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ARTICLE

Potential phylogenetic significance of the number of functional abdominal spiracles in beetle pupae, with focus on Staphylinoidea (Coleoptera)

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Abstract. The distribution of functional abdominal spiracles in pupae of Coleoptera is reviewed based on published descriptions and original observations. Aquatic Coleoptera typically have strong modifications, generally including dramatic reductions in the number of functional spiracles and often their modification into either spiracular gills or snorkels, as a response to their environment. But pupae of the great majority of Coleoptera, which are terrestrial, show broad stability across higher taxa. Most terrestrial beetles have at least the first five pairs of abdominal spiracles functional, up to and including a full set of eight pairs. However, the number is unexpectedly low in Scarabaeoidea and within Staphyliniformia, where Histeridae and all Staphylinoidea have a confirmed maximum of four pairs of spiracles. The relation between pupal size and number of functional spiracles in terrestrial pupae is explored, and it is suggested that those groups with an unexpectedly small number of functional spiracles may have passed through a "small-size bottleneck" in their ancestry. However, this hypothesis does not explain why several families of very small beetles in other groups of Coleoptera do not show a similar reduction, and little evidence was found to support a strong relation between pupal size and number of functional spiracles at lower taxonomic levels (below family). Whether pupae are exarate or obtect apparently also has little correlation with the number of functional spiracles. However, the consistency and stability of spiracular reductions in the above groups suggests that deep historical factors are involved and thus the reductions may be of phylogenetic significance. It is urged that establishing the number of functional spiracles in beetle pupae become as standard a feature of pupal descriptions as chaetotaxy and whether they are exarate or obtect.

Key-Words. Body size; Functional spiracle; Immature; Phylogeny; Pupa.

INTRODUCTION

Beetles, an enormous group of about 400,000 described species placed in more than 190 modern families, are holometabolous insects, and thus pass through four very distinct life stages: egg, larva (usually several instars), pupa and adult. Adults are the main life stage of systematic study, and are almost always the basis for the establishment of scientific names, as well as the source of a majority of systematic characters used for classification and morphology-based phylogenetic analyses, since they include a rich character set associated with movement, feeding and reproduction. Larvae, the other active and frequently encountered life stage, also have a large suite of characters that are, to a large extent, functionally independent of those of adults. This has led to the wide use of larvae by most modern systematists, especially for phylogenetic studies. The remaining two stages, eggs and pupae, are generally inactive and short-lived compared to the other two, are less often encountered and described, and so far have seldom been included in phylogenetic studies at higher taxonomic levels. For example, the most recent and comprehensive morphological phylogenetic analysis of Coleoptera as a whole (Lawrence *et al.,* 2011) used 516 phylogenetically informative characters in the analysis, but all of these were either of adults (344) or larvae (172), with no contribution from characters of eggs or pupae.

Nevertheless, eggs and pupae do possess systematically useful characters, and have been used occasionally for systematic and phylogenetic studies within smaller groups of beetles. Eggs, for example, when included in descriptions of immature stages at all, are often described in as little as two words (*e.g.,* "ovoid, white"), but Hinton (1981, based on unpublished work of D.C.R. Lincoln)

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demonstrated that, within the subfamily Staphylininae of Staphylinidae, the eggs of 43 taxa could be characterized and keyed out in a way that reflected generic and higher-level relationships within this subfamily. Pupae have received much more attention, especially through the efforts of Hinton (*e.g.,* 1946a, b, 1948, 1949, 1955a, 1971) who developed a widely accepted classification of insect pupae and drew attention to a number of pupal characters of taxonomic and phylogenetic significance for beetle pupae, such as the presence and distribution of "gin traps" and other protective devices (*e.g.,* Hinton, 1946b, 1955a). According to his classification (Hinton, 1946a, 1949), all known Coleoptera pupae are adecticous (lack articulated mandibles that can be moved), and most are exarate (with appendages such as antennae, wings and legs free of the body, and with more or less moveable abdomen and soft cuticle), while obtect pupae (appendages molded to the body, abdomen usually immobile, and with thick cuticle; see Fig. 1) occur within several beetle groups independently. Hinton (1946a) also noted that most beetle pupae occur in protected cells or even specially constructed cocoons and are terrestrial, although some are aquatic or adapted to episodic flooding. Pupae are featured prominently within some broader descriptive reviews of Coleoptera immature stages, *e.g.,* in Costa *et al.* (1988), as well as in detailed comparative studies of pupae within some groups such as Cerambycidae (*e.g.,* Duffy, 1953, 1957, 1960, 1963, 1968), Chrysomelidae (*e.g.,* Cox, 1996, 1998) and Curculionoidea (*e.g.,* Burke, 1968; May, 1994). Pupal descriptions have become not only more frequent but also more detailed and standardized over time, and now routinely include such features as the system of setae, spines or other projections that support the pupa in its cell, the presence and distribution of protective devices such as gin traps, and whether the pupa is exarate or obtect. Such pupal characters have also been used in phylogenetic studies within a few taxa, *e.g.,* in Hydradephaga (Ruhnau, 1986), Hydrophilidae (Archangelsky, 2004b), Staphylinidae: Staphylinini (Staniec & Pietrykowska-Tudruj, 2019), Tenebrionidae (Bouchard & Steiner, 2004) and Chrysomelidae (Cox, 1998).

The present study is not an attempt to review pupal characters in general for potential utility in systematic and phylogenetic studies, but rather is focused on one particular trait of Coleoptera pupae, the number and placement of abdominal spiracles that are functional. More than a century ago, Verhoeff (1918) noted that staphylinid pupae such as *Philonthus decorus* (Gravenhorst) and *Rugilus rufipes* Germar had a restricted number of functional abdominal spiracles, not the full set of eight pairs of functional spiracles that are pres-

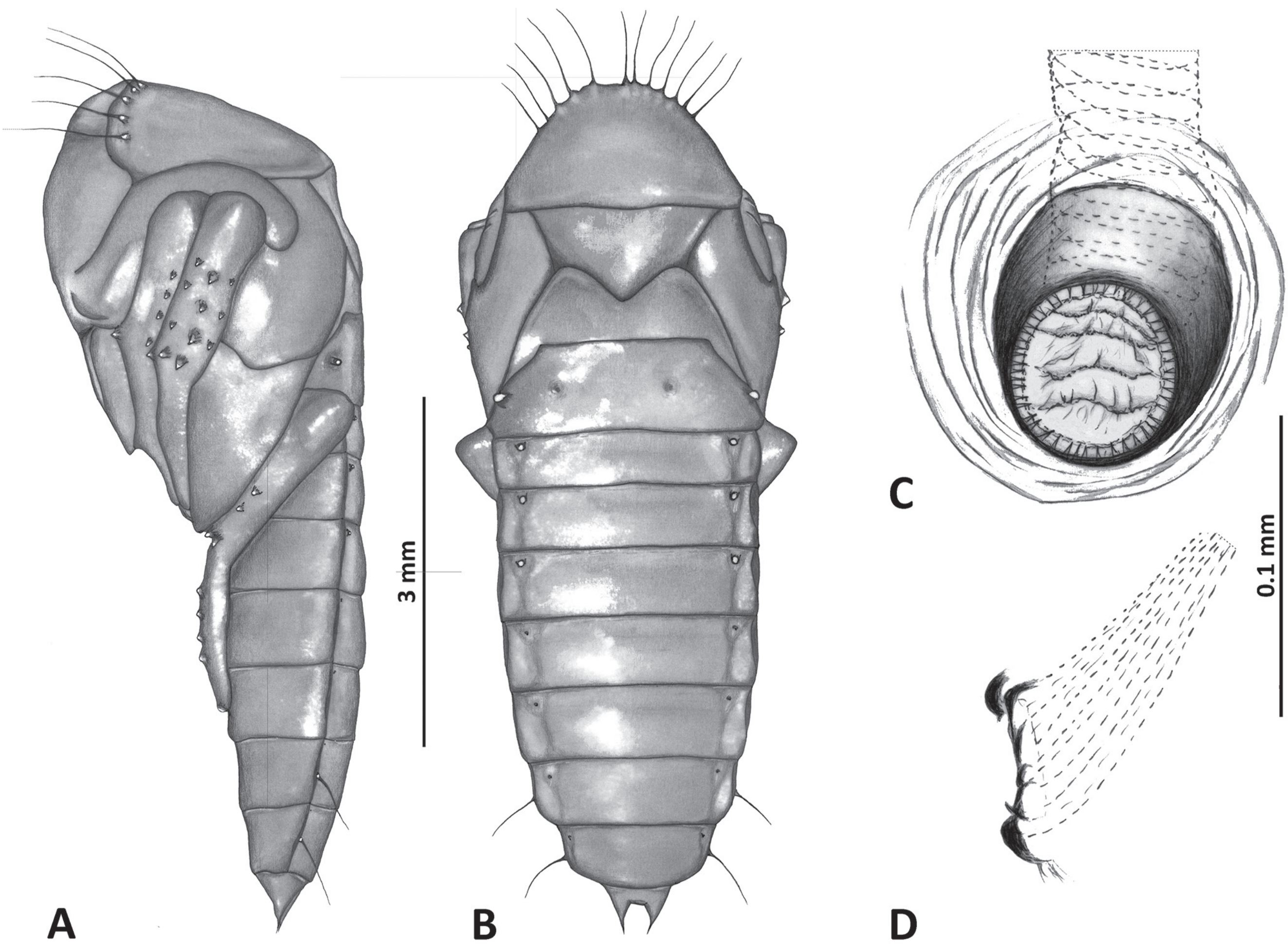

Figure 1. *Hesperus rufipennis* (Gravenhorst). Pupa (A) left lateral view, (B) dorsal view, (C) detail of functional abdominal spiracle 2, (D) detail of non-functional abdominal spiracle 6. Modified from Staniec (2004b: figs. 45, 46, 49, and 50, respectively), used with permission.

ent in larval and adult staphylinids of the same species. Verhoeff noted that the functional spiracles on abdominal segments 1-4 were evidently open and attached to functional tracheal tubes, while the more posterior spiracles were smaller and evidently closed, with vestigial tracheal tubes, or were absent (see example in Fig. 1). Paulian (1941), Emden (1957) and Hinton (1946a) also noted that this phenomenon of functional spiracular reduction in beetle pupae is common, and Paulian (1941) and Crowson (1981) suggested that the distribution of this character could have some phylogenetic significance within beetles. Unfortunately, the description of the number of functional abdominal spiracles in beetle pupae has not become as standardized as some of the other pupal characteristics noted in the previous paragraph. Some authors have noted the distribution of functional spiracles within particular groups, *e.g.,* Duffy (1953, 1957, 1960, 1963, 1968) in Cerambycidae, Cox (1996, 1998) in Chrysomelidae and Newton & Thayer (1995) and Thayer (2016) in Staphylinidae, but it is still not routine in Coleoptera.

The purpose of this review is to provide a brief summary of the distribution of functional abdominal spiracles in beetle pupae, and explore whether there may be some higher phylogenetic relevance in this distribution. The review is focused most heavily on the beetle group Staphyliniformia, and especially the families of Staphylinoidea. This survey is based on a combination of published descriptions of pupae plus my original observations of beetle pupae that have been identified at least to family.

MATERIAL AND METHODS

It should be emphasized first that whether abdominal spiracles in pupae are functional or non-functional is not the same as whether spiracles are present or absent, since non-functional spiracles can still be conspicuous and easily confused with functional ones (see, *e.g.,* Cox, 1998 for discussion of the difficulty). Functional spiracles have a distinct spiracular opening and, internally, have a distinct tracheal connection and (often) a spiracular closing apparatus; non-functional spiracles are generally smaller than functional ones and lack an opening, and the attached trachea is collapsed or not evident (see example in Fig. 1). Published descriptions that do not make this distinction must be interpreted with caution, because they frequently refer to the presence of spiracles rather than functionality and may include more apical non-functional spiracles in the count. Another frequent error is that spiracles on the first abdominal segment may be overlooked because they are often more or less covered by the metathoracic wings (although spiracles on the first segment may also be genuinely absent, as evidently the case in Hydrophiloidea). Finally, care must be taken to determine that the spiracular count is from the pupa proper, not from any immediately preceding phases such a pharate pupa or pre-pupa that may be immobile but still have the spiracles of the last larval instar functional, or from a pharate adult that is visible within the pupal cuticle (see, *e.g.,* Costa & Vanin, 1985; Hinton, 1971).

More than 840 publications containing descriptions and/or illustrations of beetle pupae were consulted. This literature survey is undoubtedly more complete for the families of Staphyliniformia, because I have maintained a card catalog of immature stages of this group and sought the relevant publications for several decades. Outside of this group, the survey is based largely on a literature search using general resources such as the Zoological Record and Google Scholar, although this approach is no doubt very incomplete in detecting pupal descriptions because pupae are often not mentioned in titles or abstracts. For example, an excellent series of papers titled "Larvae of Neotropical Coleoptera …" plus taxon name (see examples in References by Costa *et al.* or Vanin *et al.*) often also include good pupal descriptions, but this is not evident from the titles. Recent comprehensive reviews of Coleoptera immatures (*e.g.,* Lawrence, 1991) or Coleoptera as a whole (*e.g.,* the recent Coleoptera volumes of the Handbook of Zoology: Beutel & Leschen, 2016; Leschen *et al.,* 2010; Leschen & Beutel, 2014) were also consulted for pupal descriptions or citations of literature on them. Unfortunately, only a small percentage of the consulted published descriptions refer specifically to the distribution of functional spiracles in the studied pupae, although in some additional cases where the descriptions or illustrations were sufficiently detailed it was possible to infer the presence of functional spiracles (in these cases, the distribution is indicated with "?" in Table 1).

Examined pupae include some of those on which publications were based, but also many pupae present in the collections of the Field Museum of Natural History (FMNH), and a few borrowed from or studied in other collections. Some of these were identified by rearing from identifiable larvae or by association with emerged adults, but others were identified only by association with larvae and/or adults found together with them in the same microhabitat, in combination with the use of adult characters that are visible in most beetle pupae (*e.g.,* the shape of the antenna, head, eyes, and pronotum, leg and tarsal segmentation, and length of elytra are often clearly evident in pupae). Only those pupae that could be reasonably identified to family are cited in this study. In many cases of examined small lightly sclerotized pupae, where the functionality was not clear externally, the pupa was temporarily lightly cleared by warming in lactic acid and then observed with a compound microscope (Leica Dialux 22) using transmitted light. Otherwise, pupae were observed with a Leica MZ-16 dissecting microscope. Most of these pupae are stored in 70% ethanol in vials, but a few were examined as dried pinned specimens, and a few small ones were also studied as permanent microscope slides.

The functional spiracles of beetle pupae, at least of those that pupate in terrestrial habitats, generally have simple annular spiracular openings, and may or may not have an internal closing apparatus on the tracheal con-

Table 1. Distribution of functional abdominal spiracles (FASP) in Coleoptera pupae. Taxa are arranged alphabetically by suborder, series, superfamily, family, and taxon name(s), with addition of subfamily within Staphylinoidea and tribes within Staphylinidae. All modern Coleoptera families are listed even if no data were found, to highlight missing data at this level. The column "FASP" indicates the distribution of functional abdominal spiracles in pupae by segment number using Arabic numerals; a query (?) indicates doubt or an inferred distribution based on published figures or descriptions. The "Type" column indicates pupal type as exarate (Ex) or obtect (Ob), and also if the pupae are aquatic or periaquatic (Aq). "Sources" indicates published sources that are cited in References. An asterisk (*) before a taxon name indicates it is based on original personal observation (as "*orig." in Sources) and a double asterisk (**) indicates other unpublished sources also indicated in Sources.

Suborder	Series	Superfamily	Family	Subfamily: Tribe	Taxon/Taxa	FASP	Type	Sources, Notes
Adephaga			Amphizoidae					
Adephaga			Aspidytidae					
Adephaga			Carabidae		**Asaphidion pallipes; *Bembidion punctulatum; Carabus lefebvrei, C.* spp.; **Cicindela duodecimguttata; Hadrocarabus dufouri; Macrothorax rugosus; Megacephala brasiliensis;* **Paratachys bistriatus; Polpochila* sp. (Brazil); **Porotachys bisulcatus;* **Scaphinotus marginatus;* **Tachyta nana; Trichognathus marginipennis;* *Carabidae spp. (USA); Paussinae spp.	1-5, 1-6, 1-7	Ex	Cárdenas & Hidalgo, 2002; Costa *et al.*, 1988; Di Giulio *et al.*, 2007; Giglio *et al.*, 2009; Paulian, 1941; Santos, 2012; Serrano, 1992; Sturani, 1962; *orig.
Adephaga			Dytiscidae		*Acilius fraternus; Copelatus glyphicus; Hoperius planatus; Hygrotus sayi; Lancetes angusticollis; Matus ovatus; Nebrioporus ceresyi*	1-6, 1-7?	Ex	Brancucci & Ruhnau, 1985; Di Giulio & Nardi, 2006; Spangler, 1962a, 1973; Spangler & Gillespie, 1973; Wolfe, 1980; Wolfe & Roughley, 1985
Adephaga			Gyrinidae		*Aulonogyrus striatus; Gyrinus* spp.	1-3?	Ex, Aq	Saxod, 1965. Note: 1-8 visible, 1-3 very large, rest small, presumed non-functional.
Adephaga			Haliplidae		*Haliplus* spp.; *Peltodytes* spp.	2-4	Ex, Aq	Hickman, 1930
Adephaga			Hygrobiidae					
Adephaga			Meruidae					
Adephaga			Noteridae		*Noterus* sp.	1-7	Ex	Dettner, 2016
Adephaga			Rhysodidae		*Rhysodes sulcatus*	1-8	Ex	Burakowski, 1975; Note: as subfamily in Carabidae, Lawrence, 2016
Adephaga			Trachypachidae					
Archostemata			Crowsoniellidae					
Archostemata			Cupedidae					
Archostemata			Jurodidae					Note: family as *incertae sedis* in Polyphaga, Lawrence, 2016
Archostemata			Micromalthidae		**Micromalthus debilis*	1-8	Ex	Rozen, 1963; *orig.
Archostemata			Ommatidae					
Myxophaga		Lepiceroidea	Lepiceridae					
Myxophaga		Sphaeriusoidea	Hydroscaphidae		*Hydroscapha natans; Scaphydra angra*	1-3	Ob, Aq	Costa *et al.*, 1988; Reichardt, 1974; Reichardt & Hinton, 1976. Note: semiaquatic, *Scaphydra* with spiracular gills.
Myxophaga		Sphaeriusoidea	Sphaeriusidae					
Myxophaga		Sphaeriusoidea	Torridincolidae		*Hintonia britskii; Ytu zeus*	1-2	Ob, Aq	Costa *et al.*, 1988; Reichardt, 1973; Reichardt & Hinton, 1976. Note: semiaquatic, with spiracular gills.
Polyphaga	Bostrichiformia	Bostrichoidea	Bostrichidae					
Polyphaga	Bostrichiformia	Bostrichoidea	Dermestidae		*Dermestes maculatus*, **D.* sp. (USA)	1-6	Ex	Prins, 1984b; *orig.
Polyphaga	Bostrichiformia	Bostrichoidea	Endecatomidae					
Polyphaga	Bostrichiformia	Bostrichoidea	Ptinidae		*Lasioderma serricorne;* *"Anobiidae" sp. (Mexico)	1-7	Ex	Costa *et al.*, 1988; *orig.
Polyphaga	Cucujiformia	Chrysomeloidea	Cerambycidae		*Acanthoderes juno, A. melanosticta; Callipogon luctuosum; Coleoxestia waterhousei; Eutrypanus dorsalis; Lophopoeum timbouvae; Macropophora accentifer; Malacopterus pavidus; Myzomorphus quadripunctatus; Necydalis cavipennis; Oreodera glauca;*	1-5, 1-6, 1-7, 1-8	Ex	Benham, 1969; Biffi & Fuhrmann, 2013; Casari, 2016; Casari & Albertoni, 2017; Casari & Martins, 2013; Casari & Nascimento, 2019; Casari & Steffanello, 2010; Casari & Teixeira, 2014; Costa *et al.*, 1988; Cox, 1996,

Suborder	Series	Superfamily	Family	Subfamily: Tribe	Taxon/Taxa	FASP	Type	Sources, Notes
					Ortholeptura insignis; Parandra longicollis; Paratenthras martinsi; Phoebemima ensifera; Polyoza lacordairei; Prionus laticollis; Psapharochrus cylindricus, P. vetustus; Psyllotoxus griseocinctus; Pyrrhidium sanguineum; Pyrodes nitidus; Quercivir gounellei; Retrachydes thoracicus; Stenodontes spinibarbis; Tapuruia felisbertoi; Tilloglomus spectabile; [dozens of additional genera in multiple subfamilies, see Cox (1996), Duffy (1953-1968)]	1-5, 1-6, 1-7, 1-8	Ex	1998; Duffy, 1953, 1957, 1960, 1963, 1968; Leech, 1966; Mermudes & Monné, 2001; Penteado-Dias, 1982; Švácha & Lawrence, 2014d; Teixeira & Nogueira, 1993; Zajciw, 1964, 1973, 1975a, b, 1976. Note: 1-8 only in *Pyrrhidium sanguineum, teste* Švácha & Lawrence, 2014d.
Polyphaga	Cucujiformia	Chrysomeloidea	Chrysomelidae		*Altica* spp.; *Amblycerus unimaculatus; Anacassis* spp.; **Callosobruchus* sp. (USA); *Calyptocephala paralutea; Caryedes brasiliensis; Cassida* spp.; *Charidotis gemellata; Chrysophtharta* spp.; *Dicranosterna immaculata;* **Galerucella xanthomelaena; Gratiana conformis; Heterispa vinula; Laccoptera* spp.; *Lamprosoma amethystinum; Mecynodera baly; Metaxycera purpurata; Novacastria nothofagi; Pachymerus* spp.; *Paropsides umbrosa; Paropsis* spp.; *Paropsisterna* spp.; *Physocoryna scabra; Pseudolampsis darwini; Pygiopachymerus lineola; Pyrgoides* spp.; *Speciomerus rubrofemoralis; Stichotaenia* spp.; *Syphrea uberabensis; Trachymela* cf. *tincticollis; Trochalodes* cf. *hemisphaerica;* [dozens of additional genera in multiple subfamilies, see Cox (1996)]	1-5, 1-6, 1-7?, 1-8?	Ex, Ob	Buzzi, 1975, 1996; Buzzi & Miyazaki, 1992; Casari, 2005; Casari & Duckett, 1998; Casari & Teixeira, 1997, 2004, 2008, 2010, 2011; Cox, 1996, 1998; Fernandes & Buzzi, 2007; Lawrence & Reid, 2014; Ranade *et al.*, 2004; Rane & Ghate, 2005; Reid, 1992; Reid & Beatson, 2019; Świętojańska, 2005; Takizawa, 1978; Teixeira & Casari-Chen, 1992; Zhang *et al.*, 2007; *orig.
Polyphaga	Cucujiformia	Chrysomeloidea	Disteniidae		*Distenia japonica*	1-6	Ex	Švácha & Lawrence, 2014c
Polyphaga	Cucujiformia	Chrysomeloidea	Megalopodidae		*Agathomerus sellatus; Temnaspis nankinea; Zeugophora flavicollis*	1-6	Ex	Cox, 1996, 1998
Polyphaga	Cucujiformia	Chrysomeloidea	Orsodacnidae					
Polyphaga	Cucujiformia	Chrysomeloidea	Oxypeltidae		*Oxypeltus quadrispinosus*	1-5	Ex	Švácha & Lawrence, 2014b
Polyphaga	Cucujiformia	Chrysomeloidea	Vesperidae		*Vesperus sanzi*	1-5	Ex	Švácha & Lawrence, 2014a
Polyphaga	Cucujiformia	Cleroidea	Acanthocnemidae					
Polyphaga	Cucujiformia	Cleroidea	Biphyllidae		*Diplocoelus* af. *amplicollis*	1-6	Ex	Costa *et al.*, 1988
Polyphaga	Cucujiformia	Cleroidea	Byturidae					
Polyphaga	Cucujiformia	Cleroidea	Chaetosomatidae					
Polyphaga	Cucujiformia	Cleroidea	Cleridae		*Cleridae sp. (Tasmania)	1-6	Ex	*orig.
Polyphaga	Cucujiformia	Cleroidea	Lophocateridae					
Polyphaga	Cucujiformia	Cleroidea	Mauroniscidae					
Polyphaga	Cucujiformia	Cleroidea	Melyridae		*Astylus trifasciatus*	1-7	Ex	Estrada & Solervicens, 1997
Polyphaga	Cucujiformia	Cleroidea	Peltidae					
Polyphaga	Cucujiformia	Cleroidea	Phloiophilidae					
Polyphaga	Cucujiformia	Cleroidea	Phycosecidae					
Polyphaga	Cucujiformia	Cleroidea	Prionoceridae					
Polyphaga	Cucujiformia	Cleroidea	Protopeltidae					
Polyphaga	Cucujiformia	Cleroidea	Rentoniidae					
Polyphaga	Cucujiformia	Cleroidea	Rhadalidae					
Polyphaga	Cucujiformia	Cleroidea	Thanerocleridae					
Polyphaga	Cucujiformia	Cleroidea	Thymalidae		**Thymalus marginicollis*	1-6	Ex	*orig.
Polyphaga	Cucujiformia	Cleroidea	Trogossitidae		*Temnochila* sp. (Brazil), **T.* sp. (Mexico)	1-6	Ex	Costa *et al.*, 1988; *orig.
Polyphaga	Cucujiformia	Coccinelloidea	Akalyptoischiidae					
Polyphaga	Cucujiformia	Coccinelloidea	Alexiidae					
Polyphaga	Cucujiformia	Coccinelloidea	Anamorphidae					

Suborder	Series	Superfamily	Family	Subfamily: Tribe	Taxon/Taxa	FASP	Type	Sources, Notes
Polyphaga	Cucujiformia	Coccinelloidea	Bothrideridae					
Polyphaga	Cucujiformia	Coccinelloidea	Cerylonidae					
Polyphaga	Cucujiformia	Coccinelloidea	Coccinellidae		*Anovia circumclusa; Coccinella oceligera; Epilachna* spp.; Coccinellidae sp.	1-6, 1-8	Ex, Ob	Casari & Teixeira, 2015; Costa *et al.*, 1988; Forrester *et al.*, 2009; Ślipiński & Tomaszewska, 2010
Polyphaga	Cucujiformia	Coccinelloidea	Corylophidae		*Orthoperus* sp. (Brazil); *Sericoderus lateralis*	1-5	Ob	Costa *et al.*, 1988; Hinton, 1941b; Polilov & Beutel, 2010
Polyphaga	Cucujiformia	Coccinelloidea	Discolomatidae		*Discoloma modestum*	1-4	Ex	Costa *et al.*, 1988
Polyphaga	Cucujiformia	Coccinelloidea	Endomychidae		*Amphix* sp. (Brazil); *Archipines championi; Endomychus biguttatus; Lycoperdina ferruginea; Mycetina cruciata;* *Endomychidae sp. (Panama)	1-5, 1-7	Ex	Burakowski, 1997; Costa *et al.*, 1988; Leschen & Carlton, 1988; Pakaluk, 1984; Tomaszewska, 2003; *orig.
Polyphaga	Cucujiformia	Coccinelloidea	Eupsilobiidae					
Polyphaga	Cucujiformia	Coccinelloidea	Euxestidae					
Polyphaga	Cucujiformia	Coccinelloidea	Latridiidae					
Polyphaga	Cucujiformia	Coccinelloidea	Murmidiidae					
Polyphaga	Cucujiformia	Coccinelloidea	Mycetaeidae					
Polyphaga	Cucujiformia	Coccinelloidea	Teredidae					
Polyphaga	Cucujiformia	Cucujoidea	Agapythidae					
Polyphaga	Cucujiformia	Cucujoidea	Boganiidae					
Polyphaga	Cucujiformia	Cucujoidea	Cavognathidae					
Polyphaga	Cucujiformia	Cucujoidea	Cryptophagidae					
Polyphaga	Cucujiformia	Cucujoidea	Cucujidae		**Platisus* sp. (Australia)	1-6?	Ex	*orig.
Polyphaga	Cucujiformia	Cucujoidea	Cybocephalidae					
Polyphaga	Cucujiformia	Cucujoidea	Cyclaxyridae					
Polyphaga	Cucujiformia	Cucujoidea	Erotylidae		*Aegithus clavicornis; Cypherotylus californicus; Erotylus histrio; *Tritoma biguttata*	1-4, 1-5	Ex	Costa *et al.*, 1988; Graves, 1965; Teixeira & Casari, 1998; *orig.
Polyphaga	Cucujiformia	Cucujoidea	Helotidae					
Polyphaga	Cucujiformia	Cucujoidea	Hobartiidae					
Polyphaga	Cucujiformia	Cucujoidea	Kateretidae					
Polyphaga	Cucujiformia	Cucujoidea	Laemophloeidae					
Polyphaga	Cucujiformia	Cucujoidea	Lamingtoniidae					
Polyphaga	Cucujiformia	Cucujoidea	Monotomidae					
Polyphaga	Cucujiformia	Cucujoidea	Myraboliidae					
Polyphaga	Cucujiformia	Cucujoidea	Nitidulidae		*Brachypeplus glaber; Carpophilus* spp.; *Conotelus* sp. (Brazil); *Epurea guttata; Meligethes aeneus, M. ?ruficornis*	1-6	Ex	Cline *et al.*, 2013; Costa *et al.*, 1988; Kurochkin, 2005; Kurochkin & Kirejtshuk, 2003; Osborne, 1965
Polyphaga	Cucujiformia	Cucujoidea	Passandridae					
Polyphaga	Cucujiformia	Cucujoidea	Phalacridae		*Acylomus pugetanus*	1-7	Ex	Steiner & Singh, 1987
Polyphaga	Cucujiformia	Cucujoidea	Phloeostichidae					
Polyphaga	Cucujiformia	Cucujoidea	Priasilphidae					
Polyphaga	Cucujiformia	Cucujoidea	Protocucujidae					
Polyphaga	Cucujiformia	Cucujoidea	Silvanidae		**Cryptamorpha* sp. (New Zealand); *Macrohyliota sculptus; Megahyliota cryptolucidus;* **Uleiota* sp. (Australia)	1-5, 1-7?	Ex	Yoshida & Hirowatari, 2016; *orig.

Suborder	Series	Superfamily	Family	Subfamily: Tribe	Taxon/Taxa	FASP	Type	Sources, Notes
Polyphaga	Cucujiformia	Cucujoidea	Smicripidae					
Polyphaga	Cucujiformia	Cucujoidea	Sphindidae		*Aspidiphorus orbiculatus*	1-5 + ?	Ex	Burakowski & Ślipiński, 1987
Polyphaga	Cucujiformia	Cucujoidea	Tasmosalpingidae					
Polyphaga	Cucujiformia	Curculionoidea	Anthribidae		*Araecerus palmaris; Ptychoderes elongatus*	1-6	Ex	Costa *et al.*, 1988; May, 1994
Polyphaga	Cucujiformia	Curculionoidea	Attelabidae		*Attelabus nitens; Auletobius cassandrae; Eugnamptus collaris; Haplorhynchites aeneus; Hybolabus amazonicus; Merhynchites bicolor; Pselaphorhynchites perplexus*	1-6, 1-7	Ex	Hamilton, 1980, 1981, 1983; Hamilton & Kuritsky, 1981; Riedel, 2014; Vanin & Bená, 2020
Polyphaga	Cucujiformia	Curculionoidea	Belidae					
Polyphaga	Cucujiformia	Curculionoidea	Brachyceridae					
Polyphaga	Cucujiformia	Curculionoidea	Brentidae		*Apion brevicorne; Diplapion confluens; Estenorhinus angulicollis; Squamapion atomarium*	1-5, 1-6	Ex	Costa *et al.*, 1988; Gosik *et al.*, 2010; Lima *et al.*, 2020; Pawlęga *et al.*, 2019
Polyphaga	Cucujiformia	Curculionoidea	Caridae					
Polyphaga	Cucujiformia	Curculionoidea	Cimberididae					
Polyphaga	Cucujiformia	Curculionoidea	Curculionidae		*Anthonomus* spp.; *Bagous alismatis, Bagous* spp.; *Barypeithes pellucidus; Brachyderes incanus;* **Calvertius tuberosus; Cleonis pigra; Cleopomiarus* spp.; *Eudiagogus* spp.; *Eusemio* sp. (Brazil); *Larinus* spp.; *Linomadarus* sp. (Brazil); *Liophloeus tessulatus; Lixus pulverulentus; Miarus* spp.; *Mononychus* spp.; *Naupactus* sp. (Brazil); *Otiorhynchus* spp.; *Peritelus sphaeroides; Phrydiuchus* spp.; *Phyllobius* spp.; *Pityophthorus* sp. (Brazil); *Plinthus caucasicus; Rhinusa bipustulata, R. neta; Strophosoma* cf. *sus; Tanymecus palliatus; Thryogenes festucae, T. fiorii, T. nereis; Trichobaris* spp.; *Tychius subsulcatus*	1-5, 1-6, 1-7	Ex	Anderson, 1970; Arzanov, 2017, 2019; Báborská *et al.*, 2019; Bená & Vanin, 2013; Burke, 1968; Burke *et al.*, 1984; Costa *et al.*, 1988; Cuda & Burke, 1985; Gosik, 2006, 2007, 2008, 2009a, b, 2010, 2011; Gosik & Skuhrovec, 2011; Gosik & Sprick, 2012, 2013; Kovarik & Burke, 1985; Ścibior & Łętowski, 2018; Skuhrovec *et al.*, 2017, 2018, 2019; Staniec & Gosik, 2003; Szwaj *et al.*, 2018; *orig.
Polyphaga	Cucujiformia	Curculionoidea	Dryophthoridae					
Polyphaga	Cucujiformia	Curculionoidea	Nemonychidae		*Rhynchitoplesius eximius*	1-7	Ex	Costa *et al.*, 1988
Polyphaga	Cucujiformia	Lymexyloidea	Lymexylidae		*Atractocerus emarginatus*	1-7	Ex	Fulmek, 1930; Lawrence, 2010
Polyphaga	Cucujiformia	Tenebrionoidea	Aderidae					
Polyphaga	Cucujiformia	Tenebrionoidea	Anthicidae		*Cyclodinus constrictus*	1-8?	Ex	Colombini *et al.*, 1985
Polyphaga	Cucujiformia	Tenebrionoidea	Archeocrypticidae					
Polyphaga	Cucujiformia	Tenebrionoidea	Boridae		***Boros unicolor*	1-7	Ex	**Warren Steiner *in litteris* to AFN 25 November 2019
Polyphaga	Cucujiformia	Tenebrionoidea	Chalcodryidae					
Polyphaga	Cucujiformia	Tenebrionoidea	Ciidae		*Porculus vianai;* *Ciidae sp. (Tasmania)	1-5	Ex	Costa *et al.*, 1988; *orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Melandryidae		*Serropalpus coxalis*	1-7?	Ex	Hoebeke & McCabe, 1977
Polyphaga	Cucujiformia	Tenebrionoidea	Meloidae		*Meloetyphlus attacephalus*	1-7	Ex	Costa *et al.*, 1988
Polyphaga	Cucujiformia	Tenebrionoidea	Mordellidae		*Mordella* sp. (Brazil)	1-7	Ex	Costa *et al.*, 1988
Polyphaga	Cucujiformia	Tenebrionoidea	Mycetophagidae					
Polyphaga	Cucujiformia	Tenebrionoidea	Mycteridae					
Polyphaga	Cucujiformia	Tenebrionoidea	Oedemeridae		*Diplectrus vicinus; Sessinia livida*	1-7	Ex	Costa *et al.*, 1988; Duffy, 1952
Polyphaga	Cucujiformia	Tenebrionoidea	Promecheilidae					
Polyphaga	Cucujiformia	Tenebrionoidea	Prostomidae		**Prostomis* sp. (Australia)	1-7	Ex	*orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Pterogeniidae					
Polyphaga	Cucujiformia	Tenebrionoidea	Pyrochroidae		*Pyrochroidae sp. (USA)	1-7	Ex	*orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Pythidae		**Pytho seidlitzi*	1-7	Ex	*orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Ripiphoridae		*Rhipidius quadriceps*	1-6	Ob	Besuchet, 1956a

Suborder	Series	Superfamily	Family	Subfamily: Tribe	Taxon/Taxa	FASP	Type	Sources, Notes
Polyphaga	Cucujiformia	Tenebrionoidea	Salpingidae		**Diagrypnodes wakefieldi*	1-7	Ex	*orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Scraptiidae		*Scraptia triangularis*	1-7	Ex	Vanin *et al.*, 1996
Polyphaga	Cucujiformia	Tenebrionoidea	Stenotrachelidae		**Cephaloon ungulare*	1-6	Ex	*orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Synchroidae		**Synchroa punctata*	1-7	Ex	*orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Tenebrionidae		*Alphitobius diaperinus; Anaedus* sp.; *Bolitophagus reticulatus;* **Bolitotherus cornutus; Bothrotes* sp.; *Chrysopeplus expolitus; Delognatha* sp. (Brazil); *Deretus spinicollis; Derosphaerus hirtipes; Diaperis* sp.; *Dioedus* spp.; *Eumylada* spp.; *Gonocephalum reticulatum; Heterocheira martellii; Hypaulax crenata; Lagria* sp.; *Leprocaulus borneensis; Melanesthes* spp.; *Metisopus purpureipennis; Molion muelleri; Myladina unguiculina; Nilio* sp.; *Opatrum subaratum; Pachyphaleria capensis; Peneta* spp.; *Penthicus* spp.; *Phaleria testacea; Phrenapates* spp.; *Promethis* spp; *Pseudophthora fordi; Scleropatrum horridum; Temnorrhynchus retusus; Zypoetes* sp. (Panama); [multiple additional genera of Diaperinae, Pimeliinae, Stenochiinae, Tenebrioninae]	1-5, 1-6, 1-7, 2-7	Ex	Bouchard, 2019; Bouchard & Steiner, 2004; Chelazzi *et al.*, 1986; Duarte *et al.*, 1997; Jia *et al.*, 2013; Matthews *et al.*, 2010; Prins, 1984b; Purchart & Nabozhenko, 2012; Steiner, 1995; Wagner & Gosik, 2016; *orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Tetratomidae		**Eustrophinus* sp. (USA); *Mycetoma suturale;* **Penthe obliquata*	1-5, 1-8?	Ex	Burakowski, 1995; *orig.
Polyphaga	Cucujiformia	Tenebrionoidea	Trictenotomidae		***Trictenotoma formosana*	1-6	Ex	Lin & Hu, 2019, plus **Fang-Shuo Hu *in litteris* to AFN 11 October 2019
Polyphaga	Cucujiformia	Tenebrionoidea	Ulodidae					
Polyphaga	Cucujiformia	Tenebrionoidea	Zopheridae		*Noserinus dormeanus; Rhopalocerus rondanii*	1-6, 1-8?	Ex	Costa *et al.*, 1988; Ślipiński & Burakowski, 1988
Polyphaga	Derodontiformia	Derodontoidea	Derodontidae					
Polyphaga	Derodontiformia	Nosodendroidea	Nosodendridae					Note: family as *incertae sedis* in Polyphaga, Lawrence, 2016, or in its own superfamily following McKenna *et al.*, 2019
Polyphaga	Elateriformia	Buprestoidea	Buprestidae		*Agrilus planipennis; Brachys cleidecostae; Coroebus florentinus; Euchroma gigantea; Pterobothris corrosus;* *Buprestidae spp. (Chile, New Zealand)	1-5, 1-6, 1-8?	Ex	Chamorro *et al.*, 2012; Costa & Vanin, 1984; Costa *et al.*, 1988; Migliore *et al.*, 2020; Moore & Cerda, 1986; Soria Iglesias & Ocete Rubio, 1992; *orig.
Polyphaga	Elateriformia	Buprestoidea	Schizopodidae					
Polyphaga	Elateriformia	Byrrhoidea	Byrrhidae		**Cytilus* sp. (USA); **Simplocaria* sp. (USA)	1-6, 1-7	Ex	*orig.
Polyphaga	Elateriformia	Byrrhoidea	Callirhipidae					
Polyphaga	Elateriformia	Byrrhoidea	Chelonariidae					
Polyphaga	Elateriformia	Byrrhoidea	Cneoglossidae		*Cneoglossa edsoni*	1-7?	Ex	Costa *et al.*, 1999b
Polyphaga	Elateriformia	Byrrhoidea	Dryopidae		*Onopelmus guarani*	1-7	Ex	Vanin *et al.*, 1997
Polyphaga	Elateriformia	Byrrhoidea	Elmidae		*Lara avara*	1-7	Ex	Steedman, 1983
Polyphaga	Elateriformia	Byrrhoidea	Eulichadidae					
Polyphaga	Elateriformia	Byrrhoidea	Heteroceridae		*Heteroceridae sp. (Chile)	1-7	Ex	*orig.
Polyphaga	Elateriformia	Byrrhoidea	Limnichidae					
Polyphaga	Elateriformia	Byrrhoidea	Lutrochidae		*Lutrochus germari*	1-5	Ex	Costa *et al.*, 1996
Polyphaga	Elateriformia	Byrrhoidea	Protelmidae					
Polyphaga	Elateriformia	Byrrhoidea	Psephenidae		*Afroeubria* spp.; *Eubria palustris; Eubrianax* spp.; *Metaeopsephenus japonicus; Nipponeubria yoshitomii; Psephenoides* spp.; *Psephenus palpalis; Sclerocyphon fuscus;* Eubriinae spp. (South Africa, Tasmania)	1-7, 2-7, 1-3+6-7, 7 only	Ex, Aq	Hinton, 1955b, 1966; Lee & Satô, 1996. Note: semiaquatic, most with spiracular gills
Polyphaga	Elateriformia	Byrrhoidea	Ptilodactylidae		*Paralichas trivittis; Tetraglossa palpalis;* *Ptilodactylidae sp. (Panama)	1-7	Ex	Funk & Fenstermacher, 2002; Spangler, 1983; *orig.
Polyphaga	Elateriformia	Dascilloidea	Dascillidae		*Dascillus davidsoni*	1-7	Ex	Grebennikov & Scholtz, 2003

Suborder	Series	Superfamily	Family	Subfamily: Tribe	Taxon/Taxa	FASP	Type	Sources, Notes
Polyphaga	Elateriformia	Dascilloidea	Rhipiceridae		*Polymerius chilensis*	1-7	Ex	Solervicens, 2005
Polyphaga	Elateriformia	Elateroidea	Artematopodidae					
Polyphaga	Elateriformia	Elateroidea	Brachypsectridae					
Polyphaga	Elateriformia	Elateroidea	Cantharidae		*Chauliognathus flavipes, C. humeralis, C. ignaciosus, C. spinipennis; Daiphron bipartitus, D. mediofasciatum; Macromalthinus brasiliensis*	1-8	Ex	Biffi & Casari, 2017; Biffi & Rosa, 2019
Polyphaga	Elateriformia	Elateroidea	Cerophytidae					
Polyphaga	Elateriformia	Elateroidea	Drilidae					
Polyphaga	Elateriformia	Elateroidea	Elateridae		*Dipropus brasilianus; Fulgeochlizus bruchi; Ludioctenus cyprius; Pachycrepidius bicinctus; Paracalais prosectus; Pherhimius dejeani;* *Elateridae spp. (New Zealand, USA)	1-6, 1-7	Ex	Casari & Bellusci, 1996; Casari & Biffi, 2012; Casari & Costa, 1998; Casari-Chen, 1986; Rosa *et al.*, 2010, 2019; *orig.
Polyphaga	Elateriformia	Elateroidea	Eucnemidae		*Deltometopus rufipes; Dirrhagofarsus lewisi; Fornax* sp. (Brazil); *Hylis foveicollis; Xylophilus othoides*	1-8	Ex	Burakowski & Buchholz, 1991; Costa *et al.*, 1988; Ford & Spilman, 1979; Mosher, 1919; Teixeira & Casari-Chen, 1994
Polyphaga	Elateriformia	Elateroidea	Iberobaeniidae					
Polyphaga	Elateriformia	Elateroidea	Lampyridae		*Aspisoma fenestrata* sp. (Brazil); *Bicellonycha* sp. (Brazil); *Lamprohiza splendidula; Lampyris noctiluca;* **Lucidota atra; Psilocladus costae; Pyractomena borealis, P. nigripennis; Pyropyga nigricans;* ***Stenocladius yoshikawai;* *Lampyridae sp. (USA)	1-7, 1-8, 2-7	Ex	Archangelsky, 2004a, 2010; Archangelsky & Branham, 1998, 2001; Branham & Archangelsky, 2000; Costa *et al.*, 1988; Novák, 2017, 2018; Vaz *et al.*, 2020; *orig.; **Itsuro Kawashima, *in litteris* to AFN 25 January 2020
Polyphaga	Elateriformia	Elateroidea	Lycidae		*Macrolygistopterus subparallelus; Plateros floralis*	1-8	Ex	Costa & Vanin, 2012; Miller, 1997
Polyphaga	Elateriformia	Elateroidea	Omalisidae					
Polyphaga	Elateriformia	Elateroidea	Omethidae					
Polyphaga	Elateriformia	Elateroidea	Phengodidae		*Phrixothrix hirtus*	1-8	Ex	Costa *et al.*, 1999a
Polyphaga	Elateriformia	Elateroidea	Rhagophthalmidae					
Polyphaga	Elateriformia	Elateroidea	Telegeusidae					
Polyphaga	Elateriformia	Elateroidea	Throscidae					
Polyphaga	Elateriformia	Rhinorhipoidea	Rhinorhipidae					
Polyphaga	Scarabaeiformia	Scarabaeoidea	Belohinidae					
Polyphaga	Scarabaeiformia	Scarabaeoidea	Diphyllostomatidae					
Polyphaga	Scarabaeiformia	Scarabaeoidea	Geotrupidae		**Odontaeus darlingtoni*	1-2?	Ex	*orig.
Polyphaga	Scarabaeiformia	Scarabaeoidea	Glaphyridae					
Polyphaga	Scarabaeiformia	Scarabaeoidea	Glaresidae					
Polyphaga	Scarabaeiformia	Scarabaeoidea	Hybosoridae		*Ceratocanthus relucens; Cyphopisthes descarpentriesi;* *Ceratocanthinae sp. (Panama)	1-4, 2-4	Ex	Grebennikov *et al.*, 2002; Morón & Arce, 2003; *orig.
Polyphaga	Scarabaeiformia	Scarabaeoidea	Lucanidae		**Aesalus ulanovskyi; Casignetus* spp.; **Lamprima* sp. (Australia); *Pycnosiphorus* spp.; *Sclerostomus cucullatus*	1-3?, 1-4, 1-5?	Ex	Cekalovic 1982; Cekalovic & Weigert, 1974; Molino-Olmedo, 2004a, b, 2007a, b; Paulian, 1941; Silva & Grossi, 2015; *orig.
Polyphaga	Scarabaeiformia	Scarabaeoidea	Ochodaeidae					
Polyphaga	Scarabaeiformia	Scarabaeoidea	Passalidae		*Passalus punctiger; Veturius impressus;* *Passalidae spp. (Mexico, Panama)	1-4, 1-5	Ex	Costa & Fonseca, 1986; Paulian, 1941; Salazar-Niño & Serrão, 2015; *orig.
Polyphaga	Scarabaeiformia	Scarabaeoidea	Pleocomidae					
Polyphaga	Scarabaeiformia	Scarabaeoidea	Scarabaeidae		*Aegidium cribratum; Aegopsis* spp.; *Ancylonycha mindanaona; Anomala cincta, A. testaceipennis; Archedinus relictus; Chlorota paulistana; Chrysophora chrysochlora; Coelosis biloba; Copris diversus, C. incertus; Coscinocephalus tepehuanus; Cyclocephala celata, C. signaticollis, C. tucumana; Plectris brevitarsis* (as *Demodema*); *Dynastes hyllus, D. neptunus; Dyscinetus dubius; Euphoria basalis; Geniates barbatus, G. borelli; Golofa*	1-3, 1-4, 1-5, 1-6, 1-7?	Ex	Albertoni *et al.*, 2014a, 2014b; Arguez *et al.*, 2017; Barbero & Palestrini, 1992; Barbero *et al.*, 2000; Böving, 1945; Carvalho *et al.*, 2019; Costa *et al.*, 1988; Fuhrmann, 2013; Fuhrmann *et al.*, 2019; Ibarra-Polesel *et al.*, 2017a, b; Jang & Kim, 2019; Micó *et al.*, 2003; Morelli, 1990, 1992, 1996; Morón, 1987, 1991, 1993, 1995a, b; Morón & Arce, 2003; Morón &

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					pizarro, G. pusilla, G. spp.; *Hemiphileurus elbitae; Heterogomphus dilaticollis; Homophileurus luederwaldti, H. tricuspis; Homonyx chalcea; Hoplopyga brasiliensis; Inca* spp.; *Isonychus* sp. (Brazil); *Lagochile emarginata; Ligyrus nasutus; Liogenys bidenticeps; Lycomedes hirtipes; Macraspis cincta, M.* spp.; *Malagoniella argentina, M. magnifica, M. puncticollis; Megasoma elaphas; Neocorvicoana reticulata; Paraegidium costalimai; Paraheterosternus luedeckei; Pentodon quadridens; Phileurus* spp.; *Platycoelia valida; Platyphileurus felscheanus; Podischnus agenor; Scarabaeus striatus; Strategus fascinus; Trioplus cylindricus;* *Sericini sp. (Panama); Scarabaeidae spp.	1-3, 1-4, 1-5, 1-6, 1-7?	Ex	Nogueira, 2000; Morón & Pardo-Locarno, 1994; Morón & Paucar-Cabrera, 2003; Morón & Ratcliffe, 1997; Morón & Salvadori, 2006; Neita-Moreno & Morón, 2017; Neita-Moreno & Orozco, 2009; Neita-Moreno & Ratcliffe, 2009, 2010, 2011; Neita-Moreno & Yepes, 2011; Neita-Moreno *et al.,* 2014; Onore & Morón, 2004; Palestrini & Barbero, 1992, 1995; Pardo-Locarno & Morón, 2006, 2007; Pardo-Locarno *et al.,* 2006; Ramírez-Salinas *et al.,* 2001, 2010; Ratcliffe & Morón, 2005; Rodrigues *et al.,* 2016, 2017a, b; Scholtz *et al.,* 2004; Sousa & Fuhrmann, 2020; Sousa *et al.,* 2018; Souza *et al.,* 2014; Vanin & Costa, 1980, 1984; Vanin *et al.,* 1983; *orig. Note: 1-7 open in *Plectris, teste* Morón & Salvadori, 2006 (but 1-4 are much larger than 5-7)
Polyphaga	Scarabaeiformia	Scarabaeoidea	Trogidae		*Omorgus procerus* (as *Trox*)	1-4	Ex	Roffey, 1958
Polyphaga	Scirtiformia	Scirtoidea	Clambidae		**Clambus* sp. (Panama)	1-5	Ob	*orig.
Polyphaga	Scirtiformia	Scirtoidea	Decliniidae					
Polyphaga	Scirtiformia	Scirtoidea	Eucinetidae		**Eucinetus morio* sp.; **Nycteus infumatus* (as *Eucinetus*)	1-6	Ex	Leschen, 2016; *orig.
Polyphaga	Scirtiformia	Scirtoidea	Scirtidae		**Cyphon* sp. (USA?); *Elodes minuta, E. tricuspis; Microcara testacea; Ora semibrunnea; Prionocyphon serricornis; Scirtes hemisphaericus*	0?, 1-2, 1-4	Ex, Aq	Jorge *et al.,* 2019; Zwick & Zwick, 2008; *orig. Note: some semiaquatic or aquatic, with floating pupae
Polyphaga	Staphyliniformia	Histeroidea	Histeridae		**Cylistix* sp. (Canada); **Hololepta* sp. (Panama); *Margarinotus scaber;* **Onthophilus kirni;* **Parepierus* sp. (New Zealand); **Paromalus* sp. (Mexico); **Platylomalus aequalis;* **Platysoma* sp. (New Zealand); **Trypanaeus quadricollis;* **Trypeticus* cf. *terebellus*	1-4, 2-4	Ex	Kovarik, 1994; Kovarik & Caterino, 2016; Yus Ramos & Coello García, 2010; *orig.
Polyphaga	Staphyliniformia	Histeroidea	Sphaeritidae					
Polyphaga	Staphyliniformia	Histeroidea	Synteliidae		*Syntelia histeroides*	1/2-6?	Ex	Mamaev, 1974, plus *in litteris* to AFN *ca.* 2000; Newton, 2016a
Polyphaga	Staphyliniformia	Hydrophiloidea	Epimetopidae					
Polyphaga	Staphyliniformia	Hydrophiloidea	Georissidae		*Georissus crenulatus*	0?	Ex	Hansen, 2000. Note: spiracles not detected at 200X
Polyphaga	Staphyliniformia	Hydrophiloidea	Helophoridae					
Polyphaga	Staphyliniformia	Hydrophiloidea	Hydrochidae					
Polyphaga	Staphyliniformia	Hydrophiloidea	Hydrophilidae		*Ametor scabrosus;* **Berosus* sp. (Mexico); *Cercyon maritimus,* **Cercyon* sp. (New Zealand); **Cymbiodyta* sp. (Canada); *Hydrobiomorpha spinosa; Laccobius kunashiricus,* *sp. (USA); **Tropisternus lateralis*	2-6	Ex	Archangelsky, 1997; Archangelsky *et al.,* 2004; Minoshima *et al.,* 2017; Prins, 1984a; Spangler, 1962b; *orig.
Polyphaga	Staphyliniformia	Hydrophiloidea	Spercheidae					
Polyphaga	Staphyliniformia	Staphylinoidea	Agyrtidae	Agyrtinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Agyrtidae	Necrophilinae	**Necrophilus hydrophiloides*	1-2	Ex	Blaisdell, 1901; Newton, 2016b; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Agyrtidae	Pterolomatinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Hydraenidae	Hydraeninae	*Hydraena* **marginicollis, H. perkinsi*	1	Ex	Deler-Hernández & Delgado, 2017; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Hydraenidae	Ochthebiinae	*Ochthebius colveranus* (as *O. exsculptus*)	1	Ex	Beier & Pomeisl, 1959
Polyphaga	Staphyliniformia	Staphylinoidea	Hydraenidae	Orchymontiinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Hydraenidae	Prosthetopinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Jacobsoniidae					
Polyphaga	Staphyliniformia	Staphylinoidea	Leiodidae	Camiarinae	**Neopelatops* sp. (Australia)	1-2	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Leiodidae	Catopocerinae				

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Polyphaga	Staphyliniformia	Staphylinoidea	Leiodidae	Cholevinae	*Antrocharis querilhaci; Bathysciella jeanneli; Cytodromus dapsoïdes; Diaprysius serullazi; Isereus* spp.; **Platycholeus* sp. (USA); *Royerella tarissani; Sciodrepoides watsoni; Speonomus* spp.; *Troglodromus bucheti*	1-2	Ex	Deleurance-Glaçon, 1963; Kilian & Mądra, 2015; Kilian & Newton, 2017; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Leiodidae	Coloninae				
Polyphaga	Staphyliniformia	Staphylinoidea	Leiodidae	Leiodinae	**Anisotoma horni*	1-2	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Leiodidae	Platypsyllinae	*Leptinillus validus; Leptinus testaceus; Platypsyllus castoris*	1-2	Ex	Ising, 1969; Wood, 1965
Polyphaga	Staphyliniformia	Staphylinoidea	Ptiliidae	Cephaloplectinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Ptiliidae	Nossidiinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Ptiliidae	Ptiliinae	*Acrotrichis discolor, A. fascicularis, A. grandicollis, A. sanctaehelenae; Actidium coarctatum; Actinopteryx fucicola; Microptilium pulchellum; Nephanes titan; Ptenidium pusillum; Ptiliolum fuscum; Pteryx suturalis; Ptinella denticollis, *P. tenella;* *Ptiliidae sp. (Mexico)	1, 0	Ob	Costa *et al.*, 1988; De Marzo, 1996, 2012; Hinton, 1941c; Jałoszyński, 2015; *orig. Note: single pair spiracles present on metanotum near suture with abdominal tergum 1, presumed to be migrated spiracles of tergum 1 (De Marzo, 2012; Hinton, 1941c); no spiracles found by De Marzo (2012) in *Actidium coarctatum*
Polyphaga	Staphyliniformia	Staphylinoidea	Silphidae	Nicrophorinae	*Nicrophorus humator, N. investigator, *N. vespillo, N. vespilloides*	1-4	Ex	Růžička, 1992; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Silphidae	Silphinae	*Aclypea opaca* (as *Blitophaga*); *Oxelytrum discicolle; *Necrophila americana; *Oiceoptoma noveboracensis; Thanatophilus micans* (as *Silpha*), *T. sinuatus*	1-4	Ex	Blunck & Janisch, 1925; Costa *et al.*, 1988; Jakubec *et al.*, 2019; Prins, 1984a; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Aleocharinae: Homalotini	*Phanerota fasciata*	1-2	Ex	Ashe, 1981
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Aleocharinae: Lomechusini	*Pella laticollis*	1-2	Ex	Staniec *et al.*, 2009a
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Aleocharinae: Oxypodini	*Haploglossa picipennis*	1-2	Ex	Staniec *et al.*, 2010
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Apateticinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Dasycerinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Empelinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Euaesthetinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Glypholomatinae	*Glypholoma pustuliferum*	1-3	Ex	Thayer, 2000
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Habrocerinae	*"*Habrocerus" magnus* (not true *Habrocerus*]	1-4	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Leptotyphlinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Megalopsidiinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Micropeplinae	*Micropeplus fulvus*	1-2?	Ex	Hinton & Stephens, 1941
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Microsilphinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Neophoninae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Olisthaerinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Omaliinae: Anthophagini	**Brathinus nitidus;* **Microedus austinianus*	1-3	Ex	Thayer, 1985; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Omaliinae: Omaliini	**Micralymma marinum;* ***Omaliomimus* n. sp.; *Omaliopsis arenaria* (as *Omalium*); **Paraphloeostiba gayndahensis*	1-3	Ex	Prins, 1984a; *orig.; **Margaret Thayer, *in litteris* to AFN 11 November 2019
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Osoriinae: Leptochirini	**Priochirus* sp. (Mexico)	1-2	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Osoriinae: Osoriini	**Holotrochus* sp. (Panama); **Osorius* sp. (Mexico)	1-4	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Osoriinae: Thoracophorini	**Lispinus* sp. (Panama); **Nacaeus* sp. (Panama); *Thoracophorus corticinus, *T. costalis*	1-2	Ex	Burakowski & Newton, 1992; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Oxyporinae	*Oxyporus femoralis, *O. lepidus, *O. rufipennis, O. stygicus, O. vittatus*	1-4	Ex	Hanley & Goodrich, 1994; Leschen & Allen, 1988; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Oxytelinae: Blediini	*Bledius atricapillus, B. nanus*, 17 other spp.	1, 1-2	Ex	Staniec, 1998a, 1998b, 2001a

Suborder	Series	Superfamily	Family	Subfamily: Tribe	Taxon/Taxa	FASP	Type	Sources, Notes
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Oxytelinae: Oxytelini	*Anotylus caffer* (as *Oxytelus*); *Oxytelus piceus; Platystethus alutaceus, P. arenarius, P. cornutus, P. nitens*	1-4, 1-3	Ex	Prins, 1984a; Staniec, 1993, 1995, 1997, 2003b, 2003c
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Oxytelinae: Thinobiini	*Aploderus caelatus*	1-4	Ex	Staniec, 1997
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Paederinae: Lathrobiini	*Lathrobium brunnipes, L. fovulum, L. volgense; Lobrathium emarginatum;* **Medonina* sp. (Mexico); *Tetartopeus terminatus; Rugilus rufipes*	1-4	Ex	Smoleński, 1995, 1997; Verhoeff, 1918; Watrous, 1981; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Paederinae: Paederini	**Baryopsis araucana;* **Homaeotarsus* sp. (Panama); ***Monocrypta* sp. (Taiwan); *Ochthephilum fracticorne; Paederus alfierii, P. riparius*	1-4	Ex	Ahmed, 1957; Smoleński, 1995; *orig.; **Fang-Shuo Hu, *in litteris* to AFN 11 October 2019
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Phloeocharinae	**Charhyphus picipennis*	1-3	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Piestinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Proteininae: Proteinini	**Megarthrus* sp. (USA)	1-3	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Protopselaphinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Pselaphinae: Trichonychini	**Bibloporus bicolor;* **Plectophloeus fischeri*	1-3	Ex	Besuchet, 1956b; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Pseudopsinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Scaphidiinae: Scaphidiini	**Scaphidium* sp. (Mexico)	1-3	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Scaphidiinae: Scaphisomatini	**Baeocera* cf. *picea;* **Scaphidium* sp. (Mexico); **Scaphisoma americanum, S. commune* (as *castaneum*), *S. terminatum*	1-3	Ex	Ashe, 1984; Hanley, 1996; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Scydmaeninae: Mastigini	*Palaeostigus pilifer* (as *Mastigus*)	2-3?	Ex	De Marzo, 1984
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Scydmaeninae: Scydmaenini	*Scydmaenus tarsatus*	1-3?	Ex	Jałoszyński, 2012
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Solieriinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Staphylininae: Diochini	**Diochus schaumii,* **D.* sp. (Mexico)	1-4	Ob	Frania, 1992; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Staphylininae: Othiini	**Atrecus* sp. (USA); *Othius fulvipennis*	1-4	Ob	Verhoeff, 1918; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Staphylininae: Staphylinini	*Acylophorus wagenschieberi; Astrapaeus ulmi; Atanygnathus terminalis; Belonuchus rufipennis; Bisnius fimetarius, B. nitidulus;* ***Bolitogyrus rufomaculatus; Creophilus maxillosus; Emus hirtus; Erichsonius alumnus, E. cinerascens; Gabrius appendiculatus, G. astutus, G. osseticus, G. splendidulus;* **Glenus flohri; Hesperus rufipennis; Heterothops niger; Neobisnius sobrinus, N. villosulus; Ocypus fulvipennis, O. nitens, O. olens; Ontholestes murinus; Quedionuchus plagiatus; Quedius brevicornis, Q. brevis, Q. cinctus, Q. cruentus, Q. curtipennis, Q. fuliginosus, Q. fumatus, Q. humeralis, Q. laevigatus, Q. mesomelinus, Q. microps, Q. spelaeus, Q.* spp., **Q.* sp. (USA); *Philonthus albipes, P. atratus, P. caeruleipennis, P. carbonarius, P. corvinus, P. debilis, P. decorus, P. fumarius, P. fuscipennis, P. lepidus, P. longicornis, P. micans, P. misor, P. natalensis, P. nigrita, P. nitidus, P. politus, P. punctus, P. quisquiliarius, P. rectangulus, P. rubripennis, P. sericans, P. succicola, P. tenuicornis, P. umbratilis, P. varians, P.* spp.; *Platydracus cinnamopterus, P. tomentosus,* **P. violaceus, P.* sp. (South Africa); *Rabigus tenuis; Remus sericeus; Staphylinus erythropterus; Tasgius melanarius*	1-4	Ob	Kemner, 1912; LeSage, 1977; Mank, 1923; Moseley *et al.*, 2006; Orth *et al.*, 1976; Outerelo, 1978; Paulian, 1941; Pietrykowska-Tudruj & Staniec, 2006b, c, 2007, 2010, 2011, 2012; Pietrykowska-Tudruj *et al.*, 2014a, b; Prins, 1984a; Saalas, 1917; Schmidt, 1994a, b, 1996; Staniec, 1996, 1999a, b, 2001b, 2002, 2003a, d, 2004a, b, 2005a, b; Staniec & Kitowski, 2004; Staniec & Pietrykowska, 2005a, b; Staniec & Pietrykowska-Tudruj, 2007, 2008a, b, 2009, 2019; Staniec *et al.*, 2009b; Szujecki, 1965; Tawfik *et al.*, 1980; Verhoeff, 1918, 1920; *orig.; **Fang-Shuo Hu, *in litteris* to AFN 11 October 2019
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Staphylininae: Xantholinini	*Gyrohypnus fracticornis; Hypnogyra angularis;* **Nudobius cephalus; Xantholinus* spp. (Europe, South Africa)	1-4	Ob	Pietrykowska-Tudruj & Staniec, 2006a; Prins, 1984a; Staniec & Pietrykowska, 2005b; Verhoeff, 1920; *orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Steninae	**Stenus* sp. (Canada?)	1-4	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Tachyporinae: Mycetoporini	*Mycetoporini sp. (USA)	1-4	Ex	*orig.
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Tachyporinae: Tachyporini	**Coproporus ventriculus;* **Sepedophilus* spp. (USA); **Tachinomorphus grandis; Tachinus luridus* (as *flavipennis*), *T. subterraneus*	1-4, 1-3, 1-3 + 8?	Ex	Hinton, 1941a; Mank, 1923; *orig. Note: spiracles on 8 reported in *Tachinus* (Hinton, 1941a) needs confirmation of functionality
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Trichophyinae				
Polyphaga	Staphyliniformia	Staphylinoidea	Staphylinidae	Trigonurinae	**Trigonurus crotchii*	1-3	Ex	*orig.

nection (Hinton, 1949, and the surveyed literature and examined pupae). This is in contrast to the often complex and diverse structures of spiracular openings in beetle larvae (*e.g.,* Lawrence, 1991). However, no attempt to record details about the structure of pupal spiracles was made in the current survey, nor was any attempt made to record the functionality of the mesothoracic spiracles, which are normally difficult to see in pupae and seldom described or figured. Furthermore, information about the functional abdominal spiracles of the corresponding adults and larvae of the surveyed pupae would be invaluable, but was generally not available in the case of most published pupal descriptions or many of the studied pupae, and no attempt was made to include such data in Table 1.

The classification of Coleoptera used here (Table 1) is adapted from Bouchard *et al.* (2011) as updated by Lawrence (2016), but includes a few more recent changes. Any general discussion below about phylogenetic relationships of various groups of beetles is done in the context of this classification plus recent phylogenetic studies, most notably the morphological phylogeny of Coleoptera in Lawrence *et al.* (2011) and especially the molecular analyses of McKenna *et al.* (2015a) for Staphyliniformia and Scarabaeoidea and McKenna *et al.* (2015b, 2019) for Coleoptera as a whole, which generally support the monophyly of most of the listed suborders, series and superfamilies.

RESULTS

The results of this survey are summarized in Table 1 at the family level only, except that for the focus group Staphylinoidea, where the available information is more complete, subfamilies are also listed, and in Staphylinidae also tribes of some of the larger subfamilies when the pupal character could be determined. All taxa are listed alphabetically, from suborder to cited genera and species. Out of more than 840 publications including descriptions and/or figures of beetle pupae that were consulted, only about a third included explicit information about the distribution of functional spiracles, and these publications were concentrated in the six large families Staphylinidae, Scarabaeidae, Tenebrionidae, Cerambycidae, Chrysomelidae, and Curculionidae, where the indication of this characteristic has generally become a standard part of modern pupal descriptions. Original unpublished information based on my direct examination of more than 100 different available pupae is also included (taxa indicated with an asterisk in Table 1), to help confirm or expand on published information, and a few *in litteris* comments from others are added (indicated with a double asterisk and the name of the source).

All 195 modern beetle families are listed in Table 1, regardless of whether it was possible to determine the distribution of functional abdominal spiracles in pupae, in order to highlight the large gaps in knowledge of this character in Coleoptera. Pupae of perhaps two-thirds of those 195 families have been discovered and described in some way, but evidence for the distribution of functional abdominal spiracles in pupae could be found for only 93 of them, or 48%, in this survey. This does include at least one member of all modern suborders, series and superfamilies, with the exception of the small group Derodontiformia (two superfamilies if Nosodendridae is placed in its own superfamily Nosodendroidea, as in McKenna *et al.,* 2019), but in some groups like the suborder Archostemata and the polyphagan superfamilies Cleroidea, Coccinelloidea and Cucujoidea the gaps at the family level are obviously large. However, this sample is enough to highlight some apparent general patterns and conclusions, which hopefully can be tested with further discoveries and with confirmation or correction of some of the questionable entries in Table 1.

As Hinton (*e.g.,* 1946a, 1947, 1966) has already discussed extensively, beetle pupae and their corresponding larvae that are aquatic or inhabit periaquatic habitats, or that pupate in situations where periodic inundation is likely, generally have strong reductions in the number of functional spiracles, or other profound respiratory modifications such as the development of spiracular gills (*e.g.,* in Myxophaga, see Reichardt & Hinton, 1976) or snorkels (within Scirtidae, see Jorge *et al.,* 2019). Indeed, Hinton (1955b, 1966) argued that the variation in the distribution and nature of pupal spiracles and respiration in the single small aquatic family Psephenidae, or water pennies, probably exceeds the variation in the rest of Coleoptera. A thorough review focused on these modifications and specializations in non-terrestrial beetle groups would be a worthy objective on its own, but is beyond the scope of the present study.

Here the focus is more on the pattern of functional spiracles in pupae that can be broadly considered terrestrial, a habitat that characterizes the vast majority of beetle families and higher groups. These beetles pupate in situations not likely to be flooded, such as in protected shelters under bark or in soil, sometimes in specially constructed cocoons but often in simple excavated cells (or pupal chambers), but some (*e.g.,* within Coccinellidae and Chrysomelidae) also pupate in exposed situations such as attached to vegetation. The following Discussion explores in more detail some attributes of these terrestrial pupae, particularly the distribution of obtect pupae and the number and distribution of functional abdominal spiracles across the order.

DISCUSSION

As discussed by Hinton (1946a, 1949), one might expect that exposed pupae would be obtect, to provide better protection against desiccation or predation, and in fact this appears to be the case for the exposed pupae of Coccinellidae and Chrysomelidae. However (see Table 1), obtect pupae also occur in some groups that pupate in protected situations but are very small, and thus possibly more subject to desiccation (*e.g.,* Ptiliidae, Clambidae, and Corylophidae, where the average pupal size is about 1 mm). However, not all very small beetle pupae are obtect, *e.g.,* pupae of Hydraenidae, Sphindidae and Ciidae are also in the 1-2 mm size range but are exarate. More surprisingly, all of the many known pupae of the staphylinid subfamily Staphylininae are also obtect (Table 1). Staphylinine species are not small (known pupae range from 3-18 mm or larger), nor do they pupate in exposed situations, so an explanation in this case is not obvious (Hinton, 1946a, 1949). All of these multiple cases of obtect pupae in Coleoptera appear to be independently derived from exarate pupae, which are presumed to represent the ancestral condition in Coleoptera (Hinton, 1949). In the case of Staphylininae, this derivation of obtect from exarate pupae is obvious for two reasons: (1) this subfamily is nested high within the known phylogenetic tree of Staphylinidae (see, *e.g.,* Grebennikov & Newton, 2009; McKenna *et al.,* 2015a) while all other known pupae in Staphylinidae and Staphylinoidea are exarate, including the sister subfamily Paederinae; and (2) the observations of Frania (1992) that freshly eclosed staphylinine pupae are actually exarate, then quickly transform into obtect pupae with molded appendages and thick cuticle. However, the functional significance of obtection in this subfamily remains unclear.

If the "aquatic" groups of beetles are set aside, one can recognize in Table 1 a broad general pattern in the number of functional pupal spiracles in the terrestrial beetle groups. For most of these groups (in the suborders Adephaga and Archostemata, and the polyphagan series Bostrichiformia, Cucujiformia, Elateriformia and Scirtiformia, which together include the great majority of beetle families), functional spiracles are generally present on at least the first five abdominal segments, up to and including all eight segments in a few groups. The full range of these possibilities can be found within some of the largest of these families. For example, Cerambycidae, which probably includes the highest percentage of known pupae among beetle families thanks to the efforts of Duffy (1953-1968) and many later authors, exhibits all four states (1-5, 1-6, 1-7, 1-8), although only a single species of *Pyrrhidium* Fairmaire (Cerambycinae) is reported to have all eight abdominal spiracles functional (Švácha & Lawrence, 2014d). Duffy (1960) noted that although some cerambycid subfamilies such as Spondylidinae (as Aseminae) and Lepturinae appeared to have a constant number of functional spiracles (1-7 and 1-5, respectively), the number varied within the other subfamilies; he concluded that the number had little value as a subfamily character, and found no satisfactory correlation between the number present and the pupal environment. The other polyphagan families in these series nearly all have functional spiracles in the range from 1-5 to 1-7 within the larger families, or a fixed number within this range in the smaller families, while a full set of eight spiracles is generally rare or questionable and often in need of confirmation. The series Elateriformia, and especially its superfamily Elateroidea, have consistently higher numbers compared to the other groups, as already noted by Paulian (1941) and Crowson (1981), and this often includes the full set of 1-8. In this survey, only a few apparent exceptions were found to the presence of five or more functional spiracles in this huge assemblage of beetles, in Discolomatidae and within Erotylidae, where only four pairs of functional spiracles are found or reported for some genera (Table 1).

The distribution of functional abdominal spiracles in pupae of the two remaining large groups of beetles, the series Scarabaeiformia and Staphyliniformia, stands in strong contrast to the above pattern. Rather than a minimum of five pairs (on 1-5), a great majority of species in this large assemblage has a maximum of four pairs (1-4), down to a single pair (on 1), or rarely none. There are exceptions, notably Hydrophilidae with functional spiracles on segments 2-6, Synteliidae with possibly the same arrangement, and the possible presence of five pairs (1-5) in some Passalidae and Lucanidae (Paulian 1941, and observed on one unidentified passalid pupa). However, most if not all of the remaining families of Scarabaeoidea, all Histeridae, and all Staphylinoidea, have a confirmed maximum of four functional spiracles (1-4). There are a few anomalous reports of higher numbers that need further exploration, *e.g.,* Morón (1993) noted that spiracles 1-5 or 1-6 may be open in some pupae of unnamed Cetoniinae, Morón & Salvadori (2006) reported that the pupa of the melolonthine genus *Demodema* Blanchard (now a synonym of *Plectris* Lepeletier & Audinet-Serville) had spiracles 5-7 open (even though they were very small compared to the clearly open 1-4), and Fuhrmann *et al.* (2019) reported that a series of pupae of the scarab species *Cylcocephala tucumana* Bréthes included specimens with functional spiracles on either 1-4 or 1-5. Hinton (1941a) reported that a species of *Tachinus* Gravenhorst (Staphylinidae; Tachyporinae) had 1-3 plus 8 open, but my own study of the pupa (in poor condition) of the related genus *Tachinomorphus,* which seemed similar, found that the apparent 8th spiracle likely belonged to the pharate adult inside the pupal cuticle, and the pupa of another *Tachinus* species described by Mank (1923) showed conspicuous spiracles only on 1-3.

Before further discussing this unusual distribution pattern of functional pupal spiracles in beetles, it is worth considering some theoretical factors potentially relevant to the question of why pupae might benefit from reducing the number of functional spiracles compared to the corresponding larval and adult stages of the same species. First, the pupa is an inactive stage, with no food or liquid intake. Thus, its oxygen requirements should be minimal, and certainly much lower than those of the active larval and adult stages. As noted by Crowson (1981), Keister & Buck (1964) demonstrated experimentally that the oxygen consumption per unit weight of the few studied beetle pupae was found to be lower than even quiescent larvae and adults at the same temperatures. Further, because there is normally no liquid intake, pupae may be highly susceptible to desiccation unless they are in a stable saturated environment. These factors would favor reducing the number of functional spiracles in pupae as compared to adults and larvae. However, such a reduction could be constrained by the size of the pupa, as can be seen from some simple calculations. If, as a first approximation, we assume the pupa is a cube, then doubling the length of the pupa while retaining the cube shape would increase its surface area by the length squared, or 4 times, and increase its volume by the length cubed, or 8 times. The pupa's oxygen requirement would presumably be proportional to its mass (or volume), but air movement into the tracheal system would be proportional to the area of the spiracular openings (which are presumably proportional to the surface area of the pupa). In other words, with increasing pupal size, the oxygen requirement may increase faster than the ability of the tracheal system to deliver it. Therefore, larger pupae should require more, or larger, functional spiracles, or both, compared to smaller pupae, in order to meet their relatively greater oxygen needs. Thus, there is much less constraint on reduction in number of functional spiracles for small pupae than for large ones. And finally, if size increases within a group that originally has a very reduced number of functional spiracles, one might expect a secondary increase in the number of functional spiracles (which theoretically can be up to the number found in adults).

With these considerations of the potential impact of pupal size in mind, we can ask if the low numbers of functional spiracles in staphylinoids, histerids and most scarabaeoid families might be the result of one or more small-size bottlenecks in the history of these clades. According to the results of McKenna *et al.* (2015a), these three groups are each monophyletic but do not form a clade together, so the spiracular reduction to 1-4 or less is either derived independently in each of them, or the larger number in Hydrophiloidea and possibly Synteliidae (2-6) is secondarily derived from a smaller number of no more than 1-4. Modern hydrophilid pupae include a wide size range (*ca.* 2-30 mm) but are so far consistent in having functional spiracles on 2-6, but the small-sized hydrophiloid family Georissidae is reported to lack functional abdominal spiracles (Hansen, 2000).

The impact of small size on respiratory and other functional systems in insects in general has been explored by Polilov (2016), who noted that a reduction in the number of functional spiracles is a common result of extreme body size reduction in any life stage. The related idea of an ancestral small-size bottleneck has been previously proposed for the evolution of Staphylinoidea by Lawrence & Newton (1982), who suggested, based on adult characters such as simplified wing venation and a reduced number of Malpighian tubules, that ancestral staphylinoids were very small, and this is also consistent with the small size of many existing staphylinoids. The low number of functional pupal spiracles in this group is consistent with this interpretation, and even consistent with the distribution pattern of functional spiracles among the included families and within Staphylinidae. In this superfamily, following McKenna *et al.* (2015a) and prior studies, the set of relationships of families with known pupae is well established as (Hydraenidae + Ptiliidae) + ((Agyrtidae + Leiodidae) + (Silphidae + Staphylinidae)). In the first monophylum (Hydraenidae + Ptiliidae) size is always small (adults less than 1 mm to *ca.* 2 mm) and functional pupal spiracles are found only on the first abdominal segment, a highly unusual condition that occurs in spite of other differences between these families (Hydraenidae have semi-aquatic or aquatic larvae and adults and exarate pupae, while Ptiliidae are terrestrial with obtect pupae). The next monophylum, (Agyrtidae + Leiodidae), consistently has functional abdominal pupal spiracles on 1-2 only, even though size differences are substantial (*ca.* 2-3 mm for most leiodids, 10 mm or more for some agyrtids). The third and by far most diverse monophylum, (Silphidae + Staphylinidae), includes very small to very large species (less than 1 mm to over 30 mm), and includes more variation in the number of functional abdominal spiracles in pupae (1 only (rare), 1-2, 1-3, 1-4). Within this vast group, the largest species, in Silphidae and Staphylininae, consistently have spiracles 1-4 functional, while many subfamilies with smaller-sized species generally have 1-2 or 1-3 functional. The number is usually consistent within a subfamily, except for Osoriinae (where it is so far consistent within tribes) and Oxytelinae, which shows the greatest variation, even within tribes and within the single genus *Bledius* Leach. According to Staniec (2001a), most *Bledius* species have spiracles 1-2 functional, but some have only 1 functional (possibly related to the semi-aquatic habitat in this genus, in which the immature stages develop in burrows in salt flats or other situations where the burrows may be inundated frequently).

Histeridae also include many small species, especially in the subfamily Abraeinae, but most are medium-sized to large. Scarabaeoidea are even less likely candidates for a small-size ancestor, and modern species include some of the largest beetles, *e.g.*, in Lucanidae, Passalidae, and especially in the scarab subfamilies Dynastinae and Cetoniinae, where pupae can exceed 60 mm in length in genera like *Dynastes* Kirby (Morón, 1987). And yet, even these monstrous pupae have only abdominal spiracles 1-4 functional, although the spiracular openings are relatively huge.

Perhaps the strongest argument against a small-size bottleneck in the ancestors of staphylinoids, scarabaeoids and Histeridae as an explanation for the reduced number of functional abdominal spiracles in their pupae is the fact that very small terrestrial beetles outside of this group do not show a similar reduction. For example, the families Micromalthidae (in Archostemata) and Ciidae, Clambidae, Corylophidae and Sphindidae (in four different superfamilies of Polyphaga) all have pupae in the 1-2 mm size range, but all have at least the first five abdominal spiracles functional, regardless of whether they are obtect (Clambidae, Corylophidae) or exarate. Our knowledge about the fossil history of beetles has grown dramatically in recent years, and potentially it will be possible to compare the fossil history of staphyliniforms and scarabaeoids (which is now becoming clear, at least from the mid-Jurassic on) to the same history for the other "small-beetle" groups mentioned above, in order to compare the evolution of size in these groups and look for differences that might explain the differences in spiracular reduction. At present I can only suggest that small size may not be the main, or only, factor in determining the degree of spiracular reduction in terrestrial beetle pupae, and that one or more other yet-undetected characteristics of groups like the above staphyliniforms and scarabaeoids is a factor.

In any case, it does appear that these spiracular reductions occur consistently within staphylinoids, scarabaeoids and Histeridae, with only modest variations even across the large size ranges found within the modern members of these groups. Even though the cause may be uncertain, this consistency in turn suggests a strong correlation between this character and the phylogenetic evolution of these groups. This character may thus have some value in placing certain controversial taxa. For example, the small enigmatic family Jacobsoniidae was for a long time placed in or near Derodontoidea or its taxonomic predecessor Dermestoidea (Crowson, 1955, Bouchard *et al.,* 2011), but recent phylogenetic studies (*e.g.,* Lawrence *et al.,* 2011) indicated the group as a probable member of Staphylinoidea, and McKenna *et al.* (2015b, 2019) resolved Jacobsoniidae as a sister group to the monophylum (Hydraenidae + Ptiliidae). Jacobsoniid pupae are apparently unknown, but this current phylogenetic placement within Staphylinoidea leads to the prediction that they will have no more than four pairs of functional spiracles (on 1-4), and possibly only one pair as in its sister clade.

CONCLUSIONS

1) Beetle pupae have an evidently stable set of characteristics useful for study of phylogenetic relationships at various levels.
2) Some features, such as obtection and gin traps or other protective devices, are clearly of multiple origin within Coleoptera but probably useful phylogenetically at or below the family level.
3) The number of functional abdominal spiracles in pupae is usually, but not necessarily, less than in larvae and adults of the same species, sometimes dramatically so in minute species (as in the clade of Hydraenidae and Ptiliidae).
4) The number of functional abdominal spiracles may be related to body size of the most recent clade's common ancestor. Low numbers characterize some, but not all, groups with very small species, especially those associated with aquatic habitats where they are subject to strong modifications to prevent drowning (*e.g.,* in Myxophaga or Scirtidae), as well as certain non-aquatic groups that may have passed through a small-size bottleneck in their distant phylogenetic history, as has possibly independently occurred in staphylinoids, scarabaeoids and Histeridae.
5) Variation in the number of functional abdominal spiracles is much lower within modern groups of family rank or below than might be predicted from theoretical considerations related to physical size. The number is often constant within large groups of species that vary enormously in size, as in most subfamilies of Scarabaeidae, in Hydrophilidae, and in "higher" Staphylinidae (Paederinae and Staphylininae). Also, the number is not invariably reduced in minute beetles, as illustrated by the presence of a minimum of 5 pairs of functional spiracles in species of Clambidae, Ciidae, Corylophidae, Micromalthidae and Sphindidae. This suggests both that historical factors outweigh functional factors in many cases, and there is the potential for high phylogenetic information content in this character.
6) Clearly, efforts toward establishing the number of functional abdominal spiracles in more pupae of Coleoptera already seems worthwhile from a phylogenetic perspective, and describing this character should become a standard part of pupal descriptions.

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