



# The relationship between taxonomic classification and applied entomology: stored product pests as a model group

Vaclav Stejskal<sup>1,\*</sup>, Tomas Vendl<sup>1</sup>, Shiqian Feng<sup>2</sup>, Yujia Qin<sup>2</sup>, Radek Aulicky<sup>1</sup>, and Zhihong Li<sup>2</sup>

<sup>1</sup>Department of Stored Product Pest Management, Czech Agrifood Research Center, Prague, Czech Republic

<sup>2</sup>Department of Plant Biosecurity, College of Plant Protection, China Agricultural University, Beijing, China

\*Corresponding author. Czech Agrifood Research Center, Drnovska 507, 161 06, Prague, Czech Republic (Email: [vaclav.stejskal@carc.cz](mailto:vaclav.stejskal@carc.cz)).

Subject Editor: Christos Athanassiou

Received on 5 September 2024; revised on 9 January 2025; accepted on 6 February 2025

Taxonomy provides a general foundation for research on insects. Using stored product pest (SPP) arthropods as a model group, this article overviews the historical impacts of taxonomy on applied entomology. The article surveys the dynamics of historical descriptions of new species in various SPP taxa; the majority of all species (90%) were described prior to 1925, while the key pests were described prior to 1866. The review shows that process of describing new SPP species is not random but is influenced by following factors: (i) larger species tend to be described earlier than smaller and SPP moths and beetles are described earlier than psocids and mites; (ii) key economic pests are on average described earlier than less significant ones. Considering a species name as a “password” to unique information resources, this review also assesses the historical number of synonymous or duplicate names of SPP species. Pests belonging to some higher taxa Lepidoptera and Coleoptera has accumulated more scientific synonyms than those others belonging to Psocoptera and Acari. Number of synonyms positively correlated with the economic importance of SPP species. The review summarized semantic origin of SPP names showing minor proportion of names (17.6%) are toponyms (geography) or eponyms (people), while the majority (82.4%) fall into other categories (descriptive, etc.). It is concluded that awareness of taxonomic advances, including changes to species and higher taxa names, should be effectively communicated to pest control practitioners and applied entomology students, and specifically addressed in relevant textbooks, web media, and databases.

**Keywords:** stored commodities, taxonomy, synonyms, insects, Acari

## Introduction

Taxonomy is considered one of the cornerstones in biology. A decade ago, Bilton (2014) published an influential review titled “What’s in a name? What have taxonomy and systematics ever done for us?” This review comprehensively outlines the historical benefits of taxonomy for science, society, and all levels of educational systems. However, it does not fully address some current challenges. Since taxonomy is not just a static accumulation of lists and catalogues of living organism names but rather a dynamic phenomenon being affected by current political and public issues. This, for instance, includes public debates surrounding the appropriateness of certain species names, specifically those derived from people (eponyms) and geographical areas (toponyms), raising ethical concerns about such names being potentially culturally offensive or inappropriate in contemporary society (Garbino 2023, Jiménez-Mejías et al. 2024). Potential societal demands for changes in animal names, coupled with rapid

taxonomic advances often associated with large-scale changes in nomenclature and taxonomic ordering, including species renaming, may have impacts on the retrieval of species-specific relevant information in databases, affecting not only professionals but also students and the general public.

Taxonomy provides a foundation not only for general entomology but also for applied entomology and pest control. The identification and classification of species, along with an understanding of their biology, help predict their potential impact on ecosystems and agriculture, defining their pest status. The inability to accurately identify pests and access relevant information about pest species may lead to inefficacy and/or excessive use of nonspecific, broad-spectrum pesticides. The practical challenge lies in the fact that global and even local pest species diversity places high demands on entomological skills and knowledge. Out of over 1 million total described arthropods (Stork 2018, Eggleton 2020), more than 9000

are considered agricultural pests (Pimentel 2009). Additionally, each year witnesses the description of new species, some of which may become pests. Increasing species diversity is not only challenge for applied entomology; it is also crucial to have unambiguous taxonomical positions, updated taxonomy, compliance with valid taxonomical synonyms, and accurate techniques/methods of identification of the target pest species. Considering a species name as a “password” to unique information resources emphasizes the need for species and higher taxa clarity and time constancy. This clarity may be obscured for practitioners due to taxonomic ambiguity, the existence of sibling species, changes in species names due to taxonomic revision, and the proliferation of common names, as well as changes in naming species for inclusivity. Despite the general knowledge of the importance of taxonomy in entomology, there is currently no specific review available that summarizes and describes the above mentioned current impacts of dynamics of historical and current changes in taxonomy for applied entomology.

Therefore, this article aims to overview, analyze, and discuss general trends, benefits, and problems associated with the historical development of taxonomic classifications in relation to applied entomology. For this purpose, we selected a specific group of agricultural arthropods called stored product pests (SPP) (Hagstrum and Subramanyam 2009). We provide an inventory and timeline of the historical descriptions of various species and higher taxa of SPP species. One of the objectives of this review was to depict the differential rate of historical descriptions of new species in four main taxa to which SPP species belong (ie beetles, moths, psocids, and mites), as this rate is considered one of the more likely predictors of a new pest species description in the future (Costello et al. 2015). The review also attempted to survey and analyze published information regarding factors that increase the probability of the description of new pest species. There is a general discussion among taxonomists to reveal reasons why some species and taxa have tended to be described earlier than others. Thus, this work was motivated by the intention to identify which of these factors can be used to predict whether new SPP species will be discovered and described. It also addresses the problem of the proliferation of scientific and common species names for practical use and information.

## Model Group: Why Stored Product Pest Arthropods?

Stored product pest arthropods (SPPA) represent a relatively well-defined ecological group adapted to develop on dry and dried stored commodities and food (Hagstrum and Subramanyam 2009). SPPA species have been utilized as model organisms across various research fields, including toxicology, population ecology, genetics, and molecular biology (Hinton 1948, Mravinac and Plohl 2010, Rösner et al. 2020, Campbell et al. 2022, Feng et al. 2022a,b, Klingler and Bucher 2022). This group of arthropods was chosen as a demonstration model for this particular review as well. Several reasons supported this choice. Storage pests constitute an artificial polyphyletic group encompassing species from numerous families. Therefore, studying the taxonomy of storage pests can provide more general insights that are less influenced by taxon-specific phenomena. Additionally, SPP arthropods have a long history of association with humans dating back to ancient times of agriculture (Buckland 1981), and key pests gradually spread and have become cosmopolitan with broad geographical distribution (Hagstrum and Subramanyam 2009, Qin et al. 2023). Recently, Qin et al. (2023) analyzed a global presence/absence dataset, including 263 stored beetle species from 33 families in 171 countries, based on their similarities in species

assemblages and found similar pest assemblages in geographically distant countries such as the United States and China, and India and South Africa, where commodity trade is high. They also identified similar pest assemblages in geographically close countries, indicating a greater threat to each other. The analysis showed that Asia, Africa, and Oceania had the highest number of unique assemblages of SPP beetle species.

Diverse synonyms and a discontinuous rate of description can be expected in various geographical regions and historical periods. The complex historical changes in names of species taxa were also anticipated by the authors of this review due to the relatively high species richness and diversity of this ecological group. Although storage arthropods only include 2 classes (Arachnida and Insecta) and 3 insect orders (Coleoptera, Lepidoptera, Psocoptera), the species richness of the pest group is relatively high. Globally, Hagstrum and Subramanyam (2009) documented 1750 insect species, and Hughes (1961) listed 86 mite species associated with stored product food and feed commodities. Even local or national diversity of stored product pest species may be high, as indicated by the two German checklists, which are the only European inventories of arthropods associated with stored commodities (Schöller 2013, Schöller and Prozell 2014). Many species (Halstead 1969) and their developmental stages (Kucerova and Stejskal 2002) are difficult or impossible to distinguish morphologically, necessitating the implementation of molecular methods.

Given the relatively high diversity and unclear classification of certain species, it was necessary to draw upon authoritative sources that could provide comprehensive insights into the subject matter. In this regard, our review relied on several influential monographs, including works by Hinton (1945), Hughes (1959), Hagstrum and Subramanyam (2009), and Hagstrum et al. (2013). These monographs served as valuable sources for historical primary and secondary references. Additionally, our review systematically utilized literature searches through ISI Web of Science and Google Scholar. As keywords for the search, we employed various combinations of general terms (the list is provided in Supplementary Appendix file - S2) and the names of arthropod species listed in Supplementary Appendix 1, as well as in the references Hinton (1945), Hughes (1959), Hagstrum and Subramanyam (2009), Hagstrum et al. (2013), and Stejskal (2004). To delve into historical resources related to common English names, we accessed the digital library of the National Library and the institutional library of the Czech Agrifood Research Center. Finally, we conducted a literature search using the “snowball process,” reviewing the reference lists of eligible sources, following a similar approach as outlined by Swanepoel et al. (2017). This method facilitated the identification of relevant information within the “gray literature.”

The authors believe that the aforementioned features of the SPPA group make it a suitable model for reviewing the impacts and trends of historical changes in taxonomic classification on storage pest arthropods in applied entomology. However, while the review primarily focuses on SPPA species, the authors suggest that many aspects may have broader applications in other areas of applied entomology or implications for general entomology.

## Historical Development from the Early Descriptive Period to the Era of “integrated taxonomy” in Relation to Stored Pest Species

### “Integrated taxonomy” in Relation to Stored Pest Species

Scientifically based taxonomy and SPP identification approaches have undergone substantial, gradual historical development since

they were established by Linnaeus in 1758. The general taxonomy model and historical process is described as the “five ‘D’s’”: taxon discovery, delimitation, diagnosis, description, and specimen determination (Favret 2024). There have been several attempts to describe historical periods of the general taxonomic classification of arthropods. For instance, Kingsolver (1990) suggested that taxonomic research and classification of bruchids (Coleoptera: Chrysomelidae), a group including various agricultural and storage pests, can be divided into four general and partly overlapping historical periods: (i) the early descriptive period (1767 to 1874), which includes isolated descriptions of particular species; (ii) the faunal study period (1873 to 1929), which includes descriptions with detailed or broad diagnostic keys; (iii) the organizational period (1929 to 1960), which includes the development of higher classification; and (iv) the monographic and synthetic period (1962 to 1990), which includes generic revisions with keys, descriptions of new and old species, host plant associations, and geographical distributions. Since the article by Kingsolver (1990) was written more than 30 yr ago, logically it could not have included the recently emerging and rapidly evolving biochemical, molecular, and advanced zoogeographical approaches that are recognized by some authors as the most recent historical period called “integrative taxonomy” (IT) (Padial et al. 2010, Schlick-Steiner et al. 2010, Vinarski 2020). The recent holistic period is based on integrating the analysis of molecular biology (DNA/RNA), morphology, phylogeography (Ahrens et al. 2013, Gomes et al. 2015, Cao et al. 2016, Vinarski 2020), insect evolutionary history, and evolutionary ecology (OConnor 1982).

The development and adoption of new molecular techniques has substantially improved our understanding of the phylogenetic relationships and evolutionary origins of various taxa (Angelini and Jockusch 2008, Thomas et al. 2020), to which many SPP species belong. They have also helped to discriminate many previously inseparable (close/sibling/cryptic) species (Hending 2024), including SPP arthropods (Feng et al. 2018, Murillo et al. 2018), and to characterize taxa at the subspecies level (Braby et al. 2012). Machine vision, learning, and artificial intelligence (AI) also represent a significant phenomenon influencing taxonomy and species determination as parts of IT approach. Initially, these technologies were designed to assist or even replace researchers in identification tasks. Over time, their scope expanded discovery of new morpho-traits to separate of sibling or of similar species (Valdecasas 2024). The IT approach has had profound influences not only on general entomology but also on many areas of applied entomology, including stored product entomology. Yeates et al. (2011) suggested and provided a substantiation for why so-called “iterative taxonomy” should be used as a more precise term instead of “integrated taxonomy.” Since the latter is still more prevalent in the current literature, we also used this notion in this review.

### Development of Molecular Approaches for Discrimination of Species and Subspecies of SPP Species

The advanced molecular technologies help to discriminate many previously morphologically inseparable (close/sibling) species of stored product pests, such as psocids (Li et al. 2011), mites (Zélé et al. 2018), and beetles (Germain et al. 2013). Together with SEM microscopy techniques (Kucerova and Stejskal 2002), molecular approaches significantly help with not only species discrimination of sub-adult stages (eggs, pupae, and larvae) but also with discrimination of geographical groups and strains at sub-specific level (Feng et al. 2018).

The earlier molecular methods and comparative diagnostics used for SPP characterization included polymerase chain reaction (PCR) based on restriction fragment length polymorphism (RFLP) analysis.

One of the first studies conducted on SPP species included weevils from the genus *Sitophilus* by Hidayat et al. (1996), where RFLP was employed to support the discrimination of *Sitophilus oryzae* L. from its morphologically similar relative, *S. zeamais* L. Later, a multispecies PCR-RFLP study enabled rapid discrimination of the common species of stored product pests, such as the genus *Liposcelis* (Psocoptera: Liposcelididae) (Qin et al. 2008). Using PCR as the method, species-specific primers were developed for rapidly discriminating stored product pests. Thus, species-specific multiplex primers were developed to identify 5 internal feeders of grain, *R. dominica*, *S. granarius*, *S. oryzae*, *S. zeamais*, and *S. cerealella* (Solà et al. 2018), and to distinguish *L. corrodens* from ten common *Liposcelis* species (Yang et al. 2013). DNA barcoding was developed in 2003, and a partial cytochrome c oxidase I (*cox1*) sequence was proposed to play a key role in species diagnoses (Hebert et al. 2003). DNA barcoding has been used in Psocoptera (Yang et al. 2012, 2013, Cui et al. 2020) and Coleoptera (Obrepalska-Stepłowska et al. 2008, Nowaczyk et al. 2009). Due to its high sensitivity, quantitative real-time PCR has been used for the accurate identification of stored product pests (Li et al. 2011, Zhang et al. 2016). Solà et al. (2017) established quantitative real-time PCR-based techniques for the detection and quantification of the insect pest *R. dominica*. Zhang et al. (2020) described a quantitative real-time PCR-based procedure for the identification of five species of *Cryptolestes* based on the COI barcode region. The next developed approach was based on a microarray technique (gene chip) for SPP species identification because of its high throughput, high parallelism, and high sensitivity. Among storage pests Liu et al. (2017) firstly applied the gene chip method in 10 economically important stored-product pests collected from 25 geographic locations in China, the Czech Republic, and the United States. The lack of specialized taxonomic entomology experts in a particular country can be partially substituted by using quick and relatively cheap molecular identification approaches, such as LAMP (loop-mediated isothermal amplification), as demonstrated for storage psocid by Zeng et al. (2021) or for dermestid species by Rako et al. (2021).

It seems that among the most recently studied SPP taxonomic groups by molecular approaches are Lepidoptera (Vitkova et al. 2007, Liu et al. 2016, 2018, Yuan et al. 2019, Wu et al. 2020, Song et al. 2021, Künstner et al. 2022), Psocoptera and Coleoptera (e.g., Li et al. 2011, Yang et al. 2012, Feng et al. 2018, Oppert et al. 2022) followed by mites (Lan et al. 2020, 2021, Su et al. 2020). Some of the works on Psocoptera also have importance for general biology; for example, the intraspecific mitochondrial genome architecture in *L. bostrychophila* was sequenced and annotated, which helped our general understanding of the fragmentation of mitochondrial genomes (Feng et al. 2022a). The profound importance of general entomology and biology has also been studied relative to the genome sequencing of storage Coleoptera species such as *T. castaneum* (Tribolium Genome Sequencing Consortium—Richards et al. 2008, Liu et al. 2016) and *R. dominica* (Oppert et al. 2022). It is expected that understanding stored product pests at the genomic and proteomic levels will help not only in their diagnostics but also in the development of a new generation of genome disrupting and CRISPR-based gene editing control approaches (Perkin et al. 2016, Stejskal et al. 2021).

### Timeline of the Historical Descriptions of Storage Pest Species Correlates with Taxa Body Size and Rank of Economic Pest Importance

The abovementioned general historical trends also reflect a timeline of the description of arthropods associated with stored products.

The intensity of taxonomic work differed in various historical phases and time periods. In addition, it apparently also differs between particular taxonomic units (families, orders). For instance, in conspicuous groups such as beetles or moths, the description intensity was relatively gradual during the first 250 years, while in less apparent groups such as mites, there were relatively long “periods of silence” during the early descriptive period. In tiny arthropods, some of the progress may be associated with the advent of modern optical and SEM microscopy and molecular methods. Some authors analyzed the reasons why some species and taxa tended to be described earlier than others. Currently, there is a debate—mainly concerning natural diversity protection and conservation—over whether there are some general key factors (body size, geography, bias towards taxon, social aspects) enabling prediction of the rate of description of arthropod species that are still unknown and may even become extinct before they are described (Morrison et al. 2009). We conducted an overview and analysis of the timeline of the first historical SPP species description. The insect species covered by our study were based on a list of the storage pests in Hagstrum and Subramanyam (2009); it included 337 species from the orders Coleoptera, Lepidoptera, and Psocoptera. Hagstrum and Subramanyam (2009) ranked their global economic importance on a scale of 1 to 5. Only phytophagous or detritivorous species directly associated with a particular commodity (ie species depicted as (S), (F), and (C) sensu Hagstrum and Subramanyam (2009)), but not (P), ie parasitoids or predators, were involved. Because the book by Hagstrum and Subramanyam (2009) does not involve stored product mites, the pest species ( $n = 65$ ) of this group were excerpted from the following additional literature sources: Zdarkova 1967, 1979, Palyvos et al. 2008, Mostafa 2011, and Li et al. 2015.

### Temporal Dynamics of the SPP Species Historical Descriptions

Based on the survey, it was found that the earliest descriptions of SPP species originated from the father of modern taxonomy Carl Linnaeus from 1758, while the most recent ones are from the second half of the 20th century. Specifically, out of the recorded species, Linnaeus described 17% (8 out of 47) of the Lepidoptera SPP species, 8% (22 out of 274) of the Coleoptera SPP species, 13% (2 out of 16) of the Psocoptera SPP species and 3% (2 out of 65) of the mite SPP species. According to the dataset of Hagstrum and Subramanyam (2009), the most recently described SPP of Coleoptera may be considered *Cryptolestes cornutus* from 1989. Regarding Psocoptera, the most recently described species was *Liposcelis rufa* from 1950, and for mites, it was *Dedroplaelaps aegypticus* from 1985. However, it should be noted that these years of descriptions involve only species from a list of economically important pests ranked 1 to 5 in Hagstrum and Subramanyam (2009), so there is possibility that there are more recently described species of very low economic importance. For instance, there are more recent dates of descriptions of less important psocid species, such as *Liposcelis badia* from 2006 (Wang et al. 2006). In 1993, a new mite species *Tyrophagus curvipenis* was described (Fain and Fauvel 1993) that was later delineated from related species using a molecular method by Murillo et al. (2018). Even in 2011, the new mite species *Lasioseius neocepa* was described and characterized as a pest associated with stored onions in Egypt (Mostafa 2011). In the case of beetles, multiple new species were described from the end of the 20th century to the start of the 21st century; some of them are from genera or families previously known to contain several stored/urban pests and thus may be potentially harmful. Among them probably the most important are dermestid

genera *Attagenus* and *Anthrenus* (Hava 2021). In contrast, based on the available published international literature, it seems that there are few, if any, recent species descriptions regarding the SPP moths, although some species may change pest status profoundly; eg *Amyelois transitella* (Walker) (Trematerra 2022).

Reichmuth (2009) was the first to exemplify the historical timeline of the first descriptions of selected pest species of Coleoptera and Lepidoptera associated with stored products during the period 1758 to 1950. Later, Hagstrum and Phillips (2017) calculated that 15% of SPP insect species were taxonomically described prior to 1800; the majority (57%) of stored pest insect species were described between 1800 and 1899, while the more recent descriptions include 28% of stored pest species. The authors stressed that if only the 430 most damaging species are considered, the percentages for these three time periods of prior to 1800, between 1800 and 1899, and after 1899 are 37, 51, and 12%, respectively. For the purpose of this review, we extended and integrated works by Reichmuth (2009) and Hagstrum and Phillips (2017) by using more species and orders (see data and references used in Supplementary materials—Beukes et al. (2020)).

The historical process of species description is not random. Understanding the factors that influence when a species is first described (the date of first description, DoFD) may help to estimate the probability of further description in a given area and taxon. For instance, in the context of extant fishes, Costello et al. (2015) and Beukes et al. (2020) identified depth, geographic range and body size as the most important predictors of the DoFD. Costello et al. (2015) found that the number of species described has slowed for (i) large compared to small fish species, (ii) geographically widespread compared to localized species, and (iii) species occurring in the tropics and northern hemisphere compared to the southern hemisphere. Our review revealed that the historical year of the first SPP species description depended on the relation to higher taxa, body size, and the rank of economic importance of the pest.

### Average Year of SPP Species Description and Their Molecular Characterization in Relation to Belonging to a Particular Higher Taxon

Figures 1 and 2A show that the species belonging to the SPP groups Psocoptera and especially Acari were described significantly later than the SPP species belonging to Coleoptera and Lepidoptera. The average DoFDs according to their relation to certain higher taxa were as follows: Lepidoptera:  $1838 \pm 7$ ; Coleoptera:  $1848 \pm 3$ ; Psocoptera:  $1882 \pm 14$ ; and Acari:  $1909 \pm 7$ . Within Coleoptera,

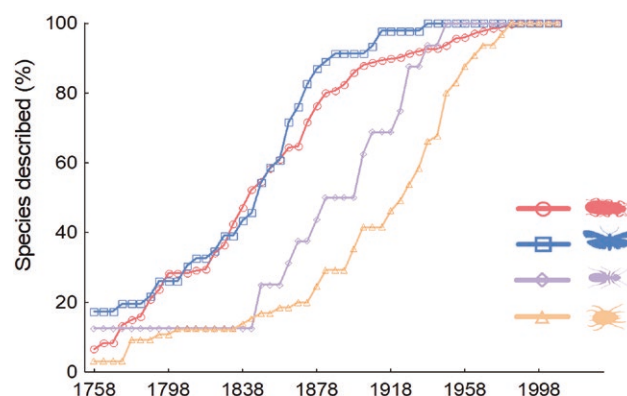


Fig. 1. Rate and dynamics of historical stored product pest species descriptions belonging to four main taxa (Lepidoptera, Coleoptera, Psocoptera, Acari).

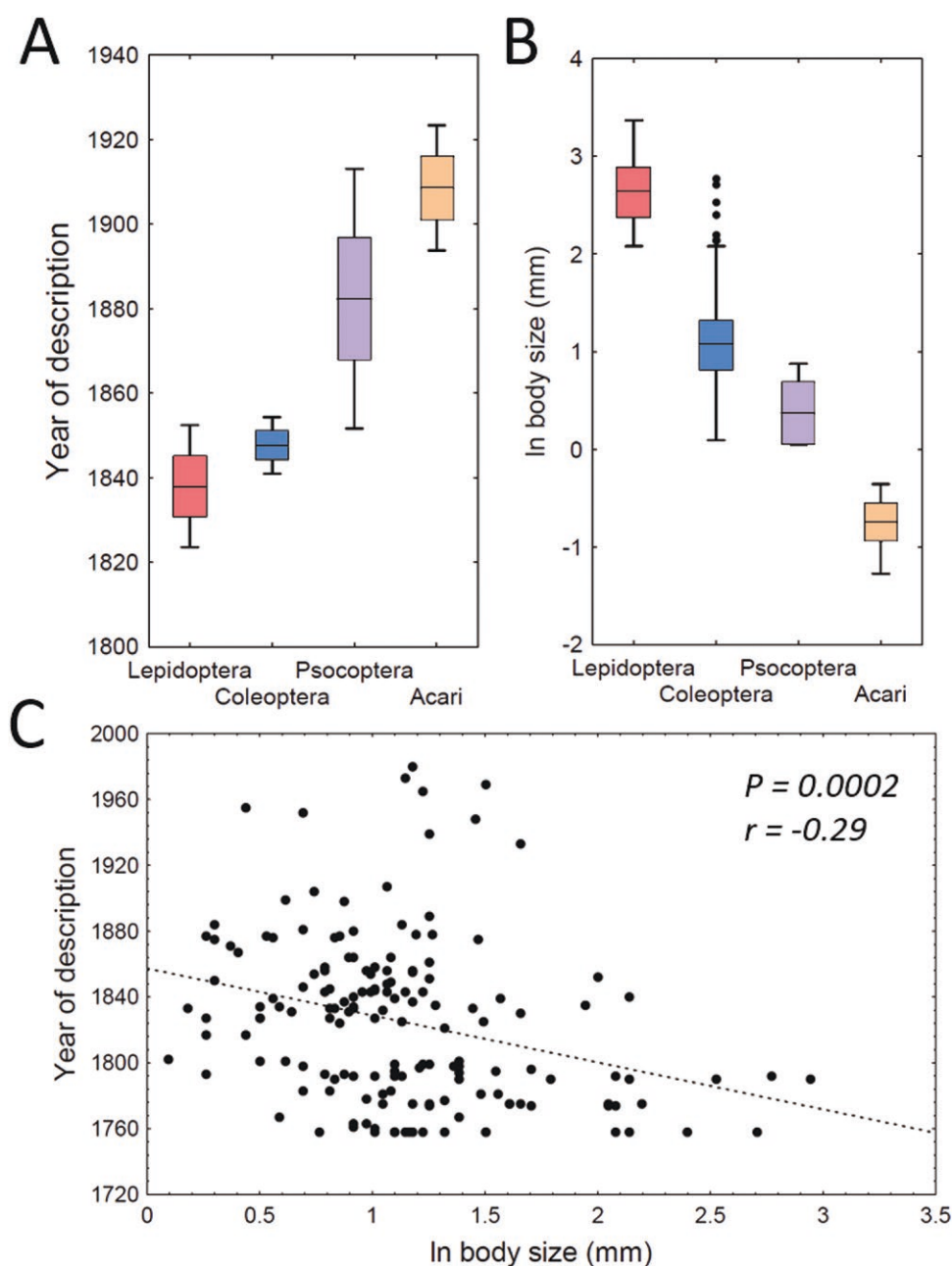


Laemophloeidae differs from other families in its significantly higher average DoFD ( $1901 \pm 16$  vs.  $1867 \pm 17$  in Laemophloeidae and the second most recently described family Curculionidae, respectively) (Table 1). Differences in DoFD between families within Lepidoptera, Psocoptera, and Acari were also observed, but these did not reach statistical significance due to their low representation in individual families. The values of DoFD for these three families are summarized in Tables 2–4.

As noted above, few new and economically important species of storage pests belonging to Lepidoptera or Coleoptera were described following the 1900s (Hagstrum and Phillips 2017). The data in this review (Fig. 1) revealed that, in comparison with beetles and moths, the historical description of storage psocids and mites came, with

some exceptions (eg Okamoto 1907), with a substantial time shift. This is in accordance with the recent bibliometric survey on papers on SPP species that psocids have been studied in more recent years (Stopar et al. 2022). The delayed interest in mite and psocid taxonomy went hand in hand with a disproportionally lower cumulative number of published “applied” studies (population dynamics and control methods, monitoring, etc.) on these groups, compared to SPP beetles and moths, although they are considered emerging pests (Stopar et al. 2022). In particular, microscopic pest mites are overlooked in comparison with moths and beetles in the context of their pest control in stored products (Stejskal and Hubert 2008).

Important information on the rate of psocid and mite descriptions and revisions are available in summary publications and



**Fig. 2.** A) Differences in the average year of descriptions of the four arthropod stored product pest orders. B) Differences in body size of the four arthropod stored product pest orders. C) Relationship between body size and year of description of stored product pest beetles. Data extracted from Weidner and Sellenschlo 2010 and Lompe 2002.

**Table 1.** Average date of first description (DoFD) for families in the order Coleoptera.

Family	Average DoFD	<i>n</i> species
Laemophloeidae	1901	12
Corylophidae	1887	1
Curculionidae	1867	11
Silvanidae	1865	13
Erotylidae	1863	3
Tenebrionidae	1857	34
Lathridiidae	1853	21
Bostrichidae	1851	14
Dermestidae	1849	50
Mycetophagidae	1848	4
Bruchidae	1847	38
Cerylonidae	1847	2
Nitidulidae	1842	17
Brentidae	1835	5
Anthiciidae	1829	2
Ptinidae	1828	22
Cryptophagidae	1826	12
Endomychidae	1801	1
Trogositidae	1795	2
Monotomidae	1793	1
Dryophthoridae	1793	4
Anthribidae	1775	1
Cleridae	1775	2
Melyridae	1775	1
Oedemeridae	1758	1

**Table 2.** Average date of first description (DoFD) for families in the order Lepidoptera.

Family	Average DoFD	<i>n</i> species
Cosmopterigidae	1882	1
Crambidae	1872	1
Gelechiidae	1846	4
Oecophoridae	1839	3
Tineidae	1839	14
Pyalidae	1834	21
Tortricidae	1807	2

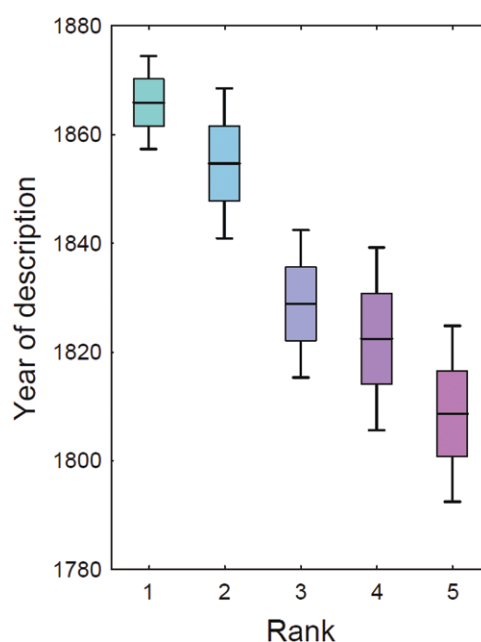
**Table 3.** Average date of first description (DoFD) for families in the order Psocoptera.

Family	Average DoFD	<i>n</i> species
Liposcelidae	1912	8
Psyllipsocidae	1872	1
Psoquillidae	1865	1
Trogiidae	1861	4
Lachesillidae	1819	2

catalogues published in 1945 to 2020: psocids (Obr 1948, Smithers 1967, Lienhard 1990, 1998, Li 2002, Lienhard and Smithers 2002, Yoshizawa and Lienhard 2010) and mites (Hughes 1959, Zdarkova 1969, Klimov and Tolstikov 2011, Dhooria 2016). This time delay in the research of psocids (Lienhard 2003) and mites (Dhooria 2016) does not apply only to storage species. Lienhard (2003) pointed out that up to the 1980s, very few Psocoptera species were known from the entire geographical territory of China. In a series of 36 papers published between 1987 and 2000, 64 new psocid genera were established, and 1468 new species were described (Lienhard 2003). At

**Table 4.** Average date of first description (DoFD) for families in the order Acari.

Family	Average DoFD	<i>n</i> species
Macrochelidae	1985	1
Triophtydeidae	1980	1
Tarsonemidae	1972	1
Echimyopodidae	1948	1
Phytoseiidae	1948	1
Ascidae	1943	4
Lardoglyphidae	1939	2
Pyroglyphidae	1936	3
Suidasiidae	1927	2
Acarophenacidae	1918	1
Ameroseiidae	1916	2
Cheyletidae	1915	14
Tydeidae	1915	2
Acaridae	1901	17
Digamaseiidae	1895	1
Laelapidae	1887	1
Stigmaeidae	1885	1
Chortoglyphidae	1879	1
Glycyphagidae	1861	6
Histiostomatidae	1839	1
Cunaxidae	1804	1
Carpoglyphidae	1758	1

**Fig. 3.** Average year of description (DoFD) in relation to global economic rank of importance by Hagstrum and Subramanyam (2009) (rank 1– the lowest economic importance, 5—the highest economic importance).

the 3rd International Congress of Acarology held in 1971, Rosický (1973), in his presidential address, described acarology as a relatively young science and stressed that up to 1963 a total of only 17,500 species of mites and ticks had been described and recorded. He claimed that the entire acarology discipline developed with a 150-yr delay in comparison with entomology. New species of economically important agricultural, dust, or stored product mites are still being described in recent decades (Nakao and Kurosa 1988).

In the last two decades, in addition to more or less sporadic descriptions of new stored product and agricultural pest species,

molecular characterization of species in all taxonomic groups, including stored product pests, has been ongoing. Regarding SPP taxa, the most turbulent taxonomy can be found in some mite species belonging to Astigmatic mites. For example, there have been long-term efforts and debates on how to resolve questions regarding *Acarus* spp. and *Tyrophagus* spp. mite groups and complexes (Robertson 1959, Griffiths 1962). Webster et al. (2004) contributed to that effort by expanding the molecular systematics of the *A. siro* (s. lato) group. Recently, efforts have been made to stabilize usage by applying the name *T. putrescentiae* to the common species; the rare species would then be known as *T. fanetzhangorum* (Klimov and OConnor 2010). Molecular phylogenetic analysis by Su et al. (2020) showed that *T. fanetzhangorum* is more closely related to *T. putrescentiae* than to *T. longior* within the genus *Tyrophagus*.

### Average Year of SPP Species Description in Relation to Body Size and Economic Importance

To ascertain the effect of body size on DoFD, we plotted the year of description to body sizes of SPP species. For this purpose, we used the SPP list and date of description used in the previous chapter of this review. Body sizes were excerpted from Lompe (2002) and Weidner and Sellenschlo (2010). If the body size was indicated as a range, the average value was computed (see Supplementary Material). Body size for a total of 218 species was recorded (ie 54% of the species in the dataset), which included the most important SPP species (27 out of 29 species from rank 5 and 32 out of 38 species from rank 4). The four main pest higher taxa differed in average body size in the order of Lepidoptera > Coleoptera > Psocoptera > Acari ( $14.6 \pm 1.0$  mm >  $3.5 \pm 0.2$  mm >  $1.6 \pm 0.15$  mm >  $0.48 \pm 0.03$  mm) (Fig. 2B). It indicated that the average body size of stored product pest species belonging to various arthropod higher taxa was inversely related to the average year of description (cf. Fig. 2A). This relationship was recorded not only among the higher taxa but also within the most represented order Coleoptera (Fig. 2C).

In addition, our overview and literature data analysis first documented that species with higher economic rank have been scientifically described earlier than less important species (Fig. 3). For instance, species ranked at value 5 (ie the most important pests) were described on average in the year  $1809 \pm 8$ , while species ranked at value 1 (ie the least important species) in year  $1866 \pm 4$ . The finding that species with greater economic importance were on average scientifically described earlier than their less economically significant counterparts implies a historical bias in the allocation of scientific attention. The prioritization of economically important species in early taxonomic research could be attributed to their direct relevance to human interests, agriculture, and trade.

### Species Name as a Unique “password” to Information Resources and SPP Species: Problems of Name Changes and Synonyms

Taxonomy and systematics are claimed to be essential keys to biological information (Koch and German 2013), thereby providing an evolutionary framework for any biological study. The binominal scientific (sometimes called Latin, although it could be based on words originating from other languages) name of a species is generally accepted as an elementary categorization unit for taxonomic classification. Individual species are further clustered into a large number of hierarchically arranged higher-order categories, such as families, orders, classes, etc. For agricultural and pest control practitioners,

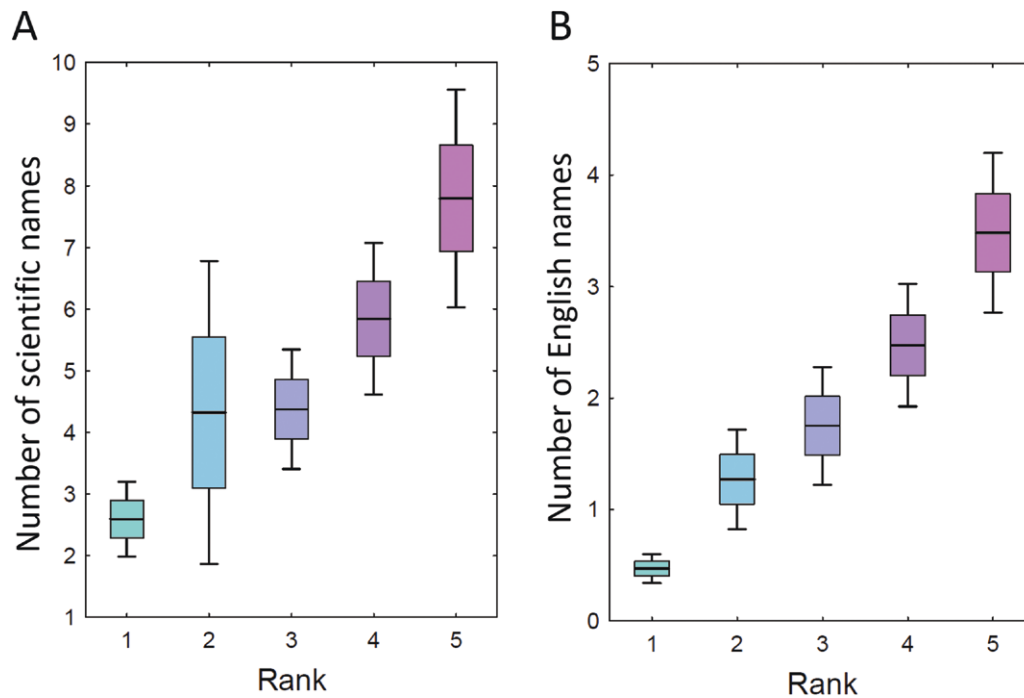
out of the taxa levels, species name is a unique “password” to information resources.

### Impacts of Name Proliferation, Name Revisions, and Name Changes (synonyms) on Practitioners

In his influential book on stored product pests, Munro (1966) stated that even taxonomic classification might differ with respect to the ultimate purpose for which is being constructed: “*Classification may serve two purposes. It may serve to indicate the origins and relationships of different groups of insects, to indicate their pedigree or phylogeny, or it may serve to enable the entomologist to group insects together, which have features in common so as to make it easier for him [one] to describe, identify and name them. A system of classification which is primarily phylogenetic may not make the identification of a particular insect easy, and a classification which aims at ease of identification may not satisfy the student of phylogeny.*” The binominal name of a species is a category of the highest practical importance, not only as a basis for initial scientific description and consequent safe identification (Munro 1966) but also from the perspective of its potential information content (Hagstrum and Subramanyam 2009). The name of a species may actually serve as the unique “keyword” or “password” to the international databases (eg CABi, WoS, Scopus, molecular DB such as GeneBank, etc.) and international journals, books, and other printed sources (eg Hagstrum and Subramanyam 2009). It allows access to historic and current species-specific information regarding identification (morphological keys, molecular markers/sequences/, etc.), biology, ecology, and pest control. However, the ability of pest association with a current common or even scientific name cannot always ensure access to the desired full information, as explained by Munro (1966): “*One of the difficulties both for the layman and the general entomologist is that the systematic entomologists, whose work is the classifying and naming of insects, frequently change the names of insects as a process that must be described as tidying-up.*” This implies the necessity for a regularly upgraded vocabulary of synonyms available for both specialists and practitioners (eg Stejskal 2004, Hagstrum and Subramanyam 2009, Hagstrum et al. 2013). For example, we found that 58% (195 out of 337 species) of stored product pest species were transferred from a genus established at the time of their description to a new or different genus.

### Number of Scientific and Common Names of Stored Product Pest Species

It is unknown what the total number of names are in various stored product pests and what the likely causes for interspecific differences are. Generally, there may be several causes of scientific name proliferation in particular species. For instance, the species may be described several times (by two or more authors) independently. In that case, according to the principle of priority of zoological nomenclature, a valid species name is the earliest published name, while the later ones are its junior synonyms. This situation frequently occurs in highly variable or widely distributed/cosmopolitan species. The latter is the case for many stored product pests, so it can be hypothesized that due to their wide geographical distribution, SPP species will “suffer” from a high “synonymy load.” However, the data for testing this hypothesis should be gathered and analyzed in future studies. It should be noted that in some specific cases, reversal of precedence could occur, and thus, a junior name could become the valid name of a species. Another cause of name proliferation may lie in taxonomic changes; a particular species may be transferred to another or newly established genus, and



**Fig. 4.** Positive trend between numbers of scientific synonyms per stored product pest species (data Suppl 1) and global rank of stored pest species importance estimated by Hagstrum and Subramanyam (2009) (rank 1– the lowest economic importance, 5—the highest rank economic importance). Horizontal lines inside the boxes indicate mean values, upper and lower box lines indicate standard errors, and whiskers indicate 0.95 confidence intervals.

thus its generic name is changed. This is especially the case for early described species, when the broad conception of genera gathering many unrelated species, even from various families, was common. We made an inventory based on various resources (mainly volumes of Catalogue of Palaearctic Coleoptera, Stejskal 2004, Hagstrum and Subramanyam, 2009 or CABI; for full inventory of synonymy resources for each species see Supplementary material). We found that 57% (156 out of 274) of SPP beetles were transferred to different genera, but in the case of Lepidoptera, it was 70% (33 out of 47); in Psocoptera, it was 38% (6 out of 16); and in Acari, it was 48% (31 out of 65).

The average number of scientific names of species belonging to various orders were: Lepidoptera— $5.5 \pm 0.6$  (min. – max.: 0–18), Coleoptera— $3.85 \pm 0.35$  (min. – max.: 0–71), and Psocoptera— $2.3 \pm 0.7$  (min. – max.: 0–10). These differences were significant (Kruskal–Wallis test;  $H_2 = 16.3$ ,  $N = 337$ ,  $P = 0.0003$ ). Post-hoc tests indicated that Lepidoptera SPP species have significantly more scientific names than both Coleoptera ( $P = 0.0011$ ) and Psocoptera ( $P = 0.012$ ). The stored product pest species with the highest number of scientific names in each group (ie beetles, moths, and psocids) comprise *Hypothenemus eruditus* (even 71 synonyms!) (Coleoptera: Curculionidae), *Setomorpha rutella* (18) (Lepidoptera: Tineidae), and *Lachesilla pedicularia* (10) (Psocoptera: Lachesillidae). Similarly, the average number of English common names varied across orders: Coleoptera— $1.1 \pm 0.1$  (min. – max.: 0–8), Lepidoptera— $2.4 \pm 0.3$  (min. – max.: 0–9), and Psocoptera— $2.1 \pm 0.7$  (min. – max.: 0–10). These differences were also statistically significant (Kruskal–Wallis test;  $H_2 = 22.3$ ,  $N = 337$ ,  $P < 0.0001$ ), driven by Lepidoptera having significantly more common names compared to Coleoptera ( $P < 0.0001$ ). Stored product pest species in each group with the highest number of English common names include *Necrobia rufipes* (8) (Coleoptera: Cleridae), *Phthorimaea operculella* (9) (Lepidoptera: Gelechiidae), and *Trogium pulsatorium* (10) (Psocoptera: Trogidae). The reason

for the higher number of scientific than English names may lie in the fact that the nonvalid scientific name becomes part of the species identity as a synonym, whereas the use of a common name is a more living process of name emergence and “extinction”—the long-term unused name commonly disappears.

We found a positive correlation between species rank and numbers of scientific (Fig. 4A) and common names (Fig. 4B). It seems that the most economically significant pest species may be more affected by synonym proliferation. This pattern may be related to the fact that species with higher economic rank have been scientifically described earlier (Fig. 3). Indeed, we found negative correlation between DoFD and number of scientific ( $r = -0.41$ ,  $P < 0.001$ ) and common ( $r = -0.37$ ,  $P < 0.001$ ) names. It can thus be speculated that the more significant and earlier described species had more time to be “loaded” with more synonyms.

#### Number of Authors of New Stored Product Pest Species Descriptions

The dynamics of species description are inherently influenced by the number of taxonomists who study a particular taxonomic unit. Therefore, we compared the number of authors for the four main SPP groups. It was found that 117 authors participated in the description of 274 beetle species (ie one author described on average 2.3 beetle species); 25 authors participated in the description of 47 moth species (one author described on average 1.9 species); 11 authors participated in the description of 16 psocid species (one author described on average 1.5 species); and 43 authors participated in the description of 65 mite species (one author described on average 1.5 species). Interestingly, the vast majority of species were described by only one author, and there were only a few species described by more than one author (7 species of Coleoptera and Acari, 1 species of Lepidoptera and none of Psocoptera), which is contradictory to the actual trend (Bebber et al. 2014).



## Number of Eponyms and Toponyms in Stored Product Pests

Although it may not be immediately apparent, taxonomy is not a rigid field of biology, as evidenced by the current discussion regarding the role of species names in contemporary society, the appropriateness of certain species names, and the potential regulation by the International Code of Zoological Nomenclature (ICZN) (eg Ceriaco et al. 2023, Guedes et al. 2023, Pethiyagoda, 2023, Roksandic et al. 2023). Despite its historical roots, taxonomy is not static; it evolves with the integration of modern methods for species identification, particularly molecular techniques (Chua et al. 2023).

While Ceriaco et al. (2023) highlight the importance of nomenclature stability, ongoing debates question the ethical appropriateness of certain scientific names, particularly those derived from people (eponyms) and geographical areas (toponyms), seen as potentially “culturally offensive and inappropriate” in today’s context (Hammer and Thiele 2021). Ceriaco et al. (2023) estimate that around 20% of all animal names are eponyms, with an additional 10% being toponyms. However, the distribution of eponyms and toponyms varies among different groups. For instance, in Microgastrinae parasitoid wasps (Hymenoptera: Braconidae), even 42% of names are derived from people, and an additional 15% from geographical areas (Moghaddam et al. 2023).

We conducted a survey to explore the use of eponyms and toponyms in naming stored product beetles. Our findings reveal that 24 out of 274 species names (ie 8.8%) are derived from people (eponyms) and the same proportion, 24 out of 274 (8.8%), are derived from geography (toponyms). The majority of species, accounting for 82.4%, are named based on descriptive features (morphology, color), biology, or host plant (such as the associated crop, for instance). The relatively low number of toponyms may be attributed to many stored product beetles having a cosmopolitan distribution, not limited to a specific region; in many cases, the original place of their occurrence is unknown.

Regarding eponyms, we could hypothesize that their scarcity in SPP beetles is due to species being more commonly named based on biological characteristics, such as the type of crop they affect. This hypothesis gains support from the observation that the number of eponyms among stored beetles decreases with their economic significance. Specifically, in groups of stored beetles with different economic importance (in ascending order, ie rank 1–5), the proportion of eponyms is 12, 9, 6, 3, and 0%. However, such a dependency is not observed for toponyms, where their proportion in economic groups 1–5 is 10, 5, 8, 7, and 15%, respectively.

## Usage of Various Taxonomic Hierarchical Levels in SPP Practice

### Practical Usage of Species vs. Family Taxa

In the practice of quarantine and stored product pest management on farms/storage sites, the central unit of interest is mainly species. The same level was described (criticized) for applied aspects of global policies of biodiversity conservation and protection programs that are mainly focused on a particular endemic/endangered species and rarely on genus or even family (Myers 2003). Although specialized identification keys and identification guides of stored product pest insects are available based on family category (eg Hinton 1945, Halstead 1986, 1993), pest control practitioners usually do not focus much on the propinquity of a particular pest species to a particular family. There are at least three hypotheses for this. First, it may be because insect families (containing species associated with

storage environments) are too abundant; there are > 1000 insect families, and stored pests belong to > 120 families (Hagstrum and Subramanyam 2009). Second, families are highly vulnerable to many taxonomic changes. Specifically, the comparison of the current taxonomic family classification (Cai et al. 2022) related to SPP species with the most recent monograph of stored pests (Hagstrum and Subramanyam 2009) revealed at least 8 family changes in only the last 13 yr. For example, the former family Anobiidae became a subfamily of Ptinidae, the former Bruchidae became a subfamily of Chrysomelidae, the former family Scolytidae became a subfamily of Curculionidae, etc.

However, a more probable reason why practitioners usually do not focus on a pest’s family status is that the family category is usually not associated with such concrete and practical information as a species category. On the other hand, there may be exceptions, such as the work by Bosquet (1990), who relatively successfully attempted to describe the economic significance of insect-selected families that exclusively include all members/species with no direct effect on the commodity. For example, he summarized the general economic status for several families of scavengers and fungivores occurring in grain stores (eg Anthicidae, Cryptophagidae, and Latridiidae). The family characteristic was so general and comprehensive that there was no need to repeat it again under the description of each species. Despite this exemption, practitioners mostly use higher categories at the level of classes or orders because of their restricted numbers. Field agricultural pests feeding on fresh plants consist of multiple orders (Stejskal and Honek 2015), whereas the storage arthropods (Hughes 1961, Hagstrum and Subramanyam 2009, Hagstrum et al. 2013) feeding on dry or semi-dry food commodities are limited to only two classes (ie Arachnida/incl. Acarina/, and Insecta), and three insect orders (Coleoptera, Lepidoptera, Psocoptera). Food industry pests or food hygiene and nuisance pests and beneficial (ie pest-predatory and -parasitic) storage arthropods include six additional orders (Zygentoma, Blattodea/including Isoptera, Orthoptera, Diptera, Hymenoptera, and Heteroptera). Higher taxa categories are frequently used for the organization of pest species in various educational materials.

### Taxonomic Classification vs. Alphabetical or Functional Categorization in Practice

There are indications that many non-specialist students and practitioners, after basic training or a simple education (Cosme et al. 2020), are able to discriminate between some main species of arthropods or at least safely recognize their association with some of the main classes and orders (eg beetles, moths, cockroaches, etc.). This general elementary taxonomic knowledge and intuition enables many published applied books and popular booklets on stored product and food industry pests to be at least partially arranged according to higher-taxa categories (eg Hinton 1945, Munro 1966, Hill 2002, Nawrot and Klejdysz 2009). However, some books are exclusively arranged in alphabetical order according to English names of insect families and species (eg Rees 2004). The illustrated key and guide by even listed the families and stored product pest species in alphabetical order solely according to the scientific names. The Canadian grain commission provides pictures and descriptions of pests at its web page that are divided into so-called “primary or secondary categories” of stored product pests; within these functional-practical categories, the species are further arranged alphabetically by order, family, and scientific name (<https://www.grainscanada.gc.ca/en/grain-quality/manage/identify-an-insect>). Other books, book chapters and atlases do not use any specific higher categories

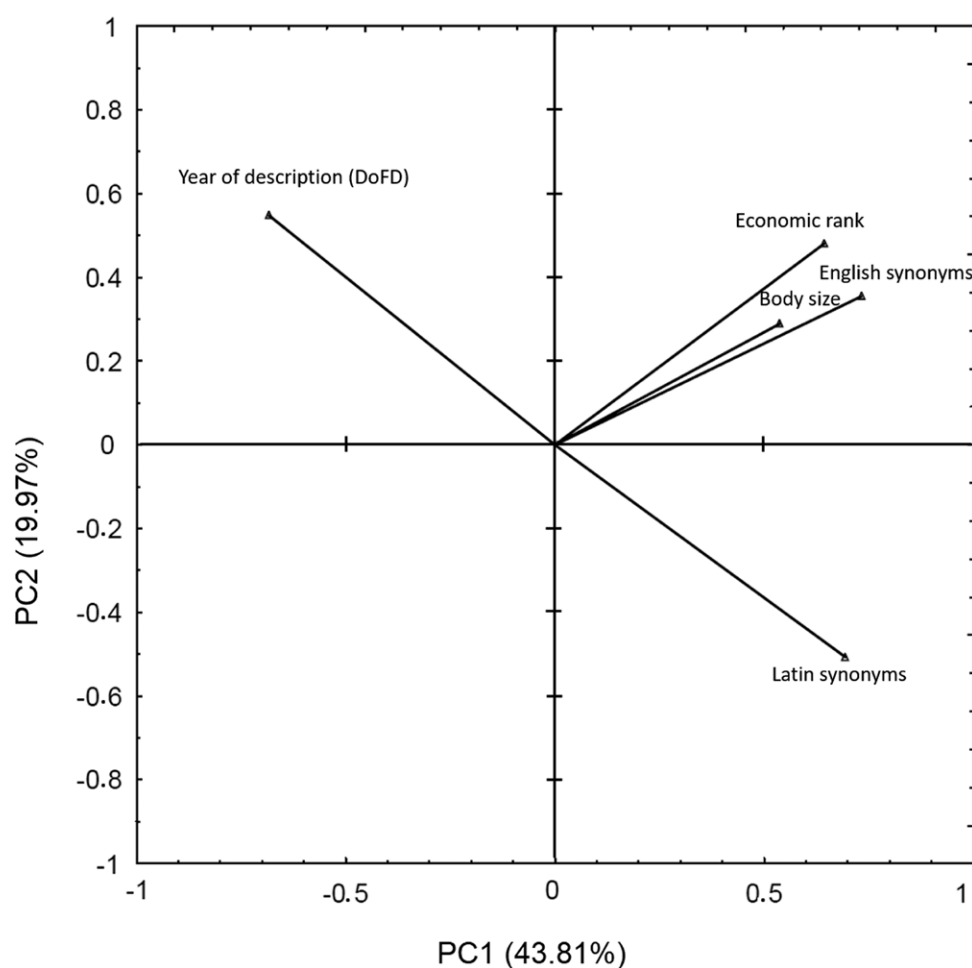
and rely on organizing and presenting individual species (Sinha and Watters 1985, Hagstrum et al. 2013) or families (Navarro and Navarro 2018) of stored product arthropods exclusively based on their alphabetical order.

The practical advantage of such an approach is that the alphabetical categorization excludes a priori conditions of knowledge regarding pest categorization into higher taxa or functional categories of non-biologically oriented readers. Some books combined taxonomic with other categorization criteria or order stored product species according to their economic importance from the most to the least important. Campbell et al. (2004) grouped stored product pest arthropod species into eleven (A–K) categories based in part on the traditionally used USDA resource (ie Agriculture Handbook Number 500): A. -Grain weevils; B. - Grain borers; C. - Grain moths; D. - Grain and flour beetles; E. Mealworms; F. - Dermestid beetles; G. Spider beetles; H. Miscellaneous I. - Flour moths, J. -Psocids; and K.- Mites. The most intuitive approach to functional categorization of stored product pest species of Coleoptera was suggested by Bosquet (1990), who grouped illustrations of stored product species according to their general morphological habitus. He suggested 7 basic categories regarding their habitus (eg category—“Spider like beetles”). The latter is similar to an approach used by ecology specialists known as the morpho-species concept. Such simplified “functional taxonomy” or “parataxonomy” approaches (Basset et al. 2004) are used in cases where individual species cannot be

assigned to scientifically rigorously named species (Lawton et al. 1998, Hamilton et al. 2010).

## Impacts and Solutions

The review documented the multifaceted challenges and implications of taxonomic changes, specifically focusing on species name revisions and synonyms, for applied entomology and pest control. These changes, while essential for scientific precision, may create barriers to accessing historical information and communicating effectively with stakeholders. In particular, the “password” phenomenon refers to the critical role species names play as keys to accessing historical information. Changes in nomenclature can disrupt access to older literature and databases, creating challenges for stakeholders, including pest control professionals, applied entomologists, and the food industry. Taxonomic changes may have direct consequences for pest management, where accurate identification and historical data access are essential. For instance, pest control professionals rely on consistent species names to implement effective measures, and disruptions caused by name changes can lead to miscommunication and inefficiencies. Similarly, farmers and other stakeholders may struggle to integrate new nomenclature into existing practices, potentially hampering pest management efforts. While students can be educated to navigate this issue, it is significantly harder to ensure effective knowledge transfer to pest control practitioners and food



**Fig. 5.** The principal component analysis describing the relationship between the date of first description (DoFD), economic importance (rank), number of scientific (Latin) and common English names (synonyms), and body size of SPP species.

industry facilities, who may lack the awareness, tools, or time to adapt to these changes. Morrison et al. (2009) documented three potential outcomes of taxonomic change: positive impacts on species reach and endangered species protection efforts, hampering impacts, or no measurable effect. Although taxonomic splits may enhance conservation efforts, name changes often have the least impact on charismatic organisms. Although there may be a similar differential influences on key (“charismatic”) or less, important pest species the real impacts remain to be analyzed in the future. Nevertheless, the potential negative impacts should be addressed and mitigated before such analysis will be available.

To mitigate these challenges, several solutions should be implemented. Publicly available synonym lists, such as those incorporated into platforms like the ESA common names database or ITIS (Integrated Taxonomic Information System), can bridge the gap between historical and current names. Training and education are essential; students in applied entomology should be taught to work with historical synonyms and understand the evolution of taxonomy. Creating custom synonym lists and employing automation tools, such as Python scripts, can further aid systematic research. Advanced search techniques, including training on platforms like Google Scholar or BioOne and using advanced queries with historical and current synonyms, can improve access to archival texts. Visualization tools like Gephi can map synonyms, providing a clear representation of the relationships between historical and modern names. Database support and funding from ministries and relevant institutions are critical for developing national and international projects aimed at creating comprehensive pest synonym databases, with platforms like GBIF (Global Biodiversity Information Facility) and ITIS playing a central role. Additionally, artificial intelligence technologies, such as BioBERT for analyzing biological texts, can automatically link historical synonyms to modern names, enhancing the efficiency of accessing relevant information from extensive datasets. Textbooks, web media, and databases should include dedicated sections addressing the implications of name changes, while collaboration with experts on platforms and utilizing community resources can increase the likelihood of finding accurate information. Regular updates to pest control guides and training materials should reflect the latest taxonomic advancements to ensure they remain relevant and effective. Moreover, awareness among students and practitioners must be increased to acknowledge that this issue exists and to account for it in their work, ensuring they are prepared to navigate and address these challenges effectively.

## Conclusions

The correct identification of stored product pests is important for several reasons. The ecology, biology, or physiology of closely related species may differ substantially, which may imply the need for different modes of chemical/physical control of the species. Species identification is tightly connected with taxonomic classification, whose focal unit is the species binominal name. It serves as a “password” to unique information resources and thus permits the acquisition of species information. However, the usage of such unique “passwords” is complicated by the existence of many scientific (Latin/Greek) and common names (synonyms). We made an inventory of synonyms of stored product pests and showed that the number of synonyms (and consequent possible difficulties with finding species information) is not random. First, it positively correlates with the species economic significance. Thus, paradoxically, in the most important SPP species, it may be more difficult to obtain complete information (if only one of its many names is entered as a keyword into automated web

search engines or electronic databases) due to a higher number of synonyms. It also seems that earlier described pest species have more synonyms than those recently described.

In accordance with studies on various animal and arthropod taxa (Costello et al. 2015), we found that the DoFD is dependent on body size in stored product pests. Concretely, Lepidoptera and Coleoptera SPPs with larger body sizes were on average described earlier than the smaller SPP species belonging to Psocoptera and Acari. This trend was found not only among orders but also within Coleoptera. In addition to body size, it was newly revealed that another factor influencing the date of first descriptions is the level of damage potential (or economic importance) of the species, as the most damaging species were described on average earlier than the less important ones. Apparently, several factors influence a species DoFD. To visualize the correlation structure of these factors and the average DoFD, we performed principal component analysis (PCA) with the DoFD, economic rank, scientific and English names, and body size of the species as variables. As a result, the PCA contrasted DoFD against all other factors that were positively correlated (Fig. 5). The elucidation of the factors influencing DoFD may play an important role in the prediction of discovering new SPP species (Costello et al. 2015). Based on our survey nonbiologically, it can be predicted that in the future, there will be a new description, especially of small-bodied mite, psocid, and beetle species with relatively low economic significance.

Difficulties posed by the existence of synonyms are restricted not only to the species level but also to higher taxonomic units. We found that in the case of stored product pest beetles, at least 8 changes occurred at the family level during the last 13 yr, which may be confusing when searching for information in pest databases, books and other resources. Although the review was primarily focused on SPP species, the authors believe that many aspects that were presented herein may also have implications for general and applied entomology.

The issue of taxonomic changes extends beyond scientific communities, potential impacting students, pest management, farmers, and food facility stakeholders. Addressing the fluidity of “name-password” phenomenon through comprehensive solutions, education, and advanced technologies is essential for ensuring the continued effectiveness of pest control practices. Stakeholders must be equipped with tools and resources to adapt to these changes seamlessly, minimizing disruption and enhancing the integration of new scientific knowledge into applied fields. Students and practitioners need to be made and trained more aware of this issue, enabling them to recognize its existence and incorporate it into their work, ensuring they are equipped to handle these challenges effectively.

## Supplementary material

Supplementary material is available at *Journal of Insect Science* online.

## Acknowledgments

This work was supported by the Ministry of Agriculture Czech Republic grant number VZRO0418 and by Chinese project No. 2018YFE0108700. The language proofreading was partially funded by the Ministry of Education, Youth, and Sports ‘Strengthening strategic management of science and research in the CRI’ project grant number CZ.02.2.69/0.0/0.0/18\_054/0014700. We are grateful to Jiri Skuhrovec for critical comments on an earlier version of the manuscript.

## Author contributions

Vaclav Stejskal (Conceptualization [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Supervision [equal], Writing—original draft [lead], Writing—review & editing [lead]), Tomas Vendl (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Shiqian Feng (Writing—original draft [equal], Writing—review & editing [equal]), Yujia Qin (Writing—original draft [equal], Writing—review & editing [equal]), Radek Aulicky (Project administration [equal], Resources [equal], Writing—original draft [equal], Writing—review & editing [equal]), and Zhihong Li (Conceptualization [equal], Supervision [equal], Writing—original draft [equal], Writing—review & editing [equal])

*Conflicts of interest.* None declared.

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