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REVIEW ARTICLE

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When a key innovation becomes redundant: Patterns, drivers and consequences of elytral reduction in Coleoptera

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Abstract

The transformation of the fore wings into strongly sclerotized protective covers (elytra) is considered a fundamental evolutionary innovation of the megadiverse order Coleoptera. Surprisingly, these multifunctional structures have been reduced in many distantly related groups of beetles. Patterns, drivers and the evolutionary implications of this modification have never been comprehensively discussed. In the present study, we surveyed the entire order Coleoptera to analyse the patterns of elytral shortening and loss, with a special focus on prevalence, forms, degree of reduction and the functional background of this significant deviation from the coleopteran ground plan. Our analysis revealed that about 20% of all extant species (roughly 88,000 out of 442,275 spp.), distributed across all four suborders, have shortened or even absent elytra. The elytral loss was more frequent within the polyphagan series Elateriformia and Staphyliniformia. Moreover, we found that elytral reduction has independently occurred multiple times in the evolutionary history of Coleoptera and that it has been driven by a wide array of selective drivers. One of the main drivers is the improved flexibility of the uncovered abdomen and the correlated increased manoeuvrability in narrow spaces, as well as the option of using the flexible abdomen as a steering organ or to facilitate mating. Another common driver is mimicry, where exposed metathoracic wings potentially improve the overall similarity to hymenopteran models. Exposure of the abdomen can facilitate the targeted release of defensive abdominal gland secretions and was most likely a crucial step towards establishing relations with social insects enhanced by chemical communication. In the Elateriformia, and rarely in other lineages, elytral loss is a consequence of paedomorphosis, related to a specific resource-allocation strategy. In many groups of beetles with reduced elytra, alternative defensive strategies can be found. This includes, for instance, aposematic coloration, chemical defence, mimicry or bioluminescence. Direct drivers of elytral loss in many groups remain unclear, and more studies are needed to understand the evolutionary background and implications of this significant morphological modification in Coleoptera.

KEYWORDS
covers, evolution, insect, novelty, paedomorphosis, reduction, wings

INTRODUCTION

A crucial character complex of Coleoptera is the strong sclerotization of the body without exposed membranes and the protection of the posterodorsal body surface by highly modified, sclerotized fore wings, the elytra (Boudinot et al., 2023a; Crowson, 1981). An obvious evolutionary benefit is greatly improved mechanical protection, enabling adult beetles to penetrate narrow crevices, and also better protection against predators, higher desiccation tolerance and a minimised effect of rapid temperature shifts (Goczał & Beutel, 2023; Linz et al., 2016). On the other hand, forming strongly developed body armour, including sclerotized elytra, is a developmentally costly endeavour as it requires high resource investment (Goczał & Beutel, 2023; Linz et al., 2016). Moreover, fully developed elytra increase weight and reduce body flexibility (Johansson et al., 2012; Kim et al., 2020; Le et al., 2014).

The formation of elytra and their tight fit with the posterior body were decisive transformations in the early evolution of Coleoptera (Boudinot et al., 2023a; Goczał & Beutel, 2023). Although the primary function of elytra is apparently mechanical protection of the body (Beutel & Leschen, 2016), these structures have been significantly modified in many lineages by various forms of selective pressure and are involved in a wide variety of functional contexts. This might include, for instance, protection and defence, thermoregulation, water saving, flight, swimming, moisture harvesting, courtship and mating, hind wing folding, the transport of symbiotic microorganisms or acoustic communication (Goczał & Beutel, 2023). Considering these functions, it appears surprising that partial or even complete elytral reduction has occurred multiple times in Coleoptera (Goczał et al., 2018; Jolivet, 2008). The group best known in this context is the megadiverse Staphylinidae or rove beetles (ca. 67,000 described spp.). However, shortened fore wings have evolved in numerous distantly related beetle lineages distributed over all four extant suborders and apparently in many different forms and functional contexts. So far, little is known about the prevalence, potential drivers and evolutionary implications of this seemingly mysterious elytral loss in Coleoptera.

The main goal of the present study is to provide a comprehensive review of the phenomenon of elytral reduction and loss across the entire order Coleoptera. The distribution among different beetle lineages will be evaluated based on solid recent phylogenetic patterns (Cai et al., 2022; McKenna et al., 2019; Zhang et al., 2018). We will also outline different forms of partial or complete reduction and address potential drivers of shortening or complete loss of the elytra. Finally, we will discuss the evolutionary implications of this modification. Our review will be a crucial first step towards a better understanding of the largely unexplored phenomenon of the loss of this key morphological innovation in Coleoptera.

Terminology and main sources

In our study, we generally consider species with elytra characterised by a truncated apical region (e.g., Micromalthidae, Hydroscaphidae, Gyrinidae, Carabidae: Brachininae, Ptiliidae and Histeridae), that is, a more-or-less transverse posterior margin, as brachelytrous (Figure 1a–c). This also applies to rare cases when the abdomen might be unusually contracted (naturally or as an artefact of preservation) and, thus, appears largely or even completely covered (Figure 1a).

Beetles with non-truncated elytra exposing more than one abdominal tergite (at least tergite VIII and a part of tergite VII; Figure 1d) are also considered to be brachelytrous according to our concept, but not cases with only the terminal tergite (normally tergite VIII) visible (e.g., Melandryidae: *Marolia* Mulsant, Cryptophagidae: *Hypocoprus* Motschulsky).

We are aware that there is a large grey zone with groups where the elytra may or may not be slightly shortened and the abdominal apex exposed, but possibly only due to hyperextension of this tagma. The definition given above may be arbitrary and ambivalent in some cases. Nevertheless, we hope that this will make our presented results transparent and open to scrutiny.

A specific and difficult case in the context of elytral reduction and coverage of the dorsal abdomen is physogastry. Because of the taxonomic richness and morphological diversity of the studied group, in rare cases (<5% of reviewed taxa), we were not able to fully reliably distinguish between physogastry (swelling of the abdomen due to the hypertrophy of fat bodies or ovaries) or pseudophysogastry (artificial swelling of the abdomen as a part of mimicry) (Jolivet, 2008) and elytral reduction. In these rare examples, physogastric or pseudophysogastric species might have been treated in our review as brachelytrous because the consequences (e.g., limited protection value of elytra) of abdominal exposure in both cases might be similar.

We follow Jolivet (2008) in using the terms 'brachelytry' (not 'brachyelytry' or 'brachelytrism') and 'brachelytrous' (not 'brachyelytrous'). We recognise two subcategories: (a) truncated type (Figure 1a–c), where the mesal edges (suture) are parallel, adjacent or connected; the posterior edge is more-or-less straight and the abdomen is not inflated, as in Micromalthidae (Archostemata), Hydroscaphidae (Myxophaga), Gyrinidae, Carabidae: e.g., Brachininae and Pseudomorphinae (Adephaga), and several groups of Staphyliniformia (Polyphaga); and (b) dehiscent type (Figure 1d), where mesal edges are diverging, the posterior edge is not straight and the abdomen is often inflated, as in many Elateroidea, Meloidae, Dascillidae and Ripiphoridae. This second type also includes cases where the elytra are vestigial (e.g., in the female of *Omalisus* Geoffroy or the male of *Phosphaenus hemipterus* (Geoffroy), Figure 1e,f).

We used the following terminology for the description of elytra and hind wings:

Macroptery/macropterous—from 'mákros' = long + 'pterón' = wing—forms with well-developed hind (flight) wings (but not referring to elytra) (Figure 1a–d,g).

Brachyptery/brachypterous—from 'brachýs' = short + 'pterón' = wing—forms with shortened hind (flight) wings (but not referring to elytra). We include here also cases where hind wings are vestigial and which could be otherwise referred to as microptery/micropterous—from 'mikrós' = small + 'pterón' = wing (Figure 1h).

Aptery/apterous—from 'a' = not, without + 'pterón' = wing—forms lacking hind (flight) wings (but not referring to elytra) (Figure 1e–f,i).

Macrelytry/macrelytrous—from 'mákros' = long + 'élytron' = elytron—forms with complete elytra (but not referring to hind wings) (Figure 1g–i).

Brachelytry/brachelytrous—from 'brachýs' = short + 'élytron' = elytron—forms with shortened elytra (but not referring to hind wings).

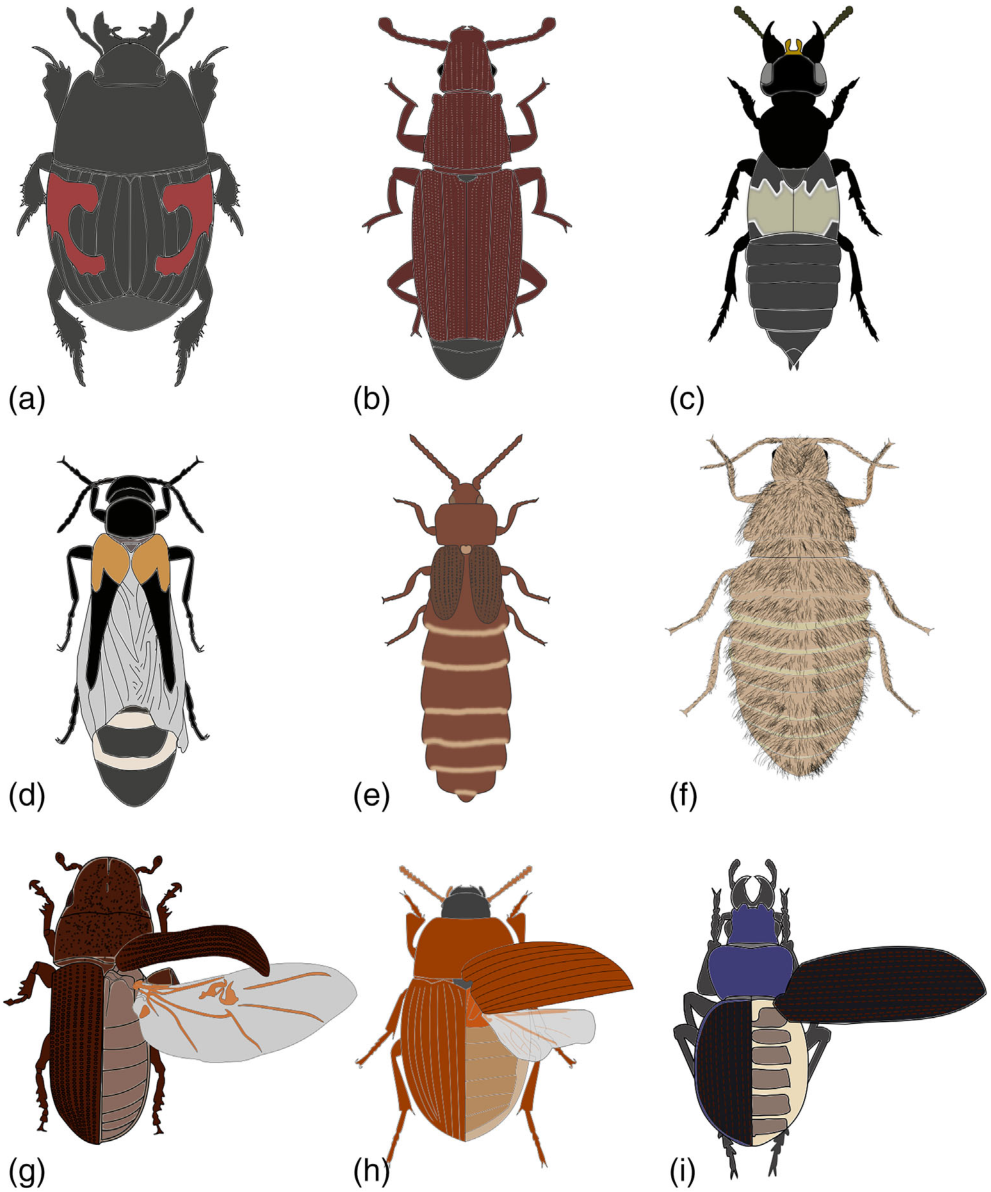

FIGURE 1 Schematic drawings of various types of wing modifications in Coleoptera. (a) Brachelytrous (truncated type) member of Histeridae; (b) Brachelytrous (truncated type) member of Monotomidae; (c) Brachelytrous (truncated type) member of Staphylinidae; (d) Brachelytrous (dehiscent type) member of Meloidae; (e) Apterobrachelytrous female of *Omalisus* Geoffroy (Elateridae); (f) Apteroanelytrous female of *Thylodrias contractus* Motschulsky (Dermestidae); (g) Macrelytrous and macropterous member of Scolytinae (Curculionidae); (h) Macrelytrous and brachypterous member of Tenebrionidae; (i) Macrelytrous and apterous member of Carabidae.

Anelytry/anelytrous—from 'a, an' = not, without + 'élytron' = elytron—forms completely lacking elytra (but not referring to hind wings) (Figure 1f). Based on analysed materials, we concluded that anelytry is a specific condition of elytra reduction, and thus, whenever we use the phrase 'elytral reduction', this also includes its rare, extreme form—anelytry.

Apteroanelytry/apteroanelytrous—forms lacking hind (flight) wings and lacking elytra (e.g., females of Elateridae: Drilini, Phengodidae and Rhagophthalmidae) (Figure 1f).

Apterobrachelytry/apterobrachelytrous—forms without hind (flight) wings and with reduced elytra (e.g., *Meloe* Linnaeus, female of *Omalisus*) (Figure 1e).

Our systematic review of elytral reduction was largely based on the three Coleoptera volumes of *Handbook of Zoology* (Beutel & Leschen, 2016; Leschen et al., 2010; Leschen & Beutel, 2014) and electronic key of Lawrence, Hastings, et al. (2010) and supplemented by a large number of other morphological studies and information from various colleagues–taxonomists (see the Systematic Review section and Acknowledgments).

We follow the latest higher level classification of extant Coleoptera by Cai et al. (2022), which was partly compiled based on prior phylogenomic analyses (McKenna et al., 2019; Zhang et al., 2018), but refer to the criticism of the analytical approach and treatment of stem-group taxa by Boudinot et al. (2023b). We keep the sequence of higher taxa in our Systematic Review section as in Cai et al. (2022), with the exception of the sequence of suborders, where we keep the traditional sequence (i.e., Archostemata, Myxophaga, Adephaga and Polyphaga; McKenna et al., 2019) because this part of the beetle tree-of-life has not yet been fully resolved.

For a reliable estimation of the prevalence of elytral loss within every extant family of beetles, we have presented the most updated and revised figures for the current number of described extant species in each family, resulting in the highest yet total number of species for Coleoptera (see Supplementary File S1 for methodological details).

SYSTEMATIC REVIEW

Below we present a taxon-by-taxon summary of the phenomenon of anelytry and brachelytry across Coleoptera. Specific examples across the order are summarised in Table 1; numbers and percentages across families, as well as a revised total number of extant, described species of beetles, are presented in Table 2.

Stem-group Coleoptera

Reduction of the elytra, either partially or completely, is unknown in Permian stem groups of Coleoptera (Boudinot et al., 2023a; Ponomarenko, 1969). The most ancestral condition in Coleoptera was outlined by Boudinot et al. (2023a) and Schädel et al. (2022): elytra broader than the abdomen and surpassing the abdominal apex posteriorly, covering the posterior body loosely in a tent-like manner (see also Goczał & Beutel, 2023). Elytra fitting closely with the abdomen forming a tightly sealed subelytral space had evolved by the Middle Permian (Boudinot et al., 2023a).

Suborder Archostemata

All species of Cupedidae and Ommatidae have fully developed elytra, covering the dorsal side of the abdomen completely (e.g., Escalona et al., 2020; Friedrich et al., 2009; Lawrence et al., 2011; Parker & Lawrence, 2001). This applies also to relict Jurodidae (Hörnschemeyer, 2005; Yan et al., 2014). The single exception is the aberrant family Micromalthidae, with a single extant species and a complex and highly unusual life cycle (Hörnschemeyer, 2005, 2009; Pollock & Normark, 2002). The elytra of the 'telephone pole beetle', *Micromalthus debilis* LeConte, are distinctly truncated, but with the posterolateral and posteromesal corners rounded. They leave abdominal tergite V partially and tergites VI–VIII completely exposed. Adults of this species are very small (1.5–2.5 mm) compared with other species of Archostemata and weakly sclerotized (Hörnschemeyer, 2005, 2009). In the context of elytral shortening, it should be noted that the number of exposed abdominal sternites in *M. debilis* has increased from the ancestral five to six or seven (Hörnschemeyer, 2005). A highly unusual feature of the species is that adult males play only a very marginal role in reproduction (or otherwise), if at all (Perotti et al., 2016; Pollock & Normark, 2002).

The brachelytrous condition evolved very early in Micromalthidae, as documented by the brachelytrous Upper Permian †*Archaeomalthus synoriacos* (Yan et al., 2019). As in the single extant species, the elytra were distinctly shortened and lacked window punctures, the latter of which is the characteristic of stem-group beetles and extant Cupedidae and Ommatidae (Boudinot et al., 2023a). It is likely that elytral shortening is correlated with the marginal role played by the adults of *Micromalthus*. Most of the year, populations consist only of larvae, which can produce offspring viviparously (Pollock & Normark, 2002). Adult females only develop under unfavourable conditions, and males only very sporadically. Considering this and the short life span of adults, strong mechanical protection is not a priority. Investment in energy and materials, including for sclerotized structures such as the elytra, is reduced.

Suborder Myxophaga

The Myxophaga comprise ca. 130 described species, placed in one extinct and four extant families (e.g.,Fikáček et al., 2020; Qvarnström et al., 2021). Lepiceridae, Sphaeriusidae and the most species-rich family Torridincolidae (54 described spp.) have fully developed elytra, entirely covering the abdomen (e.g., Lawrence et al., 2011; Reichardt, 1973). In contrast, the elytra of the extinct †Triamyxidae and the structurally very similar extant Hydroscaphidae are distinctly truncated apically, leaving abdominal tergites VI–VIII exposed (Fikáček et al., 2020; Qvarnström et al., 2021). In both groups, the posterior abdomen strongly converges to its apex. The posterior segments are ring-shaped in Hydroscaphidae and highly movable, especially laterally. Hydroscaphidae are aquatic, and this can be also assumed for the Triassic †Triamyxidae. In the case of *Hydroscapha* LeConte and related genera, shortening of the elytra is very likely correlated with the greatly increased flexibility of the posterior abdomen. Photographs and field observations (Rolf G. Beutel) show that these aquatic beetles use their posterior abdomen as a steering organ in the shallow, flowing water of hygropetric habits.

Suborder Adephaga

As in Archostemata and Myxophaga, the only form of elytral reduction in Adephaga is posterior truncation, with the mesal edges closely adjacent, leaving the posterior abdominal tergites exposed. Shortened elytra occur only in two of the 11 families: in the highly specialised aquatic Gyrinidae or whirligig beetles (Figure 1a), likely the sister taxon of the remainder of the suborder (e.g., McKenna et al., 2019; Vasilikopoulos et al., 2021), and in only a few subgroups (Gehringiinae, Brachininae, Lebiinae, Paussinae and Pseudomorphinae) of the megadiverse Carabidae, the ground beetles (e.g., Arndt et al., 2016; Lindroth, 1961–1969). In their general body shape, Gyrinidae are similar to the aquatic myxophagan Hydroscaphidae, and it is very likely that the

TABLE 1 Examples of an/brachelytrous species/genera with information about form of elytral modification (A, anelytrous; D, dehiscent; R, with rounded apices; T, truncated) and its potential drivers (?, unknown; CH, cryptic habitat; DS, enhanced targeting of defensive secretions; FW, facilitated unfolding of featherwings; IF, increased abdomen flexibility; MI, mimicry; PC, paedomorphic changes; RS, resource saving; SE, specialised ectoparasitism; SF, adaptation to specific flight style; SI, association with social insects).

	Example genus/species	Form	Potential driver(s)
Suborder Adephaga			
Gyrinidae	*Gyrinus* Linnaeus	T (♀, ♂)	IF
Carabidae	*Brachinus* Weber	T (♀, ♂)	DS
Suborder Archostemata			
Superfamily Cupedoidea			
Micromalthidae	*Micromalthus debilis* LeConte	T (♀, ♂)	RS
Suborder MYXOPHAGA			
Superfamily Sphaeriusoidea			
Hydroscaphidae	*Hydroscapha* LeConte	T (♀, ♂)	IF
Suborder Polyphaga			
Superfamily Dascilloidea			
Dascillidae	*Anorus parvicollis* Horn	A (♀)	PC, SI, CH
Superfamily Buprestoidea			
Buprestidae	*Hesperorhipis* Fall	R, D (♀, ♂)	?, MI
Superfamily Dryopoidea			
Psephenidae	*Sinopsephenoides* Yang	R, D (♀, ♂)	RS
Superfamily Elateroidea			
Incertae sedis	*Neocrowsonia* Kistner & Abdel-Galil	R, D (♂, ♀)	PC, SI
Omethidae	*Telegeusis* Horn	R, D (♂),? (♀)	PC
Jurasaidae	*Jurasai* Rosa et al.	R, D (♂), A(♀)	PC, CH
Iberobaeniidae	*Iberobaenia* Bocak et al.	D (♂),? (♀)	PC, CH
Lycidae	*Platerodrilus* Pic	A (♀)	PC
Lycidae	*Xenomorphon baranowskii* Ferreira et al.	A (♂),? (♀)	PC
Lycidae	*Cautires apterus* Bocak et al.	R, D (♂),? (♀)	PC
Cantharidae	*Ichthyurus* Westwood	R, D (♂, ♀)	MI
Lampyridae	*Lamprohiza splendidula* (Linnaeus)	A (♀)	PC
Lampyridae	*Phosphaenus hemipterus* (Geoffroy)	R, D (♂), A(♀)	PC
Phengodidae	*Phrixothrix* Olivier	R, D (♂), A(♀)	PC
Rhagophthalmidae	*Falsophrixothrix* Pic	R, D (♂),? (♀)	PC
Rhagophthalmidae	*Rhagophthalmus* Motschulsky	R (♂), A(♀)	PC
Elateridae	*Omalisus* Geoffroy	R, D (♀)	PC, CH
Elateridae	*Cebrio* Olivier	R, D (♀)	PC, CH
Elateridae	*Malacogaster* Bassi	R, D (♂), A(♀)	PC, CH
Superfamily Histeroidea			
Synteliidae	*Syntelia* Westwood	T (♀, ♂)	?
Sphaeritidae	*Sphaerites glabratus* (Fabricius)	T (♀, ♂)	?
Histeridae	*Hololepta* Paykull	T (♀, ♂)	?
Superfamily Scarabaeoidea			
Glaphyridae	*Eulasia* Truqui	T, D (♀, ♂)	?
Scarabaeidae	*Valgus* Scriba	T, D (♀, ♂)	MI
Scarabaeidae	*Pachypus* Dejan	R (♂), A(♀)	PC, CH
Superfamily Staphylinoidea			
Staphylinidae	*Anthobium* Leach	T (♀, ♂)	IF
Staphylinidae	*Thyreoxenus* Mann	T (♀, ♂)	SI

(Continues)

TABLE 1 (Continued)

	Example genus/species	Form	Potential driver(s)
Staphylinidae	*Quedius* Stephens	T (♀, ♂)	IF
Hydraenidae	*Limnebius crinifer* (Rey)	T (♀, ♂)	IF
Leiodidae	*Platypsyllus castoris* Ritsema	T (♀, ♂)	SE
Ptiliidae	*Pteryx* Matthews	T (♀, ♂)	FW
Superfamily Bostrichoidea			
Dermestidae	*Thylodrias* Motschulsky	D (♂), A(♀)	RS, PC
Superfamily Cleroidea			
Melyridae	*Carphurus* Erichson	T (♀, ♂)	?, MI
Cleridae	*Isohydnocera* Chapin	T (♀, ♂)	?, SI, MI
Trogossitidae	*Nemozoma gymnosternalis* Kolibáč	T (♀, ♂)	IF
Superfamily Lymexyloidea			
Lymexylidae	*Atractocerus* Palisot de Beauvois	R, D (♀, ♂)	?, MI, SF
Superfamily Tenebrionoidea			
Mordellidae	*Stenalia* Mulsant	R, D (♀, ♂)	?
Ripiphoridae	*Ripiphorus* Bosc	R, D (♀, ♂)	?
Ripiphoridae	*Ripidius* Thunberg	R, D (♂), A(♀)	?
Oedemeridae	*Oedemera femorata* (Scopoli)	R, D (♀, ♂)	?
Meloidae	*Sitaris* Latreille	R, D (♀, ♂)	MI, SI
Tenebrionidae	*Petria* Semenov	T (♂),? (♀)	?PC,? SI
Mycteridae	*Hemipeplus marginipennis* (LeConte)	R, D (♀, ♂)	?
Salpingidae	*Diagrypnodes* Waterhouse	R, D (♀, ♂)	IF
Anthicidae	*Leptanthicus staphyliniformis* Werner	T (♀, ♂)	?
Promecheilidae	*Chanopterus paradoxus* Boheman	T (♀, ♂)	?
Incertae sedis: Afreminae	*Afremus pickeri* Levey	T (♂),? (♀)	?
Superfamily Coccinelloidea			
Corylophidae	*Sericoderus* Stephens	T (♀, ♂)	?
Coccinellidae	*Mimolithophilus capensis* Arrow	T (♀, ♂)	?
Superfamily Nitiduloidea			
Monotomidae	*Monotoma* Herbst	T (♀, ♂)	IF
Monotomidae	*Crowsonius* Pakaluk & Ślipiński	T (♀, ♂)	?, IF, SI
Kateretidae	*Brachypterus* Kugelann	T (♀, ♂)	?
Nitidulidae	*Conotelus* Erichson	T (♀, ♂)	?
Smicripidae	*Smicrips* LeConte	T (♀, ♂)	?
Superfamily Cucujoidea			
Laemophloeidae	*Cucujinus* Arrow	T (♀, ♂)	?
Superfamily Curculionoidea			
Anthribidae	*Urodontidius enigmaticus* Louw	T (♀, ♂)	?, CH
Attelabidae	*Pterocolus* Say	T (♀, ♂)	?, CH
Curculionidae	*Ozopemon* Hagedorn	A (♂)	PC, RS
Superfamily Chrysomeloidea			
Chrysomelidae	*Arima* Chapuis	R, D (♀, ♂)	RS
Vesperidae	*Vesperus sanzi* Reitter	R, D (♀)	RS
Cerambycidae	*Necydalis* Linnaeus	R, D (♂, ♀)	MI
Cerambycidae	*Chariea longispina* Galileo & Martins	R, D (♂)	?, RS
Cerambycidae	*Miniprionus pavlovskii* (Semenov)	R, D (♀)	RS

Note: Examples of particular species are given for monospecific genera or when there is significant variation in elytral reduction within a genus.

TABLE 2 Approximate number of species meeting our criteria for anelytry or brachelytry, by beetle family.

	No. spp.	No. brach	% brach		No. spp.	No. brach	% brach
Suborder Adephaga							
Haliplidae	238	0	0	Hygrobiidae	6	0	0
Gyrinidae	882	882	100	Dytiscidae	4589	0	0
Noteridae	262	0	0	Trachypachidae	6	0	0
Meruidae	1	0	0	Cicindelidae	2910	0	0
Aspidytidae	2	0	0	Carabidae	37,702	3700	9.81
Amphizoidae	5	0	0				
Suborder Archostemata							
Crowsoniellidae	1	0	0	Micromalthidae	1	1	100
Cupedidae	36	0	0	Ommatidae	6	0	0
Suborder Myxophaga							
Lepiceridae	3	0	0	Hydroscaphidae	35	35	100
Torridincolidae	54	0	0	Sphaeriusidae	22	0	0
Suborder Polyphaga							
Jurodidae	1	0	0	Clambiformia			
Scirtiformia				Clamboidea			
Scirtoidea				Derodontidae	42	0	0
Decliniidae	2	0	0	Clambidae	170	0	0
Scirtidae	800	0	0	Eucinetidae	65	0	0
Rhinorhipiformia							
Rhinorhipoidea							
Rhinorhipidae	1	0	0				
Elateriformia							
Dascilloidea				Buprestoidea			
Dascillidae	100	15	15	Schizopodidae	7	0	0
Rhipiceridae	87	0	0	Buprestidae	15,000	20	0.13
Byrrhoidea							
Byrrhidae	500	0	0				
Dryopoidea							
Lutrochidae	21	0	0	Psephenidae	287	1	0.35
Dryopidae	280	0	0	Protelmidae	6	0	0
Eulichadidae	43	0	0	Elmidae	1500	0	0
Callirhipidae	164	0	0	Limnichidae	387	0	0
Ptilodactylidae	500	0	0	Heteroceridae	300	0	0
Cneoglossidae	9	0	0				
Chelonariidae	300	0	0				
Elateroidea							
Artematopodidae	71	0	0	Sinopyrophoridae	1	0	0
Omethidae	61	23	37.7	Lycidae	4300	250	5.81
Brachypsectridae	7	0	0	Iberobaeniidae	3	3	100
Throscidae	150	0	0	Phengodidae	312	312	100
Eucnemidae	1500	0	0	Rhagophthalmidae	66	66	100
Cerophytidae	23	0	0	Lampyridae	2500	650	26
Jurasaidae	6	6	100	Cantharidae	5600	1600	28.57
Elateridae	11,000	420	3.82				

(Continues)

TABLE 2 (Continued)

	No. spp.	No. brach	% brach		No. spp.	No. brach	% brach
Nosodendriformia							
Nosodendroidea							
Nosodendridae	104	0	0				
Staphyliniformia							
Histeroidea							
Synteliidae	7	7	100	Histeridae	4815	4815	100
Sphaeritidae	7	7	100				
Hydrophiloidea							
Hydrophilidae	3448	0	0	Georissidae	83	0	0
Helophoridae	199	0	0	Hydrochidae	276	0	0
Epimetopidae	72	0	0	Spercheidae	18	0	0
Scarabaeoidea							
Lucanidae	1774	0	0	Passalidae	850	0	0
Trogidae	335	0	0	Belohinidae	1	0	0
Glaresidae	89	0	0	Ochodaeidae	153	0	0
Pleocomidae	29	0	0	Glaphyridae	213	130	61.03
Bolboceratidae	622	0	0	Hybosoridae	695	0	0
Diphyllostomatidae	3	0	0	Scarabaeidae	35,839	3000	8.37
Geotrupidae	468	0	0				
Staphylinoidea							
Jacobsoniidae	26	0	0	Agyrtidae	73	0	0
Ptiliidae	1008	700	69.44	Leiodidae	4232	1	0.02
Hydraenidae	2160	150	6.94	Staphylinidae	66,838	63,000	94.26
Colonidae	170	0	0				
Bostrichiformia							
Bostrichoidea							
Dermestidae	1818	3	0.18	Bostrichidae	570	0	0
Endecatomidae	4	0	0	Ptinidae	2200	0	0
Cleroidea							
Rentoniidae	11	0	0	Phycosecidae	4	0	0
Byturidae	16	0	0	Prionoceridae	158	0	0
Biphyllidae	185	0	0	Mauroniscidae	30	0	0
Acanthocnemidae	1	0	0	Rhadalidae	290	1	0.34
Protopeltidae	2	0	0	Melyridae	6000	3000	50
Peltidae	8	0	0	Phloiophilidae	1	0	0
Lophocateridae	120	0	0	Chaetosomatidae	13	0	0
Trogossitidae	450	5	1.11	Thanerocleridae	38	0	0
Thymalidae	21	0	0	Cleridae	4000	200	5
Lymexyloidea							
Lymexylidae	65	30	46.15				
Tenebrionoidea							
Ripiphoridae	320	200	62.5	Stenotrachelidae	19	0	0
Mordellidae	2000	300	15	Tetratomidae	150	0	0
Aderidae	1000	0	0	Melandryidae	420	0	0
Ischaliidae	57	0	0	Synchroidae	9	0	0
Trictenotomidae	17	0	0	Prostomidae	41	0	0
Scraptiidae	500	0	0	Ciidae	650	0	0

TABLE 2 (Continued)

	No. spp.	No. brach	% brach		No. spp.	No. brach	% brach
Mycteridae	183	2	1.09	Ulodidae	39	0	0
Oedemeridae	1500	10	0.67	Archeocrypticidae	53	0	0
Boridae	4	0	0	Pterogeniidae	26	0	0
Pythidae	24	0	0	Mycetophagidae	211	0	0
Salpingidae	300	110	36.67	Tenebrionidae	30,000	4	0.01
Pyrochroidae	170	0	0	Zopheridae	1700	0	0
Lagrioididae	6	0	0	Promecheilidae	26	2	7.69
Anthicidae	3000	15	0.5	Chalcodryidae	4	0	0
Meloidae	3000	300	10	Afreminae (*incertae sedis*)	3	1	33.33
Coccinelloidea							
Bothrideridae	270	0	0	Latridiidae	1050	0	0
Cerylonidae	380	0	0	Anamorphidae	170	0	0
Murmidiidae	34	0	0	Corylophidae	285	20	7.02
Discolomatidae	400	0	0	Endomychidae	1600	0	0
Euxestidae	62	0	0	Mycetaeidae	6	0	0
Teredidae	120	0	0	Eupsilobiidae	12	0	0
Alexiidae	50	0	0	Cerasommatidiidae	9	0	0
Akalyptoischiidae	24	0	0	Coccinellidae	6000	20	0.33
Erotyloidea							
Boganiidae	16	0	0	Erotylidae	3500	0	0
Nitiduloidea							
Helotidae	83	0	0	Kateretidae	101	101	100
Sphindidae	66	0	0	Nitidulidae	4500	1100	24.44
Protocucujidae	7	0	0	Smicripidae	6	6	100
Monotomidae	248	190	76.61				
Cucujoidea							
Hobartiidae	6	0	0	Lamingtoniidae	3	0	0
Cryptophagidae	728	0	0	Tasmosalpingidae	2	0	0
Silvanidae	523	0	0	Cyclaxyridae	2	0	0
Cucujidae	70	0	0	Passandridae	112	0	0
Phloeostichidae	8	0	0	Myraboliidae	16	0	0
Agapythidae	1	0	0	Phalacridae	646	0	0
Priasilphidae	11	0	0	Laemophloeidae	532	5	0.94
Cavognathidae	9	0	0				
Curculionoidea							
Cimberididae	17	0	0	Attelabidae	2500	20	0.8
Nemonychidae	61	0	0	Caridae	6	0	0
Anthribidae	3861	70	1.81	Brentidae	4400	0	0
Belidae	372	0	0	Curculionidae	51,000	1	0
Chrysomeloidea							
Oxypeltidae	3	0	0	Megalopodidae	582	0	0
Vesperidae	71	25	35.21	Orsodacnidae	33	0	0
Disteniidae	424	0	0	Chrysomelidae	40,000	1250	3.13
Cerambycidae	38,300	1160	3.03				
Total	442,275	87,945	19.88				

Note: Family classification according to Cai et al. (2022), plus more recently published works. Total counts were obtained using sources indicated, but numbers of subspecies and fossil species were deducted where appropriate; some numbers are approximate. Numbers of an/brachelytrous species are minimum estimates in most cases; a species was included even if only one sex is an/brachelytrous. Sources cited in Supplementary File S1.

truncated elytra, which leave the last abdominal tergites uncovered (Beutel et al., 2019), have a similar evolutionary background. Gyrinidae are specialised in gliding rapidly in circles on the water surface (Larsén, 1966; Liu et al., 2018). The elytral shortening increases the flexibility of the distal abdominal region, which is used as a steering organ as in Hydroscaphidae. This is optimised by a longitudinal row of setae on the last exposed abdominal ventrite of Orectochilini (Larsén, 1966).

Apically truncated elytra also occur in some 'advanced' lineages of Carabidae, such as the Lebiini, Pseudomorphinae, Brachininae and Paussini (e.g., Jeannel, 1942; Lindroth, 1961–1969; Figure 2b). In the case of Brachininae, or bombardier beetles, the shortening of the elytra likely facilitates the release of an explosive mixture of secretions (e.g., Arndt et al., 2016). Moreover, aiming is likely improved by the increased flexibility of the posterior abdominal segments. Whether elytral shortening in the other carabid groups is linked with the release of substances produced in the pygidial defensive glands is unclear. Abdominal defensive substances are produced and released by all ground beetles, including the groups with fully developed elytra. Paussinae are mostly obligate or facultative myrmecophiles, living within the ant nests and feeding on ant larvae and workers. Within the subfamily, only members of the largest tribe, Paussini, display elytral truncation and apical abdominal exposure (Figure 2b). In some species, the elytra and/or pygidium can be filled with secretory glands and covered in trichomes, which are specialised for producing and releasing appeasement chemicals for life among ant colonies (Robertson & Moore, 2017).

Suborder Polyphaga

Superfamily Dascilloidea

Within Dascilloidea, elytral reduction is found only in the family Dascillidae, composed of two subfamilies that are probably not monophyletic as currently defined (Kundrata et al., 2021). Representatives of this family display a graded series of morphological modifications due to possible heterochronic changes resulting in paedomorphosis (occurrence of larval characters in the adult stage; Gould, 1977). While Dascillinae contain well-sclerotized forms with adults of both sexes having fully developed elytra and hind wings (although at least some females might have slightly reduced hind wings; Jin et al., 2013; Johnston & Gimmel, 2020), elytral and hind wing reductions are relatively common in the subfamily Karumiinae. Both sexes of *Genecerus* Walker are quite well sclerotized, with fully developed elytra and hind wings. In contrast, other genera in this subfamily are more-or-less soft-bodied with males having complete elytra and females having variously shortened elytra and reduced hind wings (e.g., *Anorus* LeConte, *Pleolobus* Philippi & Philippi), or soft-bodied with males usually having greatly shortened elytra and females unknown but hypothesized to be even more dramatically modified (*Karumia* Escalera) (e.g., Johnston & Gimmel, 2020; Lawrence, 2016; Paulus, 1972). Interestingly, there is great variation in elytral and hind wing reduction among species within the same genus. For example, males of *Karumia* have variously abbreviated elytra (Paulus, 1972) and females of *Anorus* display different degrees of elytral shortening and reduction of hind wings (females of *A. piceus* LeConte are brachelytrous with hind wings less than half as long as the abdomen, whereas females of *A. parvicollis* Horn have scale-like elytra hardly extending beyond the scutellar shield and no hind wings; Johnston & Gimmel, 2020). It should be noted that while Dascillinae do not occur in arid areas, Karumiinae are mostly distributed in arid and semi-arid regions and at least some are associated with subterranean termites, with females having only short periods of above-ground activity (Johnston & Gimmel, 2020; Lawrence, 2016).

Superfamily Buprestoidea

Elytral reduction in Buprestoidea is probably limited to a few tribes within Buprestidae, including Xenorhipidini (e.g., *Hesperorhipis* Fall and *Xenorhipis* LeConte) and Curidini (Buprestinae). In both males and females of *Hesperorhipis* and *Xenorhipis*, the elytra are truncated, and their apices are rounded and separated by a gap, exposing functional hind wings. A similar reduction pattern also occurs in some Curidini, for instance, in *Selagis splendens* (Macleay). However, this tribe also contains species with complete or nearly complete elytra. The drivers of the elytral shortening are unclear in this group. However, the occurrence of yellow, contrasting bands on the elytra of the diurnal, floricolous Xenorhipidini suggests that the elytral shortening may be part of a mimicry strategy.

Superfamily Dryopoidea

Elytral reduction within Dryopoidea is limited to the family Psephenidae. Representatives of the subfamily Psephenoidinae are characterised by a soft body, and at least a few species in the genera *Rhipidiomorphus* Pic and *Sinopsephenoides* Yang have more-or-less dehiscent elytra (Jeng, 2012). In *Sinopsephenoides malickyi* (Jäch & Jeng), elytra are strongly shortened and not in contact with each other, exposing the metanotum and abdomen, whereas the hind wings are functional (Jäch & Jeng, 1995). The reason for this modification is unclear, but adults do not feed and live only briefly, and some species are known to have their mating flight synchronised. This might result in limited pressure on investing in developmentally costly, strongly sclerotized elytra.

Superfamily Elateroidea

Elateroidea contain more than 25,000 described species classified in 15 extant and three extinct families. This superfamily includes lineages with a wide spectrum of morphological diversity. This includes a continuum from well-sclerotized forms with normally developed elytra and hind wings (usually groups with a clicking mechanism) to various lineages with soft-bodied species with heterochronic changes in morphology leading to a more-or-less paedomorphic appearance. The transitions from a completely sclerotized body to a more-or-less soft-

FIGURE 2 Examples of an/brachelytrous beetles. Adephaga: (a) *Gyrinus substriatus* Stephens (Gyrinidae); (b) *Paussus turcicus* Frivaldzky (Carabidae); Polyphaga: (c) *Malthodes minimus* (Linnaeus) (Elateroidea: Cantharidae); (d) *Phosphaenus hemipterus* (Geoffroy), male (Elateroidea: Lampyridae); (e) *Malacogaster* sp., female (Elateroidea: Elateridae); (f) *Margarinotus merdarius* (Hoffmann) (Histeroidea: Histeridae); (g) *Valgus hemipterus* (Linnaeus) (Scarabaeoidea: Scarabaeidae); (h) *Pachypus caesus* Erichson (Scarabaeoidea: Scarabaeidae), female; (i) *Lomechusa emarginata* (Paykull) (Staphylinoidea: Staphylinidae); (j) *Claviger testaceus* Preyssler (Staphylinoidea: Staphylinidae); (k) *Malachius bipustulatus* (Linnaeus) (Cleroidea: Melyridae); (l) *Atractocerus* sp. (Lymexyloidea: Lymexylidae); (m) *Meloe variegatus* Donovan (Tenebrionoidea: Meloidae); (n) *Arima marginata* (Fabricius) (Chrysomeloidea: Chrysomelidae); (o) *Necydalis ulmi* Chevrolat (Chrysomeloidea: Cerambycidae); (p) *Molorchus minor* (Linnaeus) (Chrysomeloidea: Cerambycidae). Photo credits: a,b,f,g,m,o by Tamás Németh; d,i,j,p by Radim Gabriš; c by Miroslav Fiala; e by Mirella Zeeders; h by Pavel & Kristián Kučera; k by Miroslav Deml, l by Arthur Anker, n by Hervé Bouyon.

bodied condition include various changes in external morphology, including the loss of mechanical coadaptation of the elytra with each other and with the pterothorax and abdomen, often leading to brachelytry and exposure of hind wings and abdominal tergites, or, more rarely, to complete reduction of elytra and hind wings (Bocak et al., 2008; Cicero, 1988; Crowson, 1972; Ferreira & Ivie, 2022; Kundrata & Bocak, 2019; Rosa et al., 2020). The soft-bodied condition is interpreted as the first step of paedomorphic transformations (Bocak et al., 2008). Females are regularly more affected than males, and their morphology spans forms with only a larviform abdomen through forms with a variously modified pterothorax, including brachelytry, brachyptery, anelytry and aptery, to completely larviform females (e.g., Bocak et al., 2008; Cicero, 1988; Crowson, 1972). Interestingly, distantly related groups within Elateroidea contain representatives with similarly modified morphologies, while, at the same time, representatives of a single clade often show various degrees of body sclerotization and morphological changes (e.g., Kundrata & Bocak, 2019; Kusy et al., 2018; Li, Kundrata, Packova, et al., 2021). It should be noted that since the abdomen in soft-bodied groups is highly flexible, capable of stretching and lengthening and again shrinking due to extensive membranes between individual segments, it exhibits great variation in length relative to the elytra among both living and variously preserved dead specimens even within a single species.

Most if not all elytral reductions in Elateroidea can be attributed to heterochronic changes. However, at least some forms may have abbreviated elytra due to their ecology, for example, termitophily. In lineages with flightless females and alate males, there is likely selective pressure, favouring reproduction against flight.

Most basal families of Elateroidea (sensu Kundrata et al., 2014), including Artematopodidae, Eucnemidae, Throscidae, Cerophytidae and Brachypsectridae, contain only members with fully developed elytra. Because Brachypsectridae have flexibly connected abdominal ventrites, sometimes the abdomen can slightly surpass the elytral apices.

Neocrowsonia Kistner & Abdel-Galil, an enigmatic, monotypic genus known from South African termite nests, was originally classified in Throscidae and is currently treated as Elateriformia *incertae sedis*. It has the elytra distinctly shortened, with apices independently rounded and separated by a broad gap, exposing much of the dorsal abdomen (Kistner & Abdel-Galil, 1986; Lawrence, Kawashima, & Branham, 2010).

In Omethidae, representatives of three traditional subfamilies (Omethinae, Matheteinae and Driloniinae) always have complete elytra, fully covering the entire dorsal abdomen, being either as long as the abdomen or even longer (Ramsdale, 2010). Five genera of the fourth subfamily, Telegeusinae (previously a separate family), are known only from males. The species are very small, highly soft-bodied, and display variously reduced mouthparts. All known males in this group have distinctly shortened elytra that expose a large portion of the abdomen (López-Pérez & Zaragoza-Caballero, 2021). There are differences in the relative length of elytra among species within a single genus (Zaragoza-Caballero & Rodríguez-Velez, 2011). The unknown females are hypothesized to be flightless and highly paedomorphic.

The recently discovered Jurasaidae contain two genera (Rosa et al., 2020). Adult males of *Tujamita* Rosa et al. have the elytra slightly shorter or as long as the abdomen, while those of *Jurasai* Rosa et al. have the elytra shorter than the abdomen, with median edges separated and apically diverging. In both genera, adult males have well-developed hind wings which are longer than the elytra (Biffi et al., 2021; Rosa et al., 2020). Females are almost completely larviform and lack both elytra and hind wings. Jurasaids live in soil for most of their lives and most probably have only short periods of above-ground activity.

'Higher' elateroids sensu Kundrata et al. (2014) comprise Iberobaeniidae, Lycidae, Cantharidae, Elateridae, and the so-called 'lampyroid clade' sensu Kusy et al. (2021), i.e., Sinopyrophoridae, Phengodidae, Rhagophthalmidae, and Lampyridae. Heterochronic changes in this group are very often pronounced, with strong morphological modifications, including dramatic reduction or even loss of elytra in various lineages.

The monogeneric Iberobaeniidae, with only three tiny species known from the Iberian Peninsula, have adult males with the elytra only weakly sclerotized and very slender, apparently not shortened but not reaching the abdominal apex, tapering towards the separately rounded apices. Females are unknown. They probably live in soil and are likely highly paedomorphic and wingless (Bocak et al., 2016; Kundrata et al., 2017).

Lycidae contain more than 4300 species classified in seven subfamilies (Kusy et al., 2019). They contain several paedomorphic lineages in which females are usually greatly modified morphologically. In cases where the paedomorphic females are known, they are larviform and completely lacking elytra and wings. In many cases, however, females are unknown and we can only hypothesise that they are also highly paedomorphic (for more information, see Kusy et al., 2019). Although females are more affected than males in the paedomorphic lineages, even the latter sometimes show more-or-less similar morphological modifications, including shortening or even loss of the elytra (Ferreira et al., 2023; Kusy et al., 2019). In Dexorinae, females are unknown but hypothesized to be paedomorphic. Bocak et al. (2013) described the brachelytrous male of *Dexoris* Waterhouse (Dexorini) with highly reduced elytra, dehiscent from the scutellar shield and exposing most abdominal tergites. Its hind wings are vestigial and nonfunctional. Some males of Mimolibnetini, for example, *Mimolibnetis ruwenzoriensis* Kazantsev, also have shortened elytra which are separated by a narrow gap and expose about half of the abdomen (Kazantsev, 2018). In Ateliinae, the females of Ateliini are also unknown but supposedly larviform. In Lycinae, paedomorphic females are reported in Leptolycini and likely also occur in some Calopterini (Ferreira, 2020; Ferreira & Ivie, 2022; Miller, 1991). Ferreira et al. (2023) recently described *Xenomorphon baranowskii* Ferreira et al. from a high-altitude region in Mexico, which represents a very rare case of anelytrous adult male in Coleoptera; the authors tentatively placed it in Calopterini. Lyropaeinae are the largest lycid group containing larviform females. Even though these are only definitively known in representatives of Platerodrilini, it appears likely that females in all other tribes are also dramatically modified. Lyropaeinae are well-known for their very large and enigmatic so-called 'trilobite larvae', which produce extremely paedomorphic females not much different from a larva and much larger than their small-bodied male counterparts (Makarov & Kazantsev, 2022; Wong, 1996). Such females were reported for *Platerodrilus* Pic (Platerodrilini), but other unusually large larvae are known in *Macrolibnetis* Pic (Platerodrilini), which supposedly turn into females of similar body mass, and also in *Lyropaeus* Waterhouse (Lyropaeini) (Masek & Bocak, 2014). In Alyculini, males have highly reduced and divergent elytra, exposing most abdominal tergites, while hind wings are fully developed (Takahashi et al., 2016). In Antennolycini, some males have somewhat shortened elytra (Kusy et al., 2019). In Metriorrhynchinae, there is only a single case of brachelytry in males. *Cautires apterus* Bocak et al. (2014) lacks hind wings and has narrow elytra, separated by a gap, which is also shortened, exposing about half of the abdomen. Its female is unknown but presumably highly paedomorphic (Bocak et al., 2014).

Cantharidae, another group with soft-bodied forms (in German 'Weichkäfer'), include approximately 5600 species in five traditionally accepted subfamilies. Most representatives have long elytra, under natural conditions usually fully covering the abdomen or exposing only one or few abdominal segments. In contrast to this ground plan condition, several groups display strongly shortened elytra, exposing a considerable portion of the abdominal tergites and/or the hind wings. Dysmorphocerinae and most Cantharinae have fully developed elytra, even though they are more-or-less shortened in some cases, often combined with reduced hind wings, as in some representatives of *Cantharis* Linnaeus, *Lycocerus* Gorham, *Pakabsidia* Wittmer, *Rhagonycha* Eschscholtz and *Themus* Motschulsky. Some species of *Podistra* Motschulsky are brachelytrous either in both sexes (e.g., the type species *Podistra alpina* Motschulsky) or only in females (originally defined subgenus *Hemipodistra* Ganglbauer) (Kazantsev, 2023). In Silinae, members of Silini usually display elytra covering the entire abdomen, but at least species of *Polemius* LeConte (subgenus *Brachypolemius* Wittmer), *Brachysilidius* Pic and *Silis* Charpentier (Constantin, 2009) have moderately to strongly shortened elytra. Tytthonyxini, which are tentatively placed in Silinae but probably represent a separate lineage sister to Malthininae (Hsiao et al., 2021), are characterised by shortened elytra (Ivie et al., 2022). Different degrees of elytral shortening also occur in most genera of Malthininae (Figure 2c), and all Ichthyurini (e.g., *Ichthyurus* Westwood; Chauliognathinae) have considerably shortened elytra. In Chauliognathini, some genera originally included in Ichthyurini are characterised by their short elytra (e.g., *Maronius* Gorham, *Belotus* Gorham, *Lobetus* Kiesenwetter and *Macromalthinus* Pic), whereas some others, like *Chauliognathus* Hentz and *Malthesis* Motschulsky, contain mostly species with long elytra although some of them are brachelytrous (Biffi, 2020; Zubair et al., 2021). We can possibly attribute morphological modifications connected with the evolution of a soft body to paedomorphic developmental patterns in Cantharidae. However, at least some taxa may have evolved shortened elytra and reduced hind wings as an adaptation to windy high-altitude habitats (e.g., Finston et al., 1997). Discoveries of different Cretaceous fossil cantharids, tentatively placed in Cantharinae and Malthininae but probably representing extinct lineages, confirmed that members of this family had already evolved variously shortened elytra during their early diversification (Hsiao et al., 2021; Li et al., 2022).

Another family with soft-bodied species, Lampyridae, or fireflies, includes about 2500 described species classified in 12 subfamilies (Ferreira et al., 2020). They represent a group with numerous morphological modifications related to paedomorphosis, including elytral and hind wing reductions. Species of various lampyrid taxa have fully developed elytra, which cover the entire dorsal abdomen or leave only the abdominal apex exposed or narrowed, and slightly dehiscent elytra separated by a narrow gap. However, in many lampyrid lineages, the elytral reductions are much stronger, especially in females.

Representatives of Cyphonocerinae, Photurinae and Psilocladinae do not show strong sexual dimorphism, with both sexes able to fly and equipped with fully developed elytra (e.g., Jeng et al., 2006). In Pterotinae, Cladodinae and Lamprohizinae, males are capable of flight and usually have complete elytra (in some cases, especially in cladodines, the elytra are narrowed and apically separated by a narrow gap), while females are larviform, for instance, in *Lamprohiza splendidula* (Linnaeus), a species with strongly reduced elytra (e.g., Bocak & Bocakova, 2006; Bocakova et al., 2022). Luciolinae usually have fully developed elytra, with only some females being brachelytrous with reduced hind wings, like some species of *Atyphella* Olliff and *Luciola* Laporte (Ballantyne & Lambkin, 2013). In Amydetinae, Cheguevariinae and Chespiritoinae, males are capable of flight and usually have complete elytra. However, species of the latter subfamily have more-or-less narrowed and dehiscent elytra, which expose a part of the dorsal abdomen and the hind wings. Females of all three groups are unknown but presumably highly paedomorphic (Campello et al., 2022; Ferreira et al., 2019, 2020). In the morphologically diverse Ototretinae, males usually do not have distinctly shortened elytra, although one or two abdominal tergites are exposed in some cases. Some females are similar to males and able to fly, whereas some others are almost completely larviform, without elytra or hind wings (e.g., *Stenocladius* Fairmaire; Ohba et al., 1997). In Lampyrinae, males usually have fully developed elytra and are able to fly. However, males of *Phosphaenus hemipterus* (Geoffroy) (Figure 2d), for instance, are brachelytrous and lack hind wings, somewhat resembling a female of the distantly related *Lamprohiza splendidula*. Females may be strongly larviform, with vestigial or completely reduced elytra and lacking hind wings, as in *Pyrocoelia pectoralis* Olivier, *Lampyris noctiluca* Linnaeus and *Phosphaenus hemipterus* (Geoffroy). Females of some species of *Pleotomodes* Green, which live in ant nests, also have reduced elytra and lack hind wings (Sivinski et al., 1998).

Phengodidae include about 300 species in 40 genera, which are placed in four subfamilies (Roza, 2022; Zaragoza-Caballero & Pérez-Hernández, 2014). All known males are winged, but with the elytra leathery rather than sclerotized, often narrowed, and slightly to extremely shortened, exposing the abdominal apex or even most tergites, with hind wings not folded beneath the elytra. For example, males of *Zarhipis* LeConte have relatively long elytra, whereas they are rather short in *Cydistus* Bourgeois. The elytra of males of *Phengodes* Illiger are not only very short but also strongly dehiscent, and in contact with each other only immediately posterior to the scutellar shield (Kundrata et al., 2019; Zaragoza-Caballero & Pérez-Hernández, 2014). The degree of elytral reduction can vary even within a single genus in this group, as in *Cydistus* (Kundrata et al., 2019) or *Cenophengus* LeConte (Vega-Badillo et al., 2021). All known females of Phengodinae and Mastinocerinae are larviform and completely lack elytra and hind wings (*Phengodes*, *Phrixothrix* Olivier and *Zarhipis*), and females of Penicillophorinae and Cydistinae are unknown but are also hypothesized to be highly paedomorphic (e.g., Kundrata et al., 2019). While the short-lived adult males probably do not feed, adult females (as well as larvae) live in soil and leaf litter and are predators, especially of millipedes (Diplopoda). Similar to the larvae and males of numerous species, females are bioluminescent (Costa & Zaragoza-Caballero, 2010).

Rhagophthalmidae, comprising about 70 species in 12 genera, are the sister group of Phengodidae (Kundrata et al., 2022). Most genera contain species with the male elytra almost covering the entire abdomen or exposing only the apex or few tergites, with the elytral apices independently rounded and separated by more-or-less broad gap, as in *Bicladodrilus* Pic, *Diplocladon* Gorham, *Dodecatoma* Westwood and *Rhagophthalmus* Motschulsky (Kazantsev, 2012; Kundrata et al., 2022; Li et al., 2008; Yiu, 2017). In some genera, such as *Rhagophthalmus*, the congeners differ in the relative length of the elytra.

Representatives of the genus *Falsophrixothrix* Pic have distinctly abbreviated elytra, exposing most of the abdomen (Kundrata et al., 2022). All known females are larviform and although they differ in the degree of paedomorphosis, they completely lack elytra and wings. They are bioluminescent like the larvae and some adult males. Similar to the larvae, adult females with known biology live in soil and leaf litter and feed on millipedes (Kawashima et al., 2010).

Elateridae, or click-beetles, are the largest family of Elateroidea with approximately 11,000 described species. Although they had been long considered a relatively uniform group with well-sclerotized bodies and the presence of a clicking mechanism, molecular phylogenetic and phylogenomic analyses have repeatedly confirmed that several more-or-less soft-bodied lineages also belong to this family (e.g., Kundrata & Bocak, 2011; Kusy et al., 2018). The 'traditional' Elateridae have well-developed elytra, although variously reduced hind wings occur in the group, as in many Dendrometrinae (Selatosomini, Dimini). The elytra of females of several subgroups are usually strongly shortened or vestigial and the hind wings highly reduced or absent. This includes Omalisinae (e.g., *Omalisus* and *Thilmanus* Gemminger), Elaterinae: Cebrionini (e.g., *Cebrio* Olivier) and Elaterinae: Aplastini (e.g., *Euthysanius* LeConte). Elytra are completely missing in females of Agrypninae: Drilini (e.g., *Malacogaster* Bassi; Figure 2e). Males of these groups may have more-or-less shortened elytra, which are in some cases dehiscent and separated by a narrow gap (Hoffmannova & Kundrata, 2022; Martínez-Luque et al., 2022; Rattu, 2020). There can be variations in elytral abbreviations within a single lineage. In Drilini, for instance, *Austroselasia* Kundrata & Bocak has the elytra usually covering the entire abdomen (or leaving only narrowed posterior tergites exposed), whereas *Malacogaster* has apparently shortened and at least apically dehiscent elytra (Kundrata & Bocak, 2019). Some elaterid groups in which both sexes share well-developed elytra and hind wings have slightly softer bodies than typical click-beetles and may also have exposed abdominal apices or slightly dehiscent apices of the elytra. This condition occurs, for example, in some Dendrometrinae and in *Paulusiella* Löbl.

The Mesozoic Cretophengodidae, known exclusively from mid-Cretaceous Burmese amber, are probably a transitional lineage between fully sclerotized groups and the phengodid clade containing soft-bodied and highly modified forms. The elytra of cretophengodids were complete and covered the entire dorsal abdomen, at least in males. However, females are unknown and hypothesized to be highly paedomorphic, as in Phengodidae (Li, Kundrata, Tihelka, et al., 2021).

The enigmatic genus *Anoeuma* Li et al., also described from Burmese amber, has been classified as Elateroidea *incertae sedis* (Li, Kundrata, Packova, et al., 2021). Males have shortened elytra, which expose about half of the abdomen and well-developed hind wings. Females are unknown but possibly also paedomorphic.

Superfamily Histeroidea

This medium-sized and clearly monophyletic superfamily (slightly less than 5000 described spp.) is the sister group of Hydrophiloidea (e.g., McKenna et al., 2019). The species of all three families, Syntelidae, Sphaeritidae and Histeridae (Figure 2f), are consistently characterised by truncated elytra, a condition reflected by the German common name 'Stutzkäfer'. The shortened elytra leave abdominal tergites VI and VII (sometimes only VII) exposed. A synapomorphy of the entire clade is that abdominal segment VIII is completely invaginated within segment VII.

The functional background of the truncated elytra is rather unclear in the case of Histeroidea. It was disputed whether a ground-living lifestyle or association with wood is ancestral for the superfamily (Hansen, 1997a). It is noteworthy that myrmecophily was already well established in Histeridae in the Cretaceous (Caterino & Maddison, 2018; Yamamoto & Caterino, 2022) and is possibly even part of the ground plan of the family, with cases of reversal. In contrast to the megadiverse Staphylinidae, the movability of the abdomen is apparently not increased, with the elytra only slightly shortened and both tagmata very broadly connected. The abdominal tergo-sternal membranes are usually wide on segments I–VI in staphyliniform groups with complete or relatively long elytra, whereas they are very short in typical brachelytrous forms, especially in Staphylinidae (Hansen, 1997b). An intermediate condition occurs in the family Histeridae, where long membranes are restricted to the proximal 3–4 segments (Hansen, 1997b). Wing-folding patches are present on tergum VI and preceding segments in the two smaller families, whereas they only occur on the permanently concealed anterior 3–4 tergites in Histeridae (Hansen, 1997b). The vestigial spines of the abdominal laterotergites of Histeridae are correlated with the presence of a ventral, sublateral, laminar locking device on the elytra, according to Hansen (1997b).

Superfamily Scarabaeoidea

Elytral reduction is rare within Scarabaeoidea and apparently restricted to only two families: the Glaphyridae and the Scarabaeidae. Elytra of several genera of Glaphyridae (e.g., *Pygopleurus* Motschulsky and *Eulasia* Truqui) are truncated and dehiscent, exposing the last 2–3 abdominal tergites and sometimes also a portion of the hind wings. Exposition of the abdomen, which is covered with coloured bands of setae, makes these anthophilous species resemble bumble bees (Sabatinelli et al., 2020), suggesting that elytral shortening might be part of a mimicry strategy. Within the very diverse family Scarabaeidae, the exposition of the last (rarely last two) abdominal tergite is relatively frequent among the Melolonthinae, Rutelinae and Cetoniinae (Figure 2g,h). In some cases, this seems to be attributed to female physogastry, but elytral shortening might also facilitate calling behaviour, copulation or oviposition. In some species of Scarabaeoidea, females adopt a specific calling position with the head and most of the body buried in soil and only the apical segments of the abdomen (equipped with pheromone-producing glands) remaining exposed (Facundo et al., 1999). In nectivorous, brightly coloured Valgini and Trichiini (Cetoniinae), elytral shortening might be part of a mimicry strategy. Bizarre examples of complete wing and elytral reduction (along with the loss of the mesoscutellar shield) in Scarabaeoidea are the females of the genus *Pachypus* Dejean (Figure 2h). These melolonthine scarabs do not feed as adults, and females spend most of their lives inside burrows. They only occasionally expose their abdomens to emit pheromones to attract males (Le Tirant & Limoges, 2017; Pacheco et al., 2022). Males have much less reduced elytra. Species of the genus *Thinorycter* Semenov & Reichardt (Dynamopodinae) are apterobrachelytrous, with truncate elytra exposing one or two abdominal tergites (Semenov-Tian-Shanskij & Reichardt, 1925). Some termitophilous species of the family Hybosoridae (*Scarabatermes amazonensis* Howden and *Scarabaeinus termitophilus* Silvestri; subfamily Ceratocanthinae) have a large, artificially swollen abdomen (pseudophysogastry) only partially covered by non-truncate elytra, but have developed hind wings (Ballerio & Grebennikov, 2016).

Superfamily Staphylinoidea

Most of the very small-to-minute Ptiliidae (minimum size ca. 0.4 mm) possess apically truncated elytra, with the exception of most members of the subfamily Nossidiinae and tribes Nanosellini and Ptiliini (Ptiliinae), whose elytra completely or nearly completely cover the abdomen. This brachelytry is likely related to the highly modified feather-like hind wings and their folding and unfolding mechanisms. The increased mobility of the exposed terminal abdominal tergites facilitates the unfolding and storage of the feather-like wings.

Complete elytra certainly belong to the ground plan of the medium-sized aquatic family Hydraenidae or minute moss beetles (ca. 2100 described spp.), which are characterised by an increased number of exposed abdominal sternites, among other features. Long elytra entirely covering the abdominal dorsum are, for instance, present in the well-known and species-rich genera *Hydraena* Kugelann and *Ochthebius* Leach (Jäch et al., 2016). Truncated elytra are an apomorphy of the genus *Limnebius* Leach, the species of which are streamlined in their body shape, in contrast to other groups of Hydraenidae (e.g., Jäch et al., 2016). The habitus of *Limnebius* strongly resembles that of the myxophagan Hydroscaphidae, with its shortened and anteriorly rounded head, the teardrop-shaped body contour and the posteriorly gradually narrowing and exposed postabdomen. The posterior abdominal segments are used as a steering organ in aquatic habitats as in *Hydroscapha* and its relatives as well as in Gyrinidae.

A remarkable case of apterobrachelytry among Leiodidae is that of the commensal *Platypsyllus castoris* Ritsema associated with beavers (Rodentia: *Castor* Linnaeus). These beetles are highly modified for life among the fur of their hosts, including having a reinforced forebody and flexible hindbody, consisting of a flattened and flexible abdomen largely exposed by the scale-like elytra (see Yavorskaya et al., 2023 for details). Other members of Platypsyllinae (e.g., *Leptinillus* Horn) may have portions of the last two abdominal tergites variably exposed.

The distinctly shortened elytra occurring in most subgroups of Staphylinidae (e.g., Kim et al., 2020; Thayer, 2016; Figure 2i,j) are of the truncated type, leaving a variable number of abdominal tergites exposed. Increased tergal sclerotization is one morphological transformation apparently correlated with the brachelytrous condition occurring in most subgroups of the family (e.g., Blum, 1979; Kim et al., 2020). Another correlated transformation is a modified pattern of hind wing folding, referred to as a ‘high grade’ folding-mechanism by Hammond (1979). This was described in detail by Blum (1979) and Haas (1998), and also discussed in Haas et al. (2000). Staphylinidae use anteriorly directed, pendulum-like movements of the abdominal apex to fold the wings into small packages and to push them under the elytra (Blum, 1979; Haas, 1998, 1999).

The shortening of the elytra in Staphylinidae results in an increased exposure of the abdominal segments including membranous areas. A character complex correlated with this is the formation of a brick-wall pattern in the abdominal intersegmental membranes. This condition has been interpreted as an apomorphic ground plan feature of Staphylinidae (Newton & Thayer, 1995). The presence of this pattern of minute sclerites increases the mechanical protection without negatively affecting intersegmental flexibility (Hammond, 1979).

Elytral shortening in rove beetles greatly increases the mobility of the abdomen, as pointed out by Blum (1979), especially in the dorsoventral and lateral directions. The flexible abdomen is used for storing but not for unfolding the membranous hind wings (see also Haas, 1998, 1999; Haas et al., 2000), for intra- and interspecific aggressions, and for specific copulatory positions in Aleocharinae (Blum, 1979). Interestingly, some staphylinids, especially in Xantholininae and Staphylininae, possess unusual diagonally intercrossing muscles in the pregenital abdomen, supposedly serially homologous with diagonal muscles in the genital segments (Blum, 1979: figs. 22–28). Similar muscular arrangements also occur in Dermaptera and some other groups with an unusually flexible abdomen; however, only the typical longitudinal and dorsoventral bundles are present in the pregenital abdomen of representatives of Omaliinae and other groups, such as for instance Aleocharinae (Blum, 1979). The evaluation of Blum (1979) suggests various degrees of specialisation within the family, with a possibly ancestral longitudinal arrangement in some groups (e.g., Omaliinae), intermediate conditions with oblique arrangements in others (e.g., Steninae, Oxyporinae) and an advanced intercrossing pattern in Xantholininae and Staphylininae (Blum, 1979).

A flexible abdomen has been suggested to increase manoeuvrability in narrow spaces (e.g., Blum, 1979; Hansen, 1997b), facilitating the invasion of leaf litter and interstitially within upper soil layers. According to Blum (1979), increased abdominal flexibility allows for wriggling–slipping movements in the substrate (‘schlängelnd-schlüpfend’). Even though this interpretation appears plausible in principle, it should be noted that numerous species of Staphylinidae and Carabidae live in very similar microhabitats, that is, forest leaf litter and the uppermost layers of the soil substrate. However, whereas strongly shortened elytra are common in rove beetles, this is only a marginal phenomenon in the similarly species-rich adephagan ground beetles, and even this modest level of shortening is rare among those inhabiting soil and leaf litter (see Adephaga). The proposed evolutionary benefits of shortened elytra, including increased flexibility of the posterior body and reduced developmental investment in sclerotized material, are arguably counterbalanced by the complicated folding of the membranous hind wings (Blum, 1979; Haas, 1999; Haas et al., 2000; Hammond, 1979).

Increased abdominal flexibility is arguably a key feature linked with elytral shortening in this family. Interestingly, however, this is secondarily abandoned by Pselaphinae (e.g., Luo et al., 2021), a highly species-rich subgroup (ca. 10,500 described spp.) formerly treated as a separate family (Figure 2j). The metathorax and abdominal base of pselaphines are broadly connected in this group (Luo et al., 2021), which includes numerous morphologically bizarre species (e.g., Chandler, 2010). Moreover, various specialised life styles have evolved in this lineage—for instance, living in deep soil or caves, or having close associations with social insects (e.g., Jałoszyński et al., 2020). The shortened elytra show a plethora of specialisation in this group (e.g., Chandler, 2010). Highly specialised forms, especially in close association with ants, also occur in the species-rich rove beetle subfamily Aleocharinae. Some extremely specialised species of Dorylomimini, Corotocini and Termitopaediini are associated with ants and termites and have reduced and/or fused elytra (Hansen, 1997b; Kistner, 1966). This includes for instance species of the genera *Mimeciton* Wasmann, *Mimanomma* Wasmann, *Corotoca* Schiødte or *Neodioxeuta* Seevers, where the elytra are missing or only present as small vestiges. It is very likely that elytral shortening, resulting in the exposition of the abdomen equipped with abdominal glands, was a crucial predisposing factor towards the establishment of a unique association with ants, which is particularly notable within the Aleocharinae (Parker et al., 2018) but also in Pselaphinae, especially but not only in Clavigeritae (e.g., Luo et al., 2021) (Figure 2j).

Superfamily Bostrichoidea

Significant elytral reduction is very rare within Bostrichoidea, being so far confirmed only in the paedomorphic, large and apteroanelytrous females of the genus *Thylodrias* Motschulsky (Trinodinae: Thylodriini) in Dermestidae (Lawrence & Ślipiński, 2010). Similar apteroanelytry might possibly occur in the closely related *Trichodryas* Lawrence & Ślipiński (Trinodinae: Trichelodini), but the females are unknown. Males of *Thylodrias* and *Egidyella* Reitter (Attageninae: Egidyellini) are macrelytrous, but the elytral apices are independently rounded and separated by a gap, exposing several abdominal tergites (Lawrence & Ślipiński, 2010). The cause of paedomorphosis and related apteroanelytry in female *Thylodrias* remains unclear. The genus belongs to a relictual lineage, Thylodriini, that originated in the Cretaceous. However, its general ecology is similar to that of other, macrelytrous Dermestidae developing in dead and dried animal matter (Motyka et al., 2022).

Superfamily Cleroidea

Examples of brachelytrous taxa can be found within several families of the Cleroidea, including Melyridae, Rhadalidae, Cleridae and Trogossitidae. Most members of the melyrid lineage (including Melyridae, Mauroniscidae and Prionoceridae) sensu Bocakova et al. (2012) are characterised by a weakly sclerotized cuticle and corresponding loss of mechanical co-adaptation of the elytra and abdomen (e.g., lack of elytral interlocking devices) (Bocakova et al., 2012, 2016; Gimmel et al., 2019). One of the two members of the subfamily Gietellinae (Rhadalidae), *Gietella fortunata* Constantin & Menier, is apterobrachelytrous, with the elytra truncate and exposing tergites VII and VIII; the other species, *Gietella faialensis* Menier & Constantin, is also apterous, but the elytra are domed and complete, though they often expose much of tergite VIII. Several soft-bodied groups within the largest group of Cleroidea, the Melyridae, contain brachelytrous species with varying degrees of elytral shortening. In the subfamily Malachiinae (Figure 2k), elytral reduction is a common phenomenon, resulting in the exposition of 1–6 posterior abdominal tergites (e.g., *Carphurus* Erichson [Carphurini] and many Lemphini), though the majority have complete elytra with 1–2 tergites variably exposed (e.g., *Anthocomus* Erichson and *Attalus* Erichson). Members of the often brightly coloured Malachiinae appear to be chemically defended, with their coloration presumably aposematic (Bocakova et al., 2016). Pairs of eversible vesicles are present in the pleural region of the pro- and metathoraxes (and on the abdomen in Carphurini); these may be involved in chemical defence among Malachiinae, which is reported to be quite powerful among some taxa (e.g., Carphurini: *Choresine* Pascoe; Dumbacher et al., 2004), perhaps removing selection pressure for elytral coadaptation and allowing much greater abdominal flexibility. Hind wings have remained functional in most of the brachelytrous taxa of Melyridae, but apterobrachelytry occurs in some genera (e.g., *Endeodes* LeConte of the Malachiinae; *Apterodasytes* Champion of the Dasytinae).

Within Cleridae, brachelytry is particularly frequent in the ant-mimicking species of the subfamily Clerinae (formerly Hydnocerinae). In many cases, for example, in the genus *Isohydnocera* Chapin, elytral truncation results in the exposition of hind wings, but some species (e.g., *Lemidia aptera* [Sharp]) are apterous. One genus of Tillinae, *Cylidrus* Latreille, contains species with the elytra apically slightly dehiscent and often fully exposing the last two abdominal tergites. Similar to the Malachiinae, diurnal Cleridae are often characterised by aposematic coloration, and some species are known to be toxic or distasteful (Bocakova et al., 2016).

Elytral reduction in Trogossitidae seems to be limited to a few species within predominantly macrelytrous genera. For instance, in *Nemozoma gymnosternalis* Kolibáč, only tergites I–III are covered by the distinctly truncated elytra, while in the majority of other species within the genus, the elytra cover the abdomen completely or almost completely (Kolibáč, 2014). Species of the genus *Nemozoma* Latreille are known to be predaceous and hunt inside the narrow and winding galleries of small wood borers (e.g., Hinson & Buss, 2016), where a flexible abdomen is likely an advantage. Evolutionary drivers of elytral reduction within Cleroidea are diverse.

Superfamily Lymexyloidea

The superfamily Lymexyloidea comprises only one small (ca. 70 extant species) monophyletic family, the Lymexylidae. In most members of the subfamily Melittommatinae, the elytral apices are rounded and separated by a gap, often exposing 1–2 abdominal tergites and part of the hind wings (Lawrence, 2010). In the Lymexylinae, represented only by *Lymexylon* Fabricius, the elytra expose 1–2 tergites and often part of a third (Wheeler, 1986). In the subfamily Atractocerinae, the elytra are extremely reduced, exposing the metatergum, abdomen and functional hind wings (Lawrence, 2010; Yamamoto, 2019; Figure 2l). Elytral reduction in Atractocerinae is a relatively old character transformation with a post-Cretaceous origin (Yamamoto, 2019). Potential benefits arising from elytral reduction in Lymexylidae are a matter of speculation. Some authors assumed that the bizarre appearance of some Atractocerinae is related to a mimicry strategy (Lawrence, 2010). Other research suggests that the minute elytra of Atractocerinae might play a similar role as dipteran halteres, resulting in the unique flight style of these beetles (Miller, 1971; Yamamoto, 2019).

Superfamily Tenebrionoidea

Within the highly diverse superfamily Tenebrionoidea, several groups have experienced different levels of elytral reduction. This process is notable in Ripiphoridae, Mordellidae, Oedemeridae, Meloidae, Tenebrionidae, Mycteridae, Promecheilidae, Salpingidae and Anthicidae; however, the exposition of the last abdominal tergite may also be observed in other families.

Elytral modification in Ripiphoridae often encompasses significant reduction in their length as well as their width, forming a wide longitudinal gap and exposing the abdomen, hind wings and often also the pterothorax (e.g., Pelecotominae [*Sharpides* Kirkaldy], Hemirhipidiinae, Ripidiinae, and Ripiphorinae [*Ripiphorus* Bosc]) (Lawrence, Falin, & Ślipiński, 2010). Slightly narrowed and dehiscent elytra can be found in several other groups, including, for instance, the tribe Macrosiagonini (Ripiphorinae). In some species characterised by brachelytrous males (e.g., *Ripidius* Thunberg), females lack elytra and hind wings and are larviform (Batelka et al., 2021). All species of Ripiphoridae studied to date are parasites of other insects during some portion of their development and use wood-boring beetles, cockroaches (Blattodea) or various hymenopterans as hosts (Lawrence, Falin & Ślipiński, 2010). The hymenopteran-like appearance of some brachelytrous Ripiphoridae, enhanced by the exposition of hind wings, might potentially deter predators relying on visual cues and evade social insect attack during oviposition near their nests.

In many groups of Mordellidae, the elytral apices are independently rounded and separated by a distinct gap, exposing 1–2 abdominal tergites, of which the last one is usually elongate and pointed (Lawrence & Ślipiński, 2010). The functional background of this modification is still unclear, though it may play a role in their 'tumbling' predator avoidance behaviour.

Members of Oedemeridae may have 1–3 or more abdominal tergites exposed by shortened or dehiscent elytra (Lawrence & Ślipiński, 2010). Brachelytrous species of *Thelyphassa* Pascoe, *Baculipalpus* Broun and *Apterosessinia* Blair (sensu stricto) are also brachypterous, whereas macrelytrous species in the same genera are macropterous (Hudson, 1975; Vázquez, 1996). Intriguingly, most brachelytrous species of Oedemeridae occur in coastal habitats (Hudson, 1975; Vázquez, 1996).

Significant elytral reduction in Meloidae, or blister beetles, can be found within Meloinae and Nemognathinae. Several genera of the first subfamily (e.g., *Meloe* Linnaeus, *Megetra* LeConte) are characterised by physogastry, shortened, dehiscent elytra with rounded apices, and a lack of metathoracic wings (i.e., apterobrachelytry; Figure 2m). Such body modification in Meloinae is attributed to both males and females, though it is often more notable in females. Within Nemognathinae, patterns of elytral reduction encompass species with dehiscent, strongly narrowed elytra separated by a longitudinal gap and exposed, functional hind wings (e.g., *Sitaris* Latreille), as well as wingless taxa characterised by minute elytra and almost the entire abdomen exposed (*Hornia* Riley, *Allendesalazaria* Martinez de la Escalera). There might be at least two different potential drivers of elytral loss in Meloidae. In the genus *Meloe*, characterised by the reduced elytra and also lacking metathoracic wings, elytral reduction might be part of a resource-saving strategy focused on maximising fecundity. Moreover, reduced mechanical protection related to elytral shortening might be compensated by chemical defence (cantharidin secretion). By contrast, in brachelytrous meloids with reduced elytra and largely exposed hind wings (e.g., *Sitaris*), elytral loss might be a part of a mimicry strategy. The characteristic coloration of *Sitaris* spp., often including contrasting yellow-to-dark-orange elements together with the exposition of hind wings, results in a hymenopteran appearance. This might be an advantage when it comes to avoiding predators or limiting aggression from aculeate hymenopterans, when meloids approach their nests for oviposition.

Among the enormous family Tenebrionidae, only one known genus has evolved brachelytry: *Petria* Semenov, of the subfamily Alleculinae. Within this family generally characterised by a thick, water-efficient cuticle allowing exploitation of arid environments, the Alleculinae represent somewhat of an exception with their much thinner cuticle. Only males of *Petria* are known, and these have abbreviated elytra that expose the last two to three abdominal tergites. Lawrence (1971) speculated that females are apterous, living underground analogous to females of the dascillid genus *Anorus*.

In the vast majority of Mycteridae, the elytra cover the entire abdomen. However, in a few species of *Hemipeplus* Latreille, the last visible tergite is exposed by slightly truncated elytra (Pollock, 2011). Little is known about the ecology and biology of *Hemipeplus*, but its species seem to be associated with grasses, palms or other monocots (Pollock, 2011). Potential drivers of elytral shortening in *Hemipeplus* remain unclear.

The small family Promecheilidae contains at least two apterobrachelytrous species and genera, *Chanopterus paradoxus* Boheman and *Perimylops antarcticus* Müller (Watt, 1970; see Johnston & Matsumoto, 2023 for images).

Interesting morphological modifications can be found within the subfamily Inopeplinae (Salpingidae), which encompasses beetles with flattened bodies and with various degrees of elytral shortening, resulting in a rove-beetle-like appearance (Ślipiński et al., 2021). This modification is most likely attributed to life under bark (Ślipiński et al., 2021) and selective pressure on higher body flexibility. Another genus of salpingids, *Aegialites* Mannerheim (subfamily Aegialitinae), which inhabit intertidal rocks in the northern Pacific region, contains species with variably truncate elytra loosely exposing the pygidium.

Within Anthicidae, the elytra often expose only the tip of the abdomen. However, in a few taxa (e.g., *Tanarthrus* LeConte), more distinct elytral reduction can be found, for instance, in *Leptanthicus staphyliniformis* Werner, where short elytra cover only half of the abdominal length (Chandler, 2010). Selection pressures for elytral shortening in some Anthicidae are unclear. However, both *Tanarthrus* and *Leptanthicus* Werner are specialist inhabitants of saline mud flats, and the elytral reduction in some *Tanarthrus* species was suggested to be related to a specific behavioural strategy of overheating avoidance, enhanced by wing-extension behaviour (Peterman, 1973). Slight exposure of the last abdominal tergite in many other Anthicidae might be related to the presence of apical elytral glands, where cantharidin (gathered from meloid beetles) is concentrated (Chandler, 2010; Hashimoto & Hayashi, 2014). Afreminae, a subfamily of three species formerly included in Anthicidae, but now included as Tenebrionoidea *incertae sedis* (Lawrence, Escalona, & Leschen, 2010), includes two species within *Afremus* Levey, one of which has the two apical tergites exposed by short elytra (Levey, 1985); the third species, *Dunbrodianus longicollis* Pic, is said to have only the ‘pygidium’ extending slightly beyond the elytra (Pic, 1904). Females of Afreminae are still unknown.

Superfamily Coccinelloidea

Brachelytry is not common in this group. In Corylophidae, some representatives of the tribes Aenigmaticini, Foadiini, Sericoderini, Stanini and Parmulini (all Corylophinae) have apically truncated elytra, exposing 1–2 abdominal tergites (Ślipiński et al., 2010). The functional background of this modification is not clear. Corylophidae are extremely small insects that inhabit various types of decaying matter, where they feed on microscopic fungi (Ślipiński et al., 2010). Regarding Coccinellidae, there are several rare brachelytrous examples such as *Ruthmuelleria* Jałoszyński & Ślipiński (Carinodulini) and *Mimolithophilus* Arrow (not assigned to tribe), the latter being flightless and living in xeric habitats under stones (e.g., Fürsch, 1996; Jaloszyński & Ślipiński, 2014).

Superfamily Nitiduloidea

In the superfamily Nitiduloidea, brachelytrous taxa occur in Monotomidae, Kateretidae, Nitidulidae and Smicripidae. Elytra are apically truncated in most Monotomidae outside of the Rhizophaginae, exposing 1–3 abdominal tergites. The vast majority of the species with truncated elytra have well-developed hind wings, but members of the genus *Crowsonius* Pakaluk & Ślipiński are apterobrachelytrous. Extant Kateretidae are exclusively brachelytrous, with the last abdominal tergite and sometimes also a part of the preceding abdominal tergite exposed, whereas the hind wings remain fully covered (Jelínek & Cline, 2010). Recently, Peris and Jelínek (2019) suggested that brachelytry represents an ancestral state for the family because all Cretaceous and one Eocene fossil species of Kateretidae share atypically short elytra and three dorsally exposed abdominal tergites. Brachelytry in Nitidulidae is particularly notable within Carpophilinae and Cillaeinae. Many members of these two subfamilies are characterised by distinct apical truncation of the elytra, often fully exposing 2–3 posterior abdominal tergites, but with the hind wings still fully covered. The family Smicripidae has only one genus, *Smicrips* LeConte, which is characterised by the elytral truncation resulting in the exposure of 1–2 abdominal tergites.

Most likely, different selective pressures have resulted in elytral shortening in different lineages of Nitiduloidea. Some Monotomidae are predators of wood-boring beetles, hunting in winding galleries where increased abdominal flexibility can improve manoeuvrability. The nearly blind, wingless species of *Crowsonius* inhabit nests of *Trigona* Jurine bees (Hymenoptera: Apidae) and are most likely efficiently dispersed via phoresy by their hosts (Pakaluk & Ślipiński, 1995). Little is known about the biology of other brachelytrous Monotomidae, but many of them are found in narrow spaces under the bark of trees and are likely fungus feeders (Majka & Bousquet, 2010). Nothing is known about potential reasons for elytral shortening in Kateretidae or Smicripidae, both of which are anthophagous as adults, with larvae also anthophagous in Kateretidae. Potential factors behind elytral reduction in some Carpophilinae and Cillaeinae (Nitidulidae) also remain unclear. However, several taxa from these groups are known to be closely associated with particular species of flower hosts (Powell et al., 2020), and thus increased flexibility of the uncovered abdomen might potentially be a result of advanced, specialised forms of anthophily.

Superfamily Cucujoidea

In the superfamily Cucujoidea, several brachelytrous taxa occur in Laemophloeidae. For example, the genus *Placonotus* Macleay contains some species with slightly truncate elytra, which expose (most of) the terminal abdominal segment, for example, *P. modestus* (Say) (Thomas 1984). Furthermore, species classified in the genus *Cucujinus* Arrow, including those in the subgenus *Paracucujinus* Lefkovitch, have similarly abbreviated elytra (Lefkovitch, 1962, 1964).

Superfamily Curculionoidea

The superfamily Curculionoidea constitutes one of the largest and most diverse groups of beetles, encompassing more than 62,000 described extant species (Oberprieler et al., 2007). The vast majority of weevil diversity is concentrated within the largest family, Curculionidae. Although weevil larvae generally live endophytically in various types of plant tissues, adults often occupy exposed microhabitats, feeding externally on plant matter. This most likely resulted in the formation of heavily sclerotized and pigmented elytra, securely shielding all of the abdomen tergites. Exceptions from this condition are extremely rare within the Curculionoidea. Although some parts of the last abdominal tergite (rarely the entire structure) might be exposed in several groups (e.g., Anthribidae, Attelabidae: Rhynchitinae: Deporaini, Belidae, Curculionidae: Dryophthorinae, Baridinae, Curculioninae: Acalyptini, Mesoptiliinae: Laemosaccini), brachelytry is very rare. Within the family Anthribidae, some members of the subfamily Urodontinae have a more-or-less exposed last abdominal tergite and sometimes also a partially uncovered preceding tergite. A good example is the enigmatic species *Urodontidius enigmaticus* Louw, which is characterised by slightly truncated elytra with apices independently rounded, and fully covered hind wings. The functional background of this modification is unclear; however, species of this subfamily feed cryptically within plant tissues (Oberprieler & Scholtz, 2018). Certain members of Anthribinae may also have the last and a portion of the preceding abdominal tergite somewhat exposed, but the elytra are not truncate. Among the Attelabidae, members of the kleptoparasitic tribe Pterocolini (Rhynchitinae) have three to more than four tergites exposed by their arcuately truncated elytra, which might be part of a suite of adaptations for digging through leaf rolls of other attelabids (Hamilton, 1998; Riedel, 2014). Certain members of the Attelabinae may, at times, have one and a portion of a second terminal tergite exposed, although the elytra are not truncate (e.g., *Euops* Schoenherr).

Within the extraordinarily diverse family Curculionidae, a spectacular example of total loss of the elytra is the paedomorphic sib-mating male of the genus *Ozopemon* Hagedorn (Scolytinae). Bizarre-looking males of this genus are characterised by a fully developed aedeagus, a strongly flattened pronotum and head, and a 10-segmented, completely uncovered larviform abdomen (Jordal et al., 2002). Females of *Ozopemon* are macrelytrous and have functional hind wings (Jordal et al., 2002). The remarkable modifications of male *Ozopemon* are attributed to the inbreeding strategy, where males do not compete for females and do not invest much in reproduction (Jordal et al., 2002). It should be also noted that many other males of sib-mating Scolytinae are characterised by miniaturisation, weak body sclerotization and loss of hind wings (Jordal et al., 2002). It seems that *Ozopemon* constitutes an extreme example of the resource-saving strategy, driven by extraordinary selection towards optimal male tissue allocation (Jordal et al., 2002), which is a direct prediction for permanently inbreeding males (Jordal et al., 2002). Males are only known from three species of *Ozopemon* so far and minute, vestigial elytra were identified only in *Ozopemon obanus* Hagedorn, while both *O. brownei* Schedl and *O. uniseriatus* Eggers lack any external trace of elytra (B. Jordal, pers. comm.).

Superfamily Chrysomeloidea

Elytral reduction is a rare phenomenon in Chrysomelidae (leaf beetles), being almost exclusively restricted to Bruchinae and Galerucinae (Jolivet, 2005a). Members of the subfamily Bruchinae are often characterised by slightly truncated elytra, exposing at least the last abdominal tergite (tergite VII), but sometimes also tergites V–VI (e.g., *Kytorhinus* Fischer von Waldheim). Spectacular examples of significant elytral reduction within Galerucinae are the genera *Arima* Chapuis (Figure 2n) or *Nyctidromas* Semenov (both Galerucini), characterised by posteriorly truncated elytra with rounded apices covering only the two first abdominal tergites. Among Alticini, two described species of desert-dwelling *Longitarsus* Berthold are apterobrachelytrous (LeSage, 1988); other brachelytrous alticines (*Hespera* Weise and *Sjoestedtinia* Weise) occur in alpine environments (Beenan & Jolivet, 2008). Within the subfamily Sagrinae, females of some *Polyoptilus* Germar are apterobrachelytrous, whereas the males have fully developed elytra (Lawrence & Reid, 2014). Among the subfamily Cryptocephalinae, the most common condition is having independently rounded elytral apices exposing a large terminal abdominal tergite and most or all of the preceding tergites. Such broad exposure of tergites without significant reduction in elytral length appears to be a secondary consequence of the body (including the abdomen) becoming more cylindrical.

Elytral reduction in leaf beetles is frequently connected with the loss of metathoracic wings (but not in Bruchinae or Cryptocephalinae) and often occurs together with physogastry (e.g., *Metacycla marginata* Chapuis). Several brachelytrous Chrysomelidae are also characterised by striking sexual dimorphism with large, wingless, physogastric females and dwarfed males, which are much rarer in populations than females (e.g., *Arima*) (Jolivet, 2005a).

Elytral reduction in Chrysomelidae seems to be a consequence of a specific resource-allocation strategy aimed at maximising female fecundity combined with resource-saving (Jolivet, 2005a, 2005b). This conception implies that the loss of flight ability and reduced protection due to an uncovered abdomen are compensated for by increased fecundity enhanced by a greater allocation of saved resources to egg production. This might be a particularly effective strategy in harsh environments (e.g., high altitudes or arid habitats), where the availability of crucial resources is strictly limited (Jolivet, 2005a, 2005b).

In the small family Vesperidae, brachelytry occurs within two subfamilies: Philinae and Vesperinae. Females of many species of *Vesperus* Dejean (e.g., *Vesperus sanzi* Reitter) are brachelytrous, physogastric and flightless, with hind wings reduced or non-functional. Similar phenomena can be found in females of some species of the genera *Heterophilus* Pu and *Mantitheus* Fairmaire (e.g., *Mantitheus pekinensis* Fairmaire). Elytral reduction in Vesperidae might be attributed to resource saving, as the brachelytrous females do not feed as adults, live only briefly, are nocturnal and occupy sheltered habitats, crawling in low vegetation (Švácha & Lawrence, 2014).

Within Cerambycidae, brachelytrous taxa can be found in several subfamilies, but they are most common within Prioninae, Necydalinae and Cerambycinae. All members of the subfamily Necydalinae (Figure 2o) are exclusively brachelytrous, with the elytra covering only the pterothorax (both in males and females), largely exposing the hind wings. In some cases, the elytra are also dehiscent. Within Prioninae, brachelytrous genera occur probably only in Anacolini and Prionini. The apparent elytral reduction also occurs in females of some Meroscelisini (e.g., *Meroscelisus*

Audinet-Serville) but is most likely attributed to physogastry. Elytral reduction in Prioninae may occur only in males (e.g., *Chariea* Audinet-Serville), only in females (e.g., *Pogonarthron* Semenov) or in both sexes but with a more far-reaching reduction in males (e.g., *Oideterus* Thomson or *Psephactus* Harold). In most cases, this is related to the exposure of the hind wings and sometimes also to a significant narrowing of the elytra. In the subfamily Cerambycinae, brachelytry occurs in many tribes and almost always in both sexes (but see, e.g., *Charassonotus hulstaerti* [Burgeon]), for instance, in Bimiini, Psebiini, Stenopterini, Hesthesini, Methiini, Molorchini (Figure 2p) or Rhinotragini. Slightly shortened and sometimes also dehiscent elytra can also be found within some members (e.g., some species of *Trypogeus* Lacordaire) of the former small subfamily Dorcasominae (now Cerambycinae: Dorcasomini). In brachelytrous Cerambycinae, the hind wings are always exposed, and sometimes the elytra are also strongly dehiscent. Brachelytry within Lepturinae is limited to a few genera within Lepturini. In some of them, including *Brachyleptura* Casey or *Nivelliomorpha* Boppe, the elytra are slightly truncated in both sexes, but the hind wings are completely covered. In contrast, in a few other genera of Lepturini (e.g., *Nanostrangalia* Nakane & Ohbayashi), elytral reduction occurs only in males, exposing a few abdominal tergites along with part of the hind wings. Exposure of the abdominal tergites is a very rare condition within the heavily sclerotized Lamiinae; however, it can be found in a few genera of Saperdini (e.g., *Gracilinitocris* Breuning).

Mimicry seems to be a major driver of elytral shortening in most Cerambycinae and Necydalinae. Several species of brachelytrous, diurnal and palynivorous species exhibit a striking resemblance to Hymenoptera (e.g., Necydalinae and Hesthesini) and exposition of hind wings might increase the similarity to the model (Švácha & Lawrence, 2014). The reason for elytral shortening in some Prioninae might be different, however. As reaching a female quickly has obvious priority for the short-lived males of some prionines, investing in protective features might be redundant. On the other hand, bright-coloured members of some Anacolini (e.g., *Oideterus* Thomson) suggest mimicry as a potential reason for the elytral reduction, at least in some groups of Prioninae. In large, brachelytrous and cryptic females of many Anacolini and Prionini, the driver of elytral reduction is unclear, though resource saving might be a potential reason. Bizarre-looking apterous females of some steppe Prioninae (e.g., *Microarthron* Pic) are known to spend their entire life cycle hidden in dead wood and only release their long, narrow, uncovered abdomens during intromission (Staněk, 1990). Increased abdominal flexibility and correlated facilitated copulation might also be a potential driver of elytral shortening in some Lepturinae.

DISCUSSION

Prevalence, forms and intensity of elytral reduction in Coleoptera

Based on a comprehensive literature review (see Supplementary File S1) and extensive consultations with taxonomic experts in particular systematic groups (see Supplementary File S1 and the Acknowledgements), we have provided here the most updated and highest yet figures for the current number of described species of Coleoptera (442,275 extant species; for methodological details, see Supplementary File S1). This was the first crucial step for a reliable estimation of the prevalence of elytral loss within every extant family of beetles. Our analysis has revealed that elytral reduction (brachelytry) is a common modification within the order Coleoptera, whereas elytral loss (anelytry) is rare (Table 1). We found examples of an/brachelytry in 53 extant families of beetles (Table 1), representing all extant suborders (percentage of species with reduced/absent elytra: Myxophaga—30.7%, Polyphaga—21.0%, Adephaga—9.8% and Archostemata—2.3%; Table 2). Within the hyperdiverse suborder Polyphaga, the highest percentage of species with reduced/absent elytra was found in the series Staphyliniformia (57.7%). Elateriformia and Cucujiformia were characterised by a small percentage of species with reduced/absent elytra (7.5% and 3.6%, respectively, Table 2), whereas the rate was marginal in Bostrichiformia (0.1%). There were no examples of elytral reduction/loss within Scirtiformia, Clambiformia, Rhinorhipiformia or Nosodendriformia (Table 2). For more details, see Table 2.

Apart from the high prevalence of an/brachelytry within extant coleopteran suborders, this phenomenon is usually limited to a small fraction of species among predominantly macrelytrous lineages (Table 2). A clear exception from this situation is the superfamilies Staphylinoidea and Histeroidea, where elytral reduction/loss is the dominant or ubiquitous condition, and also to a lesser degree in Elateroidea, where various elytral modifications have led to a wide array of patterns of elytral shortening or loss (Table 2). Obtained results highlight that brachelytry evolved many times independently, leading to the formation of similar patterns among distantly related groups (Table 1 and Figure 1). Our results also suggest that the transition from fully developed to shortened elytra can occur relatively quickly, as we found several examples of predominantly macrelytrous genera containing single or few brachelytrous species. Recently, it was also shown that the opposite transition (secondary elongation of shortened elytra) is possible and has occurred at least four times independently within the rove beetle subfamily Omaliinae (Kim et al., 2020).

Although this modification of the coleopteran groundplan already occurred in the evolution of several early diverging lineages such as the archostematan Micromalthidae (Yan et al., 2019: †*Archaeomalthus*), adephagan Gyrinidae (e.g., Beutel et al., 2020; Gustafson et al., 2017), myxophagan †Triamyxidae (Qvarnström et al., 2021), and polyphagan Elateroidea (Li et al., 2022; Li, Kundrata, Packova, et al., 2021; Li, Kundrata, Tihelka, et al., 2021) and Staphylinoidea (Chatzimanolis, 2018), Permian stem-group Coleoptera were exclusively macrelytrous (e.g., Boudinot et al., 2023a; Ponomarenko, 1969).

In general, two major types of brachelytry can be distinguished, including elytral truncation and dehiscence (Table 1 and Figure 1). The first type is characterised by a more-or-less straight posterior elytral edge and adjacent or connected sutural margins, whereas the latter is often composed of independently narrowed, apically diverging elytra, resulting in the formation of a longitudinal gap (Figure 1d). It should be further noted that, as with every continuous biological phenomenon, elytral reduction might also adopt various intermediate or overlapping forms (Table 1). Our evaluation shows that in the vast majority of brachelytrous species, the phenomenon occurs in both sexes. In contrast to this, elytral loss in many distantly related groups can be a condition found only in females (the more common scenario) or rarely only in males (Table 1).

Apart from distinctly differing general patterns of elytral reduction, brachelytry varies greatly in severity, ranging from minor truncation (e.g., Hydroscaphidae, Gyrinidae, Histeridae and Kateretidae), through a medium (e.g., *Macromalthinus*, *Molorchus*) to significant reduction (e.g., Atractocerinae, *Hornia*, *Necydalis*) or even complete loss (e.g, *Ozopemon* or *Xenomorphon* Ferreira et al. male, *Thylodrias* or *Pachypus* female, both sexes of *Mimeciton*). As elytra are modified fore wings and thus serially homologous to the membranous metathoracic alae, it is not surprising that they have maintained (at least partially) the genetic identity of flight wings (Clark-Hachtel et al., 2013). Nevertheless, elytral loss occurs independently of hind wing development. There are numerous species with shortened or even minute elytra and fully developed hind wings, as well as species with completely reduced hind wings but fully developed elytra. In rare situations, these two processes seem to occur synchronously, driven by the same, specific selective pressure on resource allocation (e.g., in paedomorphic females/rarely males). In contrast to the relatively common pattern of polymorphism in hind wing development in beetles, reflected by the condition-dependent formation of either long or minute metathoracic wings (Zhang et al., 2019), we found no evidence for a similar phenomenon in the case of elytral development.

Potential drivers of elytral reduction

Our analysis revealed that the potential drivers of elytral shortening and loss in Coleoptera are very diverse (Table 1). In three unrelated brachelytrous aquatic groups (Hydroscaphidae, Gyrinidae, *Limnebius*), the posterior abdominal segments function as a steering organ when the beetles move forward in the water. In many distinctive lineages (e.g., some Staphylinidae, Melyridae: Malachiinae, and Carabidae, e.g., Brachininae), the exposition of abdominal tergites might support the targeting of chemical defensive secretions. In highly modified beetles closely associated with social insects (e.g., some Aleocharinae and Pselaphinae), elytral shortening and related exposition of abdominal tergites (equipped with tergal secretory glands) was most likely a crucial step towards the establishment of unique social relations enhanced by chemical communication (Hölldobler & Kwapich, 2019; Naragon et al., 2022; Parker et al., 2018). Mimicry is most likely a driver of elytral shortening in many distantly related groups of diurnal anthophilous beetles (Table 1), for example, some Cerambycidae (e.g., Necydalinae), Cantharidae (e.g., Malthininae), Ripiphoridae or Meloidae (e.g., *Sitaris*), where exposed hind wings likely increase the beetles' similarity to hymenopteran models. Increased abdominal flexibility and related improved manoeuvrability in narrow spaces is a potential driver of elytral shortening in several beetle lineages, including some brachelytrous Staphylinidae, Salpingidae (Inopeplinae), Monotomidae or Nitidulidae (Carpophilinae) (Table 1). An uncovered, flexible abdomen might also facilitate copulation, which is crucial in beetles copulating in hidden spaces and only exposing the abdomen for intromission (e.g., *Microarthron komaroffi* [Dohrn]). A short life span, together with adult nonfeeding, seem to be predisposing factors to elytral reduction, at least in some groups (e.g., Phengodidae, Psephenidae: Psephenoidinae). Extreme morphological adaptation related to occupying a very specific niche might also lead to brachelytry, for instance, in the leiodid Platypsyllinae, which are closely associated with mammals (Yavorskaya et al., 2023). In the case of the short-lived, weakly sclerotized and more-or-less obsolete adults of *Micromalthus debilis* (Archostemata), developmental economy may be the reason for shortened elytra, along with generally weak body armour. Similar reasons may stand behind the elytral loss in many soft-bodied and, to various degrees, paedomorphic elateroids and dascillids.

Evolutionary implication of elytral loss

As the knowledge of the postcephalic anatomy of brachelytrous beetles is fragmentary at present, morphological effects of elytral shortening on external and internal structures are difficult to evaluate. In Adephaga, the external and internal thoracic morphology of Gyrinidae is well known (Beutel et al., 2017; Larsén, 1966; Liu et al., 2018), and the group is characterised by numerous apomorphies of the thorax and abdomen. However, this is certainly due to specialised surface-swimming habits and not related to elytral truncation (Liu et al., 2018; Yan et al., 2017). The staphylinoid Ptiliidae, also equipped with truncated elytra, are affected by miniaturisation (Yavorskaya et al., 2019). However, no specific features possibly related to shortened elytra were identified (Yavorskaya et al., 2019).

Elytral locking mechanisms such as the one formed by the mesonotal scutellar shield and metanotal alacristae are apparently scarcely affected in groups with shortened elytra with parallel mesal edges, such as rove beetles (e.g., Blackwelder, 1936: figs. 3 and 4) or Ptiliidae (Yavorskaya et al., 2019). Likewise, the elytral articulation is obviously largely or completely unmodified in Gyrinidae (Beutel et al., 2017) and brachelytrous Staphylinidae (Blackwelder, 1936: fig. 6), and probably also in other groups.

Another character system obviously affected by elytral shortening, at least in some groups, is the folding of the membranous hind wings. This has mainly been studied in Staphylinidae, where the alae are completely stored below the elytra, even in very distinctly brachelytrous species (e.g., Blum, 1979; Haas et al., 2000). Only the apical part of the hind wings is rolled in Archostemata and Myxophaga, and in some small species of Adephaga (e.g., Blum, 1979; Haas & Beutel, 2001: fig. 14), presumably a ground-plan condition in crown Coleoptera. In contrast, the more-or-less extensive distal part of the hind wings is folded in the vast majority of beetles, with or without a bending zone or marginal joint (Beutel & Haas, 2000; Haas, 1999, 1998: figs. 18 and 19). Related to elytral shortening, the folding pattern is modified in Staphylinidae, but interestingly also in rove beetle species with long elytra (Blum, 1979; Kim et al., 2020). Blum (1979) distinguished two patterns, one occurring in Omaliinae and some other groups, including taxa with long elytra, and the other in 'higher' staphylinids, such as Staphylininae, Xantholininae and Steninae. What is common to both types, likely a derived ground-plan condition of the family, is that both wings are folded differently (with the exception of *Aleochara*) and that circling and pushing movements of the abdomen play a decisive role in forming the small wing packages, which can be completely stored even below greatly shortened elytra (see also Haas, 1998, 1999).

It is very likely that the almost complete loss of elytra has resulted in the unique ('Stylopidae-like') morphology of the hind wings in Atractocerinae (Selander, 1959) and possibly led to the development of a unique flight style in this group (Miller, 1971). Furthermore, some parallel patterns in hind wing shape, especially reduction of the anal field size, were documented among several distantly related lineages of brachelytrous beetles with exposed hind wings (Goczał et al., 2018). In many cases, brachelytrous members of distantly related families were more similar to each other in hind wing shape than to their macrelytrous relatives (Goczał et al., 2018).

A modification of the abdomen obviously related to brachelytry is increased sclerotization of exposed tergites. This is a typical condition found in Staphylinidae (e.g., Blackwelder, 1936: fig. 9A). Increased tergal sclerotization is likely a common modification in brachelytrous beetles, increasing the mechanical protection of the exposed segments. However, as a gradual modification, this is not yet well documented among various groups of Coleoptera (e.g., Lawrence et al., 2011).

Knowledge of the thoracic musculature of brachelytrous beetles is fragmentary. However, looking at the extensive data presented in Larsén (1966), it is evident that the mesothoracic muscle system is scarcely affected if at all in the examined species of the staphylinoid genera *Nicrophorus* Fabricius and *Creophilus* Leach. In contrast, a distinct pattern of reduction of meso- and metathoracic muscles can be recognised in *Meloe* (Meloidae), in this case apparently related to the lost capacity of flight and not to elytral shortening.

Interesting modifications of the abdominal musculature in Staphylinidae were described by Blum (1979). Whereas a typical arrangement with parallel longitudinal and dorsoventral muscles likely belongs to the ground plan of the family (Blum, 1979: figs. 10A, B, 20 and 21), intercrossing patterns occur in the preabdomen of more advanced groups, especially in Xantholininae and Staphylininae (Blum, 1979: figs. 10D and 28A, B). The derived arrangement increases the mobility of the abdomen and, thus, facilitates the storage of the hind wings as small packages.

Reduction or loss of key protective structures might result in greatly decreased mechanical protection against predators. This problem can be overcome by the development of alternative defence strategies. The vast majority of beetles with elytra shortened or absent have developed novel defensive tactics (Goczał, 2023). In some cases, the emergence of a defensive innovation was probably a predisposition for elytral reduction. This is very likely true for some brachelytrous longhorn beetles (e.g., Molorchini, Necydalinae and Hesthesini) exhibiting a deceptive resemblance to females of aculeate Hymenoptera equipped with a stinging apparatus. It appears likely that, in some cases, a mimicry strategy and related exposition of hind wings can be a more effective defensive strategy than the costly investment in the development of highly sclerotized, long elytra. A wide range of alternative defensive strategies can be found within the largest group of brachelytrous beetles, the Staphylinidae. Alternative defensive innovations in rove beetles encompass, for instance, increased thickness of exposed abdominal tergites, fusion of exposed tergites, mimicry, enlargement of the prothorax (forming a kind of defensive shield), chemical protection (defensive glands), behavioural aspects (upward bending of the flexible abdomen) or even secretion of a specific substance disrupting water surface tension, enabling the beetle to glide over the water surface and escape from predators (Parker, 2017). A spectacular defensive strategy can be found within the flanged bombardier beetles (Carabidae: Paussinae) and the brachinine bombardier beetles (Carabidae: Brachininae), which can spray opponents with an explosive emission of hot gases when disturbed (Arndt et al., 2016; Eisner & Aneshansley, 1982). Numerous brachelytrous beetles are characterised by aposematic coloration, manifesting that they are toxic or unpalatable (e.g., some brachelytrous Cantharidae and Melyridae) (Goczał, 2023). An interesting yet poorly studied potential defensive strategy is defensive bioluminescence, which occurs in some soft-bodied and brachelytrous Phengodidae (Powell et al., 2022; Viviani & Bechara, 1997). Larviform females of Drilini (Elateridae) are known to use empty snail shells to hide, whereas many other paedomorphic elateroid females occupy cryptic niches, hiding in soil, litter or low vegetation, which might potentially largely reduce predator pressure.

AUTHOR CONTRIBUTIONS

Jakub Goczał: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; supervision; resources; funding acquisition. **Rolf G. Beutel:** Conceptualization; investigation; writing – original draft; writing – review and editing; supervision; methodology. **Matthew L. Gimmel:** Investigation; writing – original draft; validation; writing – review and editing; data curation; resources. **Robin Kundrata:** Methodology; investigation; writing – original draft; writing – review and editing; visualization; supervision; validation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

File S1. Sources used for the total numbers of described extant species in individual families in Coleoptera in Table 2.

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