eulophidae	A	Cosmopolitan	*Bruchus rufipes* Herbst, 1783	Dours 1869
					Bruchus viciae Olivier, 1795	*Zampetti & Ricci 2012*
2	*Dibrachys microgastri* (Bouché, 1834)	Pteromalidae	A	Cosmopolitan	*Bruchus brachialis* Fahraeus, 1839	Pinckney 1937

(*continued*)

Table 1. (*Continued*).

Reliability	Natural enemy	Natural enemy family	Trophic category	Natural enemy distribution	*Bruchus* species	Original data
1	*Dinarmus acutus* (Thomson, 1878)	Pteromalidae	A	Palearctic	*Bruchus affinis* Frölich, 1799	Parker 1957; Léonide 1960
					Bruchus brachialis Fahraeus, 1839	Leong & Dickanson 1975
					Bruchus emarginatus Allard, 1868	Parker 1957
					Bruchus lentis Frölich, 1799	De Luca 1962
					Bruchus luteicornis Illiger, 1794	Parker 1957
					Bruchus rufimanus Boheman, 1833	Parker 1957
					Bruchus rufipes Herbst, 1783	Parker 1957
					Bruchus sp.	Bouček 1970
					Bruchus tristiculus Fahraeus, 1839	Parker 1957
					Bruchus viciae Olivier, 1795	Parker 1957
1	*Dinarmus basalis* (Rondani, 1877)	Pteromalidae	A	Cosmopolitan	*Bruchus lentis* Frölich, 1799	De Luca 1962
					Bruchus pisorum (Linnaeus, 1758)	Chittenden 1902
					Bruchus rufimanus Boheman, 1833	*De Luca 1965*
					Bruchus sp.	*Pérez-Benavides et al. 2019*
1	*Dinarmus italicus* (Masi, 1922)	Pteromalidae	A	Palearctic	*Bruchus brachialis* Fahraeus, 1839	Parker 1957
					Bruchus luteicornis Illiger, 1794	Parker 1957
					Bruchus rufipes Herbst, 1783	Parker 1957
					Bruchus signaticornis Gyllenhal, 1833	*Zampetti & Ricci 2012*
					Bruchus tristiculus Fahraeus, 1839	Parker 1957
					Bruchus tristis Boheman, 1833	Parker 1957
1	*Dinarmus magnus* (Rohwer, 1934)	Pteromalidae	A	Cosmopolitan	*Bruchus pisorum* (Linnaeus, 1758)	Rohwer 1934
			A	Cosmopolitan	*Bruchus rufimanus* Boheman, 1833	Rohwer 1934
2	*Eupelmus messene* Walker, 1839	Eupelmidae	A	Cosmopolitan	*Bruchus brachialis* Fahraeus, 1839	*Pérez-Benavides et al. 2019*
3	*Eupelmus microzonus* Foerster, 1860	Eupelmidae	A	Palearctic	*Bruchus affinis* Frölich, 1799	Parker 1957
					Bruchus emarginatus Allard, 1868	Parker 1957
					Bruchus rufimanus Boheman, 1833	*Askew & Nieves 2000*
					Bruchus rufipes Herbst, 1783	Parker 1957
					Bruchus tristiculus Fahraeus, 1839	Parker 1957
1	*Eupelmus orientalis* (Crawford, 1913)	Eupelmidae	A	Afrotropical	*Bruchus pisorum* (Linnaeus, 1758)	*De Luca 1965*
1	*Eupelmus pulchriceps* (Cameron, 1904)	Eupelmidae	A	Nearctic	*Bruchus brachialis* Fahraeus, 1839	*De Luca 1965*
					Bruchus pisorum (Linnaeus, 1758)	*De Luca 1965*
2	*Eupelmus swezeyi* (Crawford, 1915)	Eupelmidae	A	Hawaii	*Bruchus rufimanus* Boheman, 1833	*Hagstrum & Subramanyam 2009*
3	*Eupelmus urozonus* Dalman, 1820	Eupelmidae	A	Palearctic	*Bruchus lentis* Frölich, 1799	*De Luca 1965*
					Bruchus luteicornis Illiger, 1794	*Askew & Nieves 2000*
					Bruchus rufipes Herbst, 1783	*Parker 1957*
3	*Eupelmus vesicularis* (Retzius, 1783)	Eupelmidae	A	Palearctic	*Bruchus brachialis* Fahraeus, 1839	Leong & Dickanson 1975
					Bruchus lentis Frölich, 1799	*Pérez-Benavides et al. 2019*
					Bruchus pisorum (Linnaeus, 1758)	*De Luca 1970*
					Bruchus rufipes Herbst, 1783	Parker 1957

(*continued*)

Table 1. (*Continued*).

Reliability	Natural enemy	Natural enemy family	Trophic category	Natural enemy distribution	*Bruchus* species	Original data
1	*Eurydinoteloides incerta* (Ashmead, 1893)	Pteromalidae	A	Nearctic	*Bruchus brachialis* Fahraeus, 1839	*De Luca 1965*
1	*Eurytoma lathyri* Zerova, 1979	Eurytomidae	A	Palearctic	*Bruchus affinis* Frölich, 1799	Zerova & Seryogina 2006
1	*Eurytoma lyubae* Zerova, 1995	Eurytomidae	A	Palearctic	*Bruchus* sp.	Zerova & Seryogina 2006
1	*Eurytoma obtusa* Bugbee, 1967	Eurytomidae	A	Nearctic	*Bruchus brachialis* Fahraeus, 1839	Bugbee 1967
1	*Eurytoma tylodermatis* Ashmead, 1896	Eurytomidae	A	Nearctic	*Bruchus brachialis* Fahraeus, 1839	Bridwell & Bottimer 1933
2	*Eurytoma wachtli* Mayr, 1878	Eurytomidae	A	Palearctic	*Bruchus brachialis* Fahraeus, 1839 *Bruchus laticollis* Boheman, 1833 *Bruchus rufimanus* Boheman, 1833 *Bruchus rufipes* Herbst, 1783 *Bruchus signaticornis* Gyllenhal, 1833 *Bruchus tristiculus* Fahraeus, 1839 *Bruchus tristis* Boheman, 1833	Parker 1957 Parker 1957 Parker 1957 Parker 1957 *Zampetti & Ricci 2012* Parker 1957 Parker 1957
2	*Gastrancistrus undulatus* (Ratzeburg, 1852)	Pteromalidae	A	Cosmopolitan	*Bruchus pisorum* (Linnaeus, 1758)	Leonardi 1928
3	*Laelius utilis* Cockerall, 1920	Bethylidae	A	Nearctic	*Bruchus brachialis* Fahraeus, 1839	*Hagstrum & Subramanyam 2009*
2	*Lamennaisia ambigua* (Nees, 1834)	Encyrtidae	A	Cosmopolitan	*Bruchus brachialis* Fahraeus, 1839	*De Luca 1965*
1	*Lariophagus distinguendus* (Förster, 1841)	Pteromalidae	A	Cosmopolitan	*Bruchus brachialis* Fahraeus, 1839 *Bruchus rufimanus* Boheman, 1833 *Bruchus signaticornis* Gyllenhal, 1833	*De Luca 1965* *Delucchi 1962* *Delucchi 1962*
1	*Microdontomerus anthonomi* (Crawford, 1907)	Torymidae	A	Nearctic	*Bruchus brachialis* Fahraeus, 1839 *Bruchus pisorum* (Linnaeus, 1758)	*De Luca 1965* *De Luca 1965*
3	*Pachylarthrus breviventris* Forst	Pteromalidae	A	Palearctic	*Bruchus signaticornis* Gyllenhal, 1833	*De Luca 1965*
2	*Pnigalio pecticornis* (Linnaeus, 1758)	Eulophidae	A	Palearctic	*Bruchus rufipes* Herbst, 1783	Elliot & Morley 1907; Leonardi 1928
2	*Pteromalus semotus* (Walker, 1834)	Pteromalidae	A	Palearctic	*Bruchus loti* Paykull, 1800	*Zampetti & Ricci 2012*
1	*Pteromalus sequester* Walker, 1835	Pteromalidae	A	Cosmopolitan	*Bruchus affinis* Frölich, 1799 *Bruchus atomarius* (Linnaeus, 1761) *Bruchus pisorum* (Linnaeus, 1758)	Vidal 1997 Vidal 1997 *De Luca 1965*
1	*Pteromalus* sp.	Pteromalidae	A	Cosmopolitan	*Bruchus brachialis* Fahraeus, 1839 *Bruchus lentis* Frölich, 1799	*Pérez-Benavides et al. 2019* *Pérez-Benavides et al. 2019*
2	*Pteromalus varians* (Spinola, 1808)	Pteromalidae	A	Palearctic	*Bruchus rufipes* Herbst, 1783 *Bruchus signaticornis* Gyllenhal, 1833	Menault 1886 Menault 1886
1	*Pyemotes ventricosus*	Pyemotidae	PR	Cosmopolitan	*Bruchus pisorum* (Linnaeus, 1758) *Bruchus rufimanus* Boheman, 1833	*De Luca 1965* *De Luca 1965*
3	*Semiotellus mundus* (Walker, 1834)	Pteromalidae	A	Palearctic	*Bruchus rufipes* Herbst, 1783 *Bruchus viciae* Olivier, 1795	*De Luca 1965* *Zampetti & Ricci 2012*

(*continued*)

Table 1. (*Continued*).

Reliability	Natural enemy	Natural enemy family	Trophic category	Natural enemy distribution	*Bruchus* species	Original data
3	*Stenomalina micans* (Olivier, 1813)	Pteromalidae	A	Palearctic	*Bruchus pisorum* (Linnaeus, 1758)	*De Luca 1965*
					Bruchus rufimanus Boheman, 1833	*De Luca 1965*
					Bruchus rufipes Herbst, 1783	*De Luca 1965*
					Bruchus signaticornis Gyllenhal, 1833	*De Luca 1965*
					Bruchus viciae Olivier, 1795	*Zampetti & Ricci 2012*
3	*Systasis encyrtoides* Walker, 1834	Pteromalidae	A	Palearctic	*Bruchus pisorum* (Linnaeus, 1758)	De Gaulle 1908
2	*Tetrastichus* sp.	Eulophidae	A	Palearctic	*Bruchus signaticornis* Gyllenhal, 1833	Carles 1943
2	*Torymus* sp.	Torymidae	A	Cosmopolitan	*Bruchus rufipes* Herbst, 1783	Parker 1957
2	*Triaspis brucivora* (Rondani, 1877)	Braconidae	A	Palearctic	*Bruchus atomarius* (Linnaeus, 1761)	Rondani 1877
					Bruchus lentis Frölich, 1799	Rondani 1877
1	*Triaspis facialis* (Ratzeburg, 1852)	Braconidae	A	Palearctic	*Bruchus lentis* Frölich, 1799	Balevski 1989
1	*Triaspis forbesii* (Dalla Torre)	Braconidae	A	Palearctic	*Bruchus rufimanus* Boheman, 1833	Hagstrum & Subramanyam 2009
1	*Triaspis luteipes* (Thomson, 1874)	Braconidae	A	Palearctic	*Bruchus affinis* Frölich, 1799	Lichtenstein & Picard 1919; Fahringer 1934
					Bruchus lentis Frölich, 1799	De Luca 1965
					Bruchus rufimanus Boheman, 1833	Gimingham 1922
					Bruchus signaticornis Gyllenhal, 1833	Carles 1943
1	*Triaspis obscurella* (Nees, 1816)	Braconidae	A	Palearctic	*Bruchus lentis* Frölich, 1799	Tobias 1986
					Bruchus rufimanus Boheman, 1833	Tobias 1986
1	*Triaspis pallipes* Nees (1816)	Braconidae	A	Cosmopolitan	*Bruchus affinis* Frölich, 1799	Tobias 1986
					Bruchus atomarius (Linnaeus, 1761)	Marshall 1890; Fahringer 1934; Telenga 1941; Tobias 1986
					Bruchus luteicornis Illiger, 1794	Papp 1998
					Bruchus rufimanus Boheman, 1833	De Luca 1962
1	*Triaspis stictostiba* Martin, 1956	Braconidae	A	Nearctic	*Bruchus rufimanus* Boheman, 1833	Krombein 1958
1	*Triaspis striatula* (Nees, 1816)	Braconidae	A	Palearctic	*Bruchus atomarius* (Linnaeus, 1761)	Tobias 1986
					Bruchus rufipes Herbst, 1783	Tobias 1986
					Bruchus signaticornis Gyllenhal, 1833	Tobias 1986
					Bruchus sp.	Perris 1873
2	*Triaspis thomsoni* Fahringer, 1934	Braconidae	A	Palearctic	*Bruchus atomarius* (Linnaeus, 1761)	De Luca 1962
					Bruchus brachialis Fahraeus, 1839	De Luca 1965
					Bruchus rufipes Herbst, 1783	Domenichini 1951
					Bruchus signaticornis Gyllenhal, 1833	De Luca 1962

(*continued*)

Table 1. (*Continued*).

Reliability	Natural enemy	Natural enemy family	Trophic category	Natural enemy distribution	*Bruchus* species	Original data
1	*Triaspis thoracica* (Curtis, 1860)	Braconidae	A	Cosmopolitan	*Bruchus affinis* Frölich, 1799	Parker 1957; Papp 1998
					Bruchus atomarius (Linnaeus, 1761)	Curtis 1860; Fahringer 1934; Telenga 1941
					Bruchus brachialis Fahraeus, 1839	Parker 1957
					Bruchus dentipes (Baudi, 1886)	Morris 1928; Tahhan & van Emden 1989
					Bruchus emarginatus Allard, 1868	Parker 1957
					Bruchus laticollis Boheman, 1833	Parker 1957
					Bruchus lentis Frölich, 1799	Marshall 1890; Fahringer 1934; Telenga 1941; Parker 1957; Tobias 1986; Balevski 1989; Papp 1998
					Bruchus loti Paykull, 1800	Parker 1957
					Bruchus luteicornis Illiger, 1794	Parker 1957; Balevski 1989; Papp 1998
					Bruchus pisorum (Linnaeus, 1758)	Fahringer 1934; Telenga 1941; Rozsypal 1956; Parker 1957; Capek et al. 1982; Tobias 1986; Papp 1998
					Bruchus rufimanus Boheman, 1833	Marshall 1890; Fahringer 1934; Monastero 1938; Telenga 1941; Parker 1957; Tobias 1986
					Bruchus rufipes Herbst, 1783	Parker 1957; Papp 1998
					Bruchus signaticornis Gyllenhal, 1833	Zampetti & Ricci 2012
					Bruchus tristiculus Fahraeus, 1839	Parker 1957
					Bruchus tristis Boheman, 1833	Parker 1957
					Bruchus ulicis Mulsant & Rey, 1858	Parker 1957
					Bruchus venustus Fähraeus, 1839	Papp 1998
					Bruchus viciae Olivier, 1795	Parker 1957; Tobias 1986
2	*Trichomalopsis leguminis* (Gahan, 1937)	Pteromalidae	A	Nearctic	*Bruchus pisorum* (Linnaeus, 1758)	Gahan 1937
2	*Trichomalus statutus* (Foerster, 1841)	Pteromalidae	A	Palearctic	*Bruchus signaticornis* Gyllenhal, 1833	*Zampetti & Ricci 2012*
					Bruchus tristis Boheman, 1833	*Hoffmann 1945*
1	*Trimeromicrus maculatus* Gahan, 1914	Pteromalidae	A	Nearctic	*Bruchus* sp.	Gibson 2013
1	*Uscana semifumipennis* Girault, 1911	Trichogrammatidae	A	Cosmopolitan	*Bruchus pisorum* (Linnaeus, 1758)	*De Luca 1965*
					Bruchus rufimanus Boheman, 1833	Steffan 1954
					Bruchus sp.	DeSantis 1997
1	*Uscana senex* (Grese, 1923)	Trichogrammatidae	A	Palearctic	*Bruchus affinis* Frölich, 1799	Steffan 1954
					Bruchus lentis Frölich, 1799	Karpova 1950
					Bruchus pisorum (Linnaeus, 1758)	*Steffan 1954*
1	*Zelus renardii* Kolenati, 1857	Reduviidae	PR	Palearctic	*Bruchus rufimanus* Boheman, 1833	*Hagstrum & Subramanyam 2009*

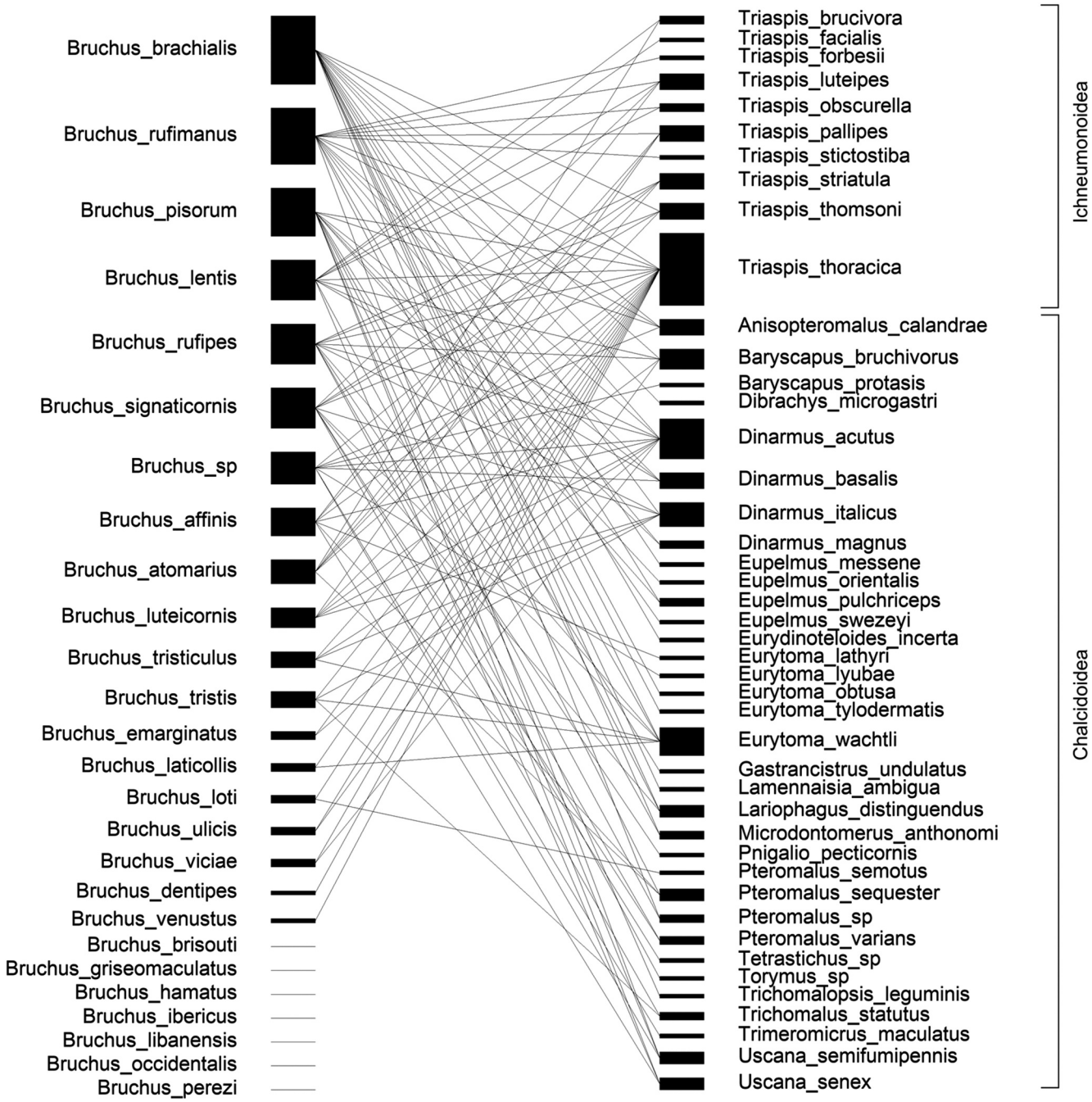

Figure 1. Known interactions between Hymenoptera parasitoids (right column) and the *Bruchus* species (left column). Only the interactions deemed "Reliable" and "To be confirmed" are presented. Design RStudio (Dormann et al. 2008; R Core Team 2019).

and *Pteromalus leucopezus* Ratzeburg, 1844 (Perris 1873).

These *Sigalphus* species have now been transferred to the genus *Triaspis* (Braconidae). *Hormius rubiginosus* has been synonymized with *Chremylus elaphus* Haliday, 1833 (Braconidae), now known as a moth parasitoid (Mason 1948), and *Pteromalus leucopezus* was renamed as *Cecidostiba fungosa* (Geoffroy, 1785) (Pteromalidae), a common parasitoid associated with cynipid galls on various *Quercus* (Nieves & Askew 1988). On the other hand, the nomenclature regarding the bruchid names was significantly modified: for instance, among the five species cited by E. Perris, only *B. signaticornis* remains valid.

These data show that initial works, although providing important information, should be considered with

caution, because of common misidentifications resulting from the absence of easy exchanges between biologists at that time.

In Europe, the main studies on bruchid beetle natural enemies were carried out during the second half of the twentieth century by Parker (1957) and Léonide (1960). Their data result from leguminous plant rearing, associating bruchid beetles and parasitoids that emerge from the seeds. The authors underlined that caution is required about their data: some interactions are uncertain as other insects, together with their parasitoids, had emerged from the reared seeds.

Within the same decade, De Luca (1965) drafted a world catalogue of the interactions between seed beetles and other living organisms. It consists of three lists of the Bruchinae species and their parasites, predators and parasitoids linked, ordered by Bruchinae species, natural enemy species and countries. His work has been widely used in further studies.

In 1981, J. R. Steffan was the first author to undertake a synthesis of known data about on the seed beetles' parasitoids, with a critical analysis of the data available at that time and called "The parasites of Bruchids" (Steffan 1981). It is mainly based on the catalogues published by De Luca (1965) and Peck (1963). The synthesis has a worldwide coverage, as for de Luca's list. Peck's list concerns the New World fauna.

Subsequent authors mainly used the data provided by de Luca together with a few scattered papers. Lastly, the list of Chalcidoidea associated with Bruchinae, published in 2019, is an important work on a global scale, limited to the Chalcidoidea superfamily (Pérez-Benavides et al. 2019).

This chronology highlights a longstanding knowledge of the interactions between natural enemies and seed beetles. It also demonstrates that these interactions have been poorly studied, even though seed beetles are considered as major pests in leguminous crops. This may be due to the apparent difficulty of identifying *Bruchus* species.

However, it should be noted that in other regions, particularly in Africa and Central America, more studies on the potential of Hymenoptera species to regulate Bruchinae populations have been carried out. They mostly focus on Bruchinae other than the genus *Bruchus*, mainly the species attacking stored seeds (Hetz & Johnson 1988; Delobel 1989; Van Huis et al. 1990; Ouedraogo et al. 1996; Sanon et al. 2005).

Comments on the list

When restricting the genus *Bruchus* to the 25 species mentioned in Europe, 166 *Bruchus*–natural enemy interactions were found in the literature (Table 1). These interactions involve 64 natural enemy species, of which 48 are considered 'reliable' or 'to be confirmed'. The remaining 16 are 'unreliable' and are not included in the following quantitative comparisons.

More or less regulated, or more or less studied *Bruchus* species. Data distribution is very heterogeneous: the interactions refer to 18 *Bruchus* species, seven species not being associated with any natural enemy. Two *Bruchus* species are linked with only one parasitoid species, whereas 17 natural enemies are cited as associated with *Bruchus brachialis* Fåhraeus, 1839.

This disparity is not adequately explained by the fact that some species are more exposed to parasitism and predation than others. It is more likely due to the relative agronomic importance of the *Bruchus* species, and therefore to the number of relevant studies of which they are the subject (Steffan 1981). Among the five species having the most interactions are found: (i) *B. brachialis*, well studied in the USA; (ii) *B. pisorum*, the main pea crop pest found across the world; (iii) *B. rufimanus*, which feeds on broad bean; and (iv) *B. lentis* Frölich, 1799, which feeds on lentil and has been studied in detail by De Luca (1956).

This heterogeneity leads to the conclusion that knowledge related to the natural enemies of *Bruchus* remains incomplete and that analysis of literature data only gives a first glimpse of the number and identity of the species involved.

Strong prevalence of parasitoids over predators. First, it is interesting to look at the distinction between the two groups of natural enemies: predators and parasitoids.

Several predation observations are reported in the literature. The predator species of *Bruchus* belong to various arthropod groups: Spiders, Hymenoptera, mites and Hemiptera. They represent five species out of the 48 considered "reliable" or "to be confirmed" in the list (Table 1).

The remaining 90% of natural enemy species are parasitoids. They are exclusively Hymenoptera, belonging to three superfamilies: the Ichneumonoidea, the Chalcidoidea and the Chrysidoidea.

Generalist predators from various taxonomic groups. Among the predators, the two most cited groups are detailed here. References to the first of these, mites, are erratic observations, which mention consumption of *Bruchus* eggs or first instar larvae by generalist predator mites. A noteworthy species is *Pediculoides ventricosus* (Newport, 1850) (Pyemotidae), a generalist mite which sometimes attacks seed beetles (Larson et al. 1938; Nicoli & Sempe 1969).

Secondly, the genus *Cerceris*, belonging to the Crabronidae, is noteworthy; its females hunt adult bruchid beetles, among others, bringing them into a burrow

dug in the ground, where the larvae are fed. No species is particularly associated with the Bruchinae, but *C. interrupta* (Panzer, 1799), *C. quadricincta* (Panzer, 1799) and *C. rubida* (Jurine, 1807) consume a limited number of prey taxa including Bruchinae (Bitsch et al. 1997).

Other citations of predation concern more generalist organisms, such as some spiders and even birds, which frequently consume *Bruchus* adults, especially when cultivated leguminous plants are harvested.

Hymenoptera parasitoids, the most numerous natural enemies. Hymenoptera parasitoids account for most citations of the natural enemy species of *Bruchus*. They are included in the superfamilies Ichneumonoidea and Chalcidoidea, plus one species of Chrysidoidea, which is grouped together with Chalcidoidea in the discussion.

Figure 1 summarises the interactions between parasitoids and *Bruchus* species. On the one hand, it is interesting to note that two thirds of parasitoid species only parasitise one or two *Bruchus* species. This means that either the parasitoids are restricted to a small number of hosts or, more likely, that a large part of the species' biology has yet to be studied.

On the other hand, some species are mentioned as parasitising many *Bruchus* species. This is notably the case for the species *Triaspis thoracica* (Curtis, 1860), which is cited in relation to 17 species of *Bruchus*, i.e. three quarters of the *Bruchus* species in Europe. It can be concluded that this species is a usual parasitoid of bruchid beetles.

The composition of the two superfamilies of *Bruchus* parasitoids is described below:

- The Ichneumonoidea group comprises the Ichneumonidae and the Braconidae. Only the latter family includes *Bruchus* parasitoids, which are cited from three genera: *Triaspis, Bracon* and *Chremylus*.
- Chalcidoidea are small parasitoid Hymenoptera. They are divided into 22 families worldwide, of which at least 19 are found in Europe (Goulet & Huber 1993; Delvare 2018). It appears that the species listed as being related to the genus *Bruchus* account for 31 species, among seven families. Although identification to species level remains difficult for some taxonomic groups and the biology of many species is still poorly known, some genera have been well studied.

The rest of the discussion is the subject of the two following sub-sections. The purpose of the first one is to cite and explain the removal of some species from the *Bruchus* parasitoid list. The second one provides details on the different species of Braconidae and Chalcidoidea considered as truly associated with seed beetles.

***Taxa removed from the list of* Bruchus *natural enemies or considered as highly dubious*.** There are three main reasons for some interactions being false, or at least very doubtful: most commonly, misidentification of the parasitoid species; misidentification of the host; and incorrect association between parasitoid and host, due either to the presence of other organisms during the rearing experiments or to the hyperparasitism behaviour of some parasitoid species (Noyes 1994).

Concerning the Braconidae, the genus *Chremylus* is cited by De Gaulle (1908) and Leonardi (1928) and then repeated in several studies. However, it is followed in de Luca's catalogue (1965) by the annotation "Parasite les Microlépidoptères et non les Bruchides selon M. Ferrière" (i.e. "Parasites Microlepidoptera and not bruchid beetles according to M. Ferrière") (De Luca 1965). This genus is therefore not considered as a *Bruchus* parasitoid.

Several individuals of the genus *Bracon* have been found parasitising *Etiella zinckenella* (Treitschke, 1832) caterpillars in broad bean pods infested with *Bruchus* larvae (pers. obs.). The same applies to Parker's (1957) and Léonide's (1960) rearings. Citations associating this genus with *Bruchus* should therefore be treated with caution, as the *Bracon* individuals could have fed on caterpillars and not seed beetles.

Graham (1969) briefly cites one species of Ichneumonidae, *Bathyplectes curculionis* (Thomson, 1887), as a *Bruchus pisorum* parasitoid. But no other citation of *Bathyplectes* – Bruchinae has been found in literature. *B. curculionis* seems to be a parasitoid linked to the genus *Hypera* (Curculionidae), and not to the genus *Bruchus*.

Concerning the Chalcidoidea, the discussion is divided by family:

a. Encyrtidae

The genus *Lamennaisia* comprises four cosmopolitan species, including *L. ambigua* (Nees, 1834), which is thought to be a parasitoid of *Bruchus brachialis*. However, in an article by Noyes and Hayat (1984), the biology of the genus is still considered unknown.

b. Eurytomidae

In the genus *Eurytoma*, the species *E. wachtli* Mayr, 1878 is cited as a parasitoid of several *Bruchus* species (Parker 1957). However, in more recent studies it is mostly associated with Curculionidae and xylophagous beetles (Zerova 2010). Its link with *Bruchus* is thus considered as dubious. For the other *Eurytoma* species, see next paragraph.

c. Eupelmidae

Three species of the genus *Eupelmus* are cited from the *Bruchus* but are associated with Cynipidae in more recent articles: *E. microzonus* (Förster, 1860), *E. urozonus* Dalman, 1820 and *E. vasicularis* (Retzius, 1783) (Askew & Nieves 2000; Fusu 2010). For the other *Eupelmus* species, see paragraph below.

d. Eulophidae

Chrysocharis pentheus (Walker, 1939) was described in the genus *Entedon*, and is cited as a parasitoid of *Bruchus rufipes* (Dours 1869). In recent studies, *C. pentheus* is rather associated with leaf-mining Lepidoptera and Diptera Agromyzidae (Hansson 1985), its link with the *Bruchus* thus being considered incorrect (Askew & Coshan 1973; Mafi & Ohbayashi 2010).

The two *Aprostocetus* quoted in literature – respectively *A*. (*Aprostocetus*) *aethiops* (Zetterstedt, 1838) and *A*. (*Aprostocetus*) *claviger* (Thomson, 1878) – as parasitoids of Bruchinae (under *Tetrastichus*) do not develop on them, but on Cynipidae on *Quercus* (Graham 1987).

e. Pteromalidae

Cecidostiba fungosa (Geoffroy, 1785), is currently considered as a Cynipidae parasitoid according to Nieves & Askew (1988).

Pachylarthrus breviventris Förster is an enigmatic species cited as a parasitoid of *Bruchus signaticornis* in de Luca's catalogue (1965). But no mention of this species is found in the original reference given by de Luca, i.e. a work by Elliot & Morley (1907). The genus *Pachylarthrus* is now a synonym of *Halticoptera*, whose species are known as parasitoids of Diptera (Pintureau 2012).

Pteromalus varians (Spinola, 1808) is only cited once in 1886 (Menault 1886). The host list of this parasitoid species mentions four species of Curculionidae, one of Cerambycidae and one of Tischeriidae (Lepidoptera), but no Bruchinae (Todorov et al. 2014). The data are thus considered as dubious.

Stenomalina micans (Olivier, 1813) is not associated with *Bruchus* species, but with Diptera and other insects living in the herbaceous plant stems (Bouček & Rasplus 1991).

The species *Semiotellus mundus* (Walker, 1834), cited as parasitoid of *Bruchus viciae* in Zampetti & Ricci (2012), should be considered as a Cecydomiidae parasitoid and therefore excluded as a *Bruchus* parasitoid (Hui & Da-Wei 1999).

The same is true of the species *Systasis encyrtoides* Walker, 1834, which is a parasitoid of Cecydomiidae and Agromyzidae (Xiao & Huang 2001).

Trichomalopsis leguminis (Gahan, 1937) (Pteromalidae) was recently cited as a parasitoid of *Bathyplectes curculionis* (Thomson, 1887) (Ichneumonidae), which is itself a parasitoid of *B. pisorum*; other species of this genus are parasitoids of various Diptera (Chloropidae, Sarcophagidae) or secondary parasitoids of Lepidoptera through Braconidae, Ichneumonidae or Tachinidae (Graham 1969). Its interaction with *Bruchus* is dubious (Gibson & Floate 2001).

The species *Trichomalus statutus* (Foerster, 1841) is associated in the literature with Diptera. However, the other *Trichomalus* species are mostly known as Curculionidae parasitoids (Delucchi & Graham 1956). The interaction with *Bruchus* is therefore considered as dubious.

f. Torymidae

The genus *Torymus* is known as a parasitoid of Diptera and Hymenoptera. Two species are recorded from Coleoptera, on *Fraxinus* (Graham & Gijswijt 1998). The link with *Bruchus* is not certain and needs to be confirmed.

g. Bethylidae (Chrysidoidea)

Lastly, the only Chrysidoidea of the list, *Laelius utilis* Cockerall, 1920, is a North American Hymenoptera which is better associated with Dermestidae than with Bruchinae according to recent studies (Mertins 1985).

Information on biology, ecology and distribution of the Bruchus *parasitoids*

a. Pteromalidae

Genus *Dinarmus* Thomson, 1878

Occurs only in the Old World. Some species were described from Africa by Risbec (1951) in the genus *Bruchobius* and were then placed in the genus *Dinarmus*. However, study of the type specimens shows they belong to others genera (Delvare comm. pers.). Risbec's species excluded, *Dinarmus* appears to be mostly a seed beetle specialist, laying the egg directly in a larva or a nymph of the host (Rasplus 1989), whether on arboreous legumes, in stored seeds, or in crops (Rasplus 1990).

However, some data associate *Dinarmus* with Curculionidae. That is a scheme found for other seed beetle parasitoids, which are specialists on Coleoptera, mostly phytophagous (Cerambycidae, Curculionidae, Brentidae), xylophagous and those developing in seeds.

Genus *Anisopteromalus* Rutschka, 1912

The same range of hosts is found for the *Anisopteromalus* species as for the genus *Dinarmus*, with numerous citations concerning stored product beetles, including Bruchinae (Rasplus 1988). *A. calandrae* is mostly known as parasitoid of the genus *Callosobruchus* (Bruchinae), which develops in dry seeds (Bellows 1985; Baur et al. 2014). The association with *Bruchus* is therefore probable, but perhaps associated with the post-harvest period.

Genus *Lariophagus* Crawford, 1909

The same comment is made for *L. distinguendus* (Förster, 1841). This species is a parasitoid that develops in various hosts of the order Coleoptera, but mainly in closed environments as agricultural products storage, seeds, and others (Niedermayer et al. 2016). Association with *Bruchus* is therefore probable, but perhaps associated with the post-harvest period.

Genus *Eurydinoteloides* Girault, 1913

The species *E. incerta* (Ashmead, 1893) occurs in the Nearctic region. It is a parasitoid of seed beetles at the

larval stage, and is linked to more than 30 Coleoptera species, like Apioninae and Bruchinae (Boe et al. 2019).

Genus *Dibrachys* Förster, 1856
This genus includes species with an extremely wide range of hosts, distributed all over the world. *D. microgastri* is known as parasitoid of Diptera, Hymenoptera, Lepidoptera, Neuroptera and Coleoptera, and uses only the pupal stage of the hosts (Peters & Baur 2011). The interaction with *B. brachialis*, reported by Pinckney (1937), should however be confirmed by new observations.

Genus *Gastrancistrus* Westwood, 1833
Little information is available about the species *Gastrancistrus undulatus* (Ratzeburg, 1852). It is cited as parasitoid of *Bruchus pisorum* in the USA (Kingsolver 2004) and in Italy (De Luca 1965).

Genus *Pteromalus* Swederus, 1795
It is one of the most diverse Pteromalidae genera, with more than 300 described species in Europe. *Pteromalus sequester* Walker, 1835 is cited as parasitoid of *Bruchus*. De Luca (1965) questions this relationship; however, more recent studies consider it as valid (Pérez-Benavides et al. 2019). This species has a wide distribution and is also known as parasitoid of Diptera and Apioninae on *Cytisus scoparius* (Fabaceae) (Graham 1969).

Another species is cited as a parasitoid of a *Bruchus* species, *P. semotus* (Walker, 1834). Although it appears to be mostly associated with Lepidoptera, its link with *Bruchus* is possible.

Genus *Trimeromicrus* Gahan, 1914
This genus includes one species, *T. maculatus* Gahan, 1914, found across North America. It feeds on numerous Curculionidae and *Bruchophagus* (Eurytomidae), as primary parasitoid and hyperparasitoid. One unidentified species of *Bruchus* is known as a host (Gibson 2013).

b. Eulophidae
Genus *Baryscapus* Förster, 1856
This genus includes more than 60 species, distributed across the Old World. The species feed on very different hosts, belonging to Hemiptera, Neuroptera, Coleoptera, Hymenoptera, Lepidoptera and Diptera (Askew & Shaw 2005). *Baryscapus bruchivorus* (Gahan, 1942) is cited from five *Bruchus* species in Europe, *Baryscapus protasis* Graham, 1991 is also associated with *Bruchus*. Another *Baryscapus* species, *B. bruchidii* (Erdös, 1951) is linked to Bruchinae, via the genus *Bruchidius* (Pérez-Benavidez et al. 2019).

It is likely that the *Tetrastichus* sp. mentioned by Carles belongs to this genus (Carles 1943).

Genus *Pnigalio* Schrank, 1802
Included in the genus *Pnigalio*, *P. pecticornis* (Linnaeus, 1758) has a worldwide distribution. It is a parasitoid of several insect orders: Coleoptera, Diptera, Lepidoptera and Hymenoptera.

c. Eupelmidae
Genus *Eupelmus* Dalman, 1820
It is a cosmopolitan genus gathering 344 valid species. Their identification is complex, and they attack a very large number of species, of several different orders: Hymenoptera, Lepidoptera and Coleoptera (Steffan 1981). Some species are cited from *Bruchus*, mostly in the New World.

Some other species, from the Old-World tropics, as *E. vuilleti* (Crawford, 1913) and *E. orientalis* (Crawford, 1913), are seed beetle parasitoids, feeding on Bruchinae and Apioninae (Rasplus 1990). More generalist species, as *E. cushmani* (Crawford, 1908) in the Nearctic region and *E. gamellus* Al khatib, 2015 (probably confused with *E. urozonus* Dalman concerning the seed beetle interactions, Delvare comm. pers.) in Europe, have dozens of hosts cited, among them some Bruchinae (Gibson 2011; Gibson & Fusu 2016).

d. Eurytomidae
Genus *Eurytoma* Illiger, 1807
In this genus, only *E. lathyri* Zerova, 1979, *E. lyubae* Zerova, 1995, *E. obtusa* Bugbee, 1967 and *E. tylodermatis* Ashmead, 1896 can reliably be associated with *Bruchus*. Some other *Eurytoma* species, belonging to the *robusta* group, are associated with Bruchinae in Africa (Gates & Delvare 2008).

e. Torymidae
Genus *Microdontomerus* Crawford, 1907
In the family Torymidae, the North American species *Microdontomerus anthonomi* (Crawford, 1907) is cited as having many hosts, all of which develop within plant tissue. Several species of Bruchinae are mentioned as hosts of *M. anthonomi* (Turner et al. 1990).

f. Trichogrammatidae
Genus *Uscana* Girault, 1911
In most articles, this genus is considered as Bruchinae specific. However, some species are cited from other hosts: *U. diagenae* (Risbec, 1951) is a Tetigoniidae parasitoid, *U. hodzhevanishvilii* Fursov, 1987 a Buprestidae parasitoid, as for *U. johnstoni* (Waterston, 1926). However, most of the *Uscana* species are parasitoids on Bruchinae eggs (Steffan 1954; Pintureau 2012).

g. Braconidae
Genus *Triaspis* Haliday, 1838
Triaspis is a cosmopolitan genus, comprising a great number of species. The known biology shows that most species are specific to Coleoptera, including *Bruchus*, which is also true for the genus *Dinarmus*. They are egg-larval parasitoid, meaning that the parasitoid egg is laid in the host egg, and the parasitoid larva then feeds on the host larva (Parnell 1964; Jimenez et al. 1997).

Conclusion and prospects

This literature review on the natural enemies of the genus *Bruchus* highlights a particular link between these pests and parasitoid Hymenoptera. In fact, although five species of predators have been identified, 44 species of parasitoid Hymenoptera are the focus of attention in the context of biological control. Among the most recurrent parasitoids, we can note the species of the genus *Triaspis* (Braconidae) and the genus *Dinarmus* (Pteromalidae).

Sixteen species are removed from the list of natural enemies associated with *Bruchus* species, according to new data found in the literature and consultation of the original citations. Fifteen are considered as dubious and need a confirmation. Lastly, 29 natural enemy species are considered as truly linked to *Bruchus* species.

Given the low amount of information available on some species, it is important to note that knowledge on the links between natural enemies and *Bruchus* species can still be improved. Studies of natural enemies should be conducted to better understand their behaviour, ecological requirements, geographic distribution, and host range. This is an important step before setting up biological control strategies, which need accurate data on beneficial species in order to implement appropriate supportive measures.

An interesting contribution could be made by including other Bruchinae genus like *Bruchidius*, and extending the study area to Africa and Asia, allowing to have a complete view of the trophic network.

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