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To cite this version:

Andrea Battisti, Andre A. Walker, Mizuki Uemura, Myron P. Zalucki, Anne Sophie A. S. Brinquin, et al.. Look but do not touch: the occurrence of venomous species across Lepidoptera. Entomologia Generalis, 2024, 44 (1), pp.29-39. 10.1127/entomologia/2023/2295 . hal-04520674

HAL Id: hal-04520674
https://hal.inrae.fr/hal-04520674v1

Submitted on 25 Mar 2024

Entomologia Generalis
Published online February 2024

Open Access
Early Access Review Article

Look but do not touch: the occurrence of venomous species across Lepidoptera

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With 2 figures and 3 tables

Abstract: Lepidoptera can cause several health issues in humans and domestic animals due to their setae, which are defensive adaptations that protect them from predators. The diversity of venomous Lepidoptera has been explored in several reviews starting from the first comprehensive attempt in 1984 by Kawamoto and Kumada (KK) who compiled a list of 228 species based on previous reviews; however, KK did not cite the original publications for listed species. In this review we validated and updated the KK table. The updated list of venomous Lepidoptera includes 5 superfamilies, 14 families, 208 genera, and 576 species, representing a two-fold increase for genera and 2.9-fold for species with respect to KK. The total number of species in the genera including at least one venomous species, which we argue is likely closer to the true number of venomous species, is 7 times higher (3,620). GBIF (Global Biodiversity Information Facility) occurrences for venomous species are 1–4 orders of magnitude higher than those of confamilial non-venomous species. The presence of venomous structures is independent of the relatedness of the clades or geographic region; venom is produced by many species of Zygaenoidea, Lasiocampoidea and Bombycoidea but only by some specialized groups in Papilionoidea and Noctuoidea. There are likely to be multiple evolutionary origins of venom within Lepidoptera, but the exact number is difficult to estimate. The knowledge gap between medical and natural history fields needs to be addressed with novel approaches to study ecology and toxicology. This review offers health practitioners a tool to better understand the origin of the reactions observed and to improve the identification of the causal agents.

Keywords: defence; hair; health; predation; seta; spine; toxin; urticaria

1 Introduction

Several Lepidoptera are known for the ability to inject venom into human and animal tissues, causing various types of adverse reactions. Venomous Lepidoptera have been known since prehistoric times as a contaminant of silk textiles produced from Lepidoptera in Africa (Pomeroy 1921) and used in initiation practices in tribal populations of South America (Rotberg 1971). The existence of venomous Lepidoptera is acknowledged in earlier work of medicine, dating back to the time of Dioscorides (40–90 A.C.) and associated with the larvae of the pine processionary moth, *Thaumetopoea pityocampa* (Denis et Schiffermüller) (Notodontidae), which were used as a poison to murder people (Roques & Battisti 2015). Matthioli (1562) and Réaumur (1736) provided detailed descriptions of the link between the setae and adverse reactions, including accurate illustrations of the setae (Fig. 1). Since then, the awareness that Lepidoptera could represent a threat to human health has increased, with the pioneering work of Stargardt (1903) and many others to follow.

DOI: 10.1127/entomologia/2023/2295

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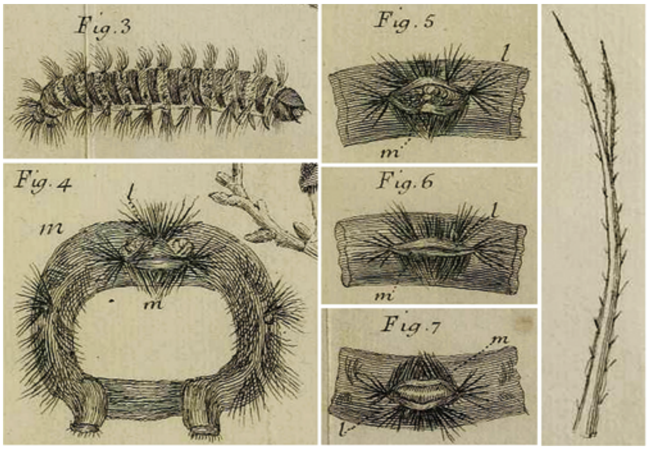

Fig. 1. Illustrations taken from Réaumur (1736) with the description of the larva of the pine processionary moth *Thaumetopoea pityocampa* ('Fig. 3') and the dorsal pads or integumental folds of abdominal segments 1–9. 'Fig. 4' shows a section of an abdominal segment of the larva with the representation of the integumental fold, closed in the figure. 'Fig. 5' details the integumental fold with the two sides 'l' and 'm' open, showing cottonwool like matter inside. 'Fig. 6' details the integumental fold with the two sides 'l' and 'm' closed. 'Fig. 7' details the integumental fold with the two sides 'l' and 'm' open, and the cottonwool like matter removed. Setae shorter than normal ones are aligned on both sides of the pad and are likely the urticating or venomous setae drawn at right, not described in the caption of the original plate although presented at pp. 155–156 of the text, where it is reported that the setae are numerous and detachable.

Despite a growing body of literature on the medical importance of venomous Lepidoptera, the biological and ecological roles of these defensive systems have remained largely understudied. Lepidoptera produce at least 11 types of defensive setae ranging from easily detached miniscule hairs to hollow spines filled with liquid venom. Battisti et al. (2011) defined true setae (detachable) and modified setae (non-detachable) as derived from the typical insect hair, while spines are more complex structures occurring in much lower density. True setae, modified setae, and spines are considered to be urticating, i.e., able to induce an adverse sensation or reaction in another animal, and are thought to do so through the delivery of chemical toxins or allergens, which is the defining character of venoms (Fry et al. 2009). While the diversity of these different systems deserves further investigation and clarification, this review focusses on occurrence of urticating species across Lepidoptera, and hence we use urticating and venomous as interchangeable terms below.

It has been assumed that hairs or setae of Lepidoptera larvae may deter vertebrate predators (Buckner 1966) while there could be predators specializing on hairy and venomous larvae (Barbaro & Battisti 2011) and moths (Collins & Watson 1983). The difficulties encountered in detecting the effects of venomous structures of Lepidoptera on predators considerably limit the information available on the ecology and evolution of these defensive systems, as no other function has been hypothesized so far (Battisti et al. 2011). There is, however, limited experimental evidence that venomous setae protect from parasitoids (Kageyama & Sugiura 2016), as well as invertebrate and vertebrate predators (Murphy et al. 2010; Sugiura & Yamazaki 2014; Uemura et al. 2017).

The diversity of the venomous Lepidoptera has been explored in several reviews, all of them based on medical or veterinary evidence of impact. The first overviews of the species known to be associated with reactions in humans were produced by Weidner (1937) for the Palaearctic, Pesce & Delgado (1971) for the Nearctic, and Southcott (1978) for the Australian realm. The biology and venoms of Lepidoptera were last comprehensively reviewed by Alexander (1984) and by Kawamoto & Kumada (1984). The latter (abbreviated in this paper as KK) provided a list of 228 irritating species, including their geographic distribution, compiled based on previous reviews and original publications that were not associated with species listed in their main table. The KK list has been used as the main reference by all more recent reviews and compilations, which mainly address the medical aspects of venomous Lepidoptera. These reviews (Diaz 2005; Hossler 2009 and 2010ab, Villas-Boas et al. 2018; Mullen & Zaspel 2019; Seldeslachts et al. 2020) occasionally added a few more species that had appeared in the literature. Simultaneously, a large body of information was reviewed in South America for Lepidoptera of medical importance (e.g., Specht et al. 2004, 2005a, 2005b, 2006, and many other regional studies), which unfortunately has not been incorporated in the recent reviews (ibidem).

The focus of this paper is to validate and update the KK table. The medical and veterinary impacts will not be reviewed because they require a specific analysis, as well as the determination of the nature of the toxins associated with the hairs. The aim is to provide an updated list of venomous species, to explore their distribution within Lepidoptera families, to discuss the biological and ecological importance of defensive hairs and provide guidance to medical and veterinary practitioners on important information that needs to be collated as evidence of venomous reactions.

2 Methods

The KK table of irritating Lepidoptera (Kawamoto & Kumada 1984) was used as a starting point, as it summarizes all the reviews available in 1984. Another review published in the same year (O' Donel Alexander 1984) and more recent reviews (Vassal 1989; Hossler 2009; Villas-Boas et al. 2018; Mullen & Zaspel 2019) that built on the KK table were also used, and species added accordingly. Firstly, the species names were updated by searching on the Global Biodiversity Information Facility (GBIF Secretariat 2023) to the currently accepted names. Secondly, as the KK table does not provide references to justify the purported medical effects for each species mentioned, Google Scholar was searched using the terms "genus name and urtic*" and "genus name and venom*", to identify the original literature for each species mentioned in the KK table and to find additional species. Thirdly, instead of blindly following the order of a 'systematic search', papers resulting from the Google Scholar search were thoroughly scrutinized to identify any issues with the former attribution of the species to the category. This often resulted in genera and species being dropped or added to the list. To estimate the overall number of venomous lepidopteran species beyond those that have been specifically reported in the literature, we considered species congeneric to those reported as venomous as likely to be venomous. The assumption has been previously validated for important genera of venomous Lepidoptera such as *Euproctis* (Kawamoto et al. 1978) and *Thaumetopoea*.

Fourthly, for each genus identified as containing at least one species of medical importance, occurrence records for all species in that genus were extracted from GBIF (GBIF 2023). Although this database is not complete and geographically heterogenous (e.g. Garcia-Rosello et al. 2023), a preliminary analysis of searching for venomous species of Lepidoptera in different parts of the world showed that the results were satisfactory for the review work. To improve data consistency, we only used records with accepted taxonomic names at the species level. Records without geographic coordinates or specimens derived from molecular sequences (unranked records) were discarded. The number of occurrence records was then compared with those of species not belonging to venomous genera in each family. The frequency of venomous species at family level was then plotted on the most up-to-date phylogeny of Lepidoptera based on genomic data (van Nieukerken et al. 2011; Kawahara et al. 2019; Mayer et al. 2021).

Biological and ecological information related to the venomous stage, the type of offending hair (true seta, modified seta, spine), the native distribution, the host plant, the solitary/gregarious behaviour, the occurrence of outbreaks, was summarized at family level based on literature and the HOSTS database (Robinson et al. 2023).

3 Updated species list, phylogeny and bio-ecology of venomous Lepidoptera

3.1 Venomous Lepidoptera list update

The list of venomous Lepidoptera includes 5 superfamilies, 14 families, 208 genera and 576 species (Table 1 and Supplementary Appendix 1). These results represent a

Table 1. List of venomous Lepidoptera identified in the review of Kawamoto & Kumada (1984) and those retrieved in the current review. Superfamilies and families are listed according to the phylogenetic order (van Nieukerken et al. 2011; Kawahara et al. 2019; Mayer et al. 2021).

Superfamily and Family	Total number (van Nieukerken et al. 2011)		Number of venomous taxa			
			K&K 1984 (verified)		Present review	
	Genera	Species	Genera	Species	Genera	Species
Total number of taxa			103	200	208	576
Zygaenoidea (12 families)	**500**	**2954**	**35**	**54**	**84**	**187**
Limacodidae	301	1672	24	34	59	105
Megalopygidae	23	232	4	12	4	19
Aididae	2	6	1	1	2	5
Somabrachyidae	4	8	0	0	2	2
Zygaenidae	170	1036	6	7	17	56
Papilionoidea (7 families)	**559**	**6152**	**5**	**10**	**10**	**18**
Nymphalidae	559	6152	5	10	10	18
Noctuoidea (6 families)	**3739**	**41879**	**29**	**71**	**55**	**161**
Notodontidae	704	3800	6	15	9	28
Erebidae	1760	24569	21	47	44	124
Nolidae	186	1738	1	1	1	1
Noctuidae	1089	11772	1	8	1	8
Lasiocampoidea (1 family)	**224**	**1952**	**16**	**24**	**26**	**83**
Lasiocampidae	224	1952	16	24	28	83
Bombycoidea (10 families)	**231**	**2782**	**18**	**41**	**33**	**127**
Eupterotidae	53	339	1	1	2	2
Anthelidae	9	94	1	1	2	4
Saturniidae	169	2349	16	39	29	121

two-fold increase for genera and 2.9-fold increase for species compared to the KK table, while the superfamilies remained the same and the families increased by one-fold (Somabrachyidae, Zygaenoidea).

The 576 species recognized as venomous, although greater in number than the estimate from previous reviews, are much smaller than the total number of species included in the genera with at least one venomous species identified, i.e., 3,620 (according to current accepted species in GBIF). There are good reasons to believe that this larger number is closer to the actual number of venomous Lepidoptera. While not necessarily true in every single case, examination of well-studied genera show that they usually share the same defensive traits, as shown by analysis of some genera such as *Thaumetopoea* (Basso et al. 2017), and in the general morpho-physiological traits shared at the genus level (Burns & Strauss 2011). The lack of literature records for many species that are likely to be venomous can be explained by: i) The high diversity of species in a genus (e.g., 195 species known in *Euproctis*, 174 in *Acronicta* and 90 in *Hylesia*), with several of them being rare, their taxonomy in need of further study, and their biology poorly characterized; ii) The lack of accurate identification of urticaria-causing species, which are often assumed to be the species previously reported to cause envenomation; and iii) The difficulty in relating clinical symptoms to the causing agent, especially when there is a time lag between exposure and manifestation, or when the venomous agent is dispersed in the environment (Battisti et al. 2011).

Two main factors must be considered when interpreting the medical and veterinary reports of impacts caused by Lepidoptera species, which are strictly related to the nature of the venomous seta. When the setae are attached to the integument (spine and modified seta), the reaction (pain) is immediate and generally associated with the identification of the agent that can be later assigned to a specific taxon. If the seta is detachable (true seta), the reaction (irritation) is somewhat delayed, with the exception of sensitive individuals. In such cases, it may be difficult to link the symptom to the exposure, in both presence and absence of contact with the insect. Adding further complexity to the situation, the modified and true setae produced by the larvae are often embedded in the cocoon (typically in Lasiocampidae, but also in other families). Setae are also produced by female moths to envelop egg masses in certain families such as Erebidae, Notodontidae, Saturniidae, and Zygaenidae. Contacts with cocoons and egg masses are another source of exposure that is difficult to assess. In addition, the larvae of some families (e.g., Limacodidae) may simultaneously carry three types of setae (e.g., Faucheux 2000) that may induce distinct symptoms. The medical literature is full of syndromes associated with the exposure to caterpillars, cocoons, moths, and eggs (e.g., Pesce & Delgado 1971; O' Donel Alexander 1984; Mullen & Zaspel 2019). However, it is important to clarify that reactions should be linked to the responsible seta more than the developmental stage of the Lepidoptera. We still know very little about the diversity of the setae associated with Lepidoptera and their occurrence among developmental stage and species within and among families.

The analysis of GBIF occurrences per species reveals a notable contrast between genera that include venomous species and those that do not within the same superfamilies. Genera containing at least one venomous species are observed much more frequently than their non-venomous counterparts, regardless of their taxonomic placement (Table 2 and Appendix 1). The differences can range from 1 to 4 orders of magnitude. This disparity may result from their importance as causing health problems and from traits that make venomous species particularly interesting for the entomologists and the general public, which will be discussed in the next paragraphs. Clinical symptoms in humans are unlikely to be closely connected with the primary function of these setae as defensive adaptations since humans are not the main predators of caterpillars. Nevertheless, there are well documented case studies of the effect of setae on humans: pine processionary moths (*Thaumetopoea* spp.) in Europe (e.g., Battisti et al. 2011 and 2017), bag-shelter moths (*Ochrogaster* spp.) in Australia (e.g., Cawdell-Smith et al. 2012; Walker et al. 2023a), and saturniid moths (*Hylesia* spp. and *Lonomia* spp.) in South America (e.g., Villa-Ruano et al. 2023; González et al. 2023), to name just a few examples. The number of taxa capable of causing subtle adverse effects is greatly underestimated. The emphasis on medical effects has led to the oversight of many relevant aspects of the ecology and biology of these species, which are crucial for assessing the risks associated with these species.

3.2 Venomous taxa in the phylogeny of Lepidoptera

Venomous Lepidoptera are generally characterized by medium to large body size and they are not found in the basal taxa of Ditrysia as well as in other clades consisting predominantly of small or small to medium size Lepidoptera (e.g., Gelechoidea and Pyraloidea) (Table 3). Among superfamilies characterized by larger body size, they are only absent in Geometroidea (Fig. 2). In the other superfamilies, venomous larvae are present occasionally (Papilionoidea) or in about half of the families. Species that are venomous in the moth stage are restricted to one family of Zygaenoidea, two families of Noctuoidea and one family of Bombycoidea (Table 1 and Fig. 2).

When the percentage of genera including at least one venomous species, either as a larva or moth, is considered over the total number of genera in a family, large differences appear among superfamilies (Fig. 2). The families included in Zygaenoidea, Lasiocampoidea and Bombycoidea have higher percentages of venomous genera than those in Papilionoidea and Noctuoidea. Although the results are

Table 2. Number of occurrences in the GBIF database (accessed on 18th August 2023) for species belonging to venomous genera (e.g., with at least one species venomous in the genus) and for species in genera not known to be venomous in each superfamily and family of venomous Lepidoptera.

	Number of GBIF occurrences		
	per species in venomous genera	**per species in non venomous genera**	**ratio venomous / non venomous**
Zygaenoidea	**789.4**	**85.6**	**9.2**
Limacodidae	352.4	31.0	11.4
Megalopygidae	337.1	19.0	17.7
Aididae	85.0	38.0	2.2
Somabrachyidae	7.5	2.0	3.8
Zygaenidae	2003.5	186.8	10.7
Papilionoidea	**89662.3**	**369.9**	**242.4**
Nymphalidae	89662.3	369.9	242.4
Noctuoidea	**7272.3**	**23.1**	**315.5**
Notodontidae	2939.7	0.7	4219.4
Erebidae	6356.4	32.5	195.4
Nolidae	3836.5	133.8	28.7
Noctuidae	128353.0	13.9	9223.9
Lasiocampoidea	**3811.4**	**32.7**	**116.4**
Lasiocampidae	3811.4	32.7	116.4
Bombycoidea	**321.1**	**16.0**	**20.1**
Eupterotidae	82.5	0.3	241.8
Anthelidae	1839.0	47.8	38.5
Saturniidae	300.0	17.0	17.6

biased by the limited knowledge of the actual occurrence of venomous structures in the taxa, the difference is striking and warrants careful consideration. It seems that the presence of venomous structures is a shared trait in many Zygaenoidea, Lasiocampoidea and Bombycoidea, while it occurs only in some specialized groups in Papilionoidea and Noctuoidea. Interestingly, in those specialized groups (e.g., Arctiinae and Lymantryiinae in the Erebidae, and Thaumetopoeinae in the Notodontidae), the occurrence of venomous structures is present in almost all the species considered so far.

The presence of venomous structures is independent of the relatedness of the clades and on the geographic region of the different groups, indicating that it is a trait that has evolved independently several times, presumably under similar selection conditions. The recent analyses of toxins produced by closely related families of Zygaenoidea show that those of Limacodidae likely have an independent origin from those of Megalopygidae (Walker et al. 2021 and 2023b). A thorough analysis at the level of superfamilies or families could shed light on how the venomous traits have evolved. The occurrence of venomous setae in a fossil first instar noctuid larva is known since the Eocene (45–55 million years ago) from Baltic amber (Poinar & Vega 2019), although more data would be required to formulate precise hypotheses about the origin of this defence system of Lepidoptera. It is likely that the evolution has been driven by predators, so a retrospective analysis should include these organisms and their putative relationships to the ancestors of the present-day venomous Lepidoptera. The detailed study of the toxins involved in the defence system of the various species may shed light on the evolution of the trait, as suggested by Walker (2020) and Walker et al. (2021 and 2023b). The lack of venomous species within a superfamily of large ditrysian Lepidoptera (Geometroidea) provides a valuable possibility to explore how natural selection has shaped the evolution of the defence structures in the order.

3.3 Biological and ecological significance

A few traits of venomous Lepidoptera that are important for their biology and ecology are summarized in Table 3. The larva is generally the stage producing venomous setae of three major types: true seta, modified seta and spine, according to Battisti et al. (2011), which can be present simultaneously on the same individual (e.g., some Limacodidae, Faucheux 2000) and generally increase in density/number with the larval instar (Perkins et al. 2016). The moths only produce true setae in the female anal tuft, which is present in only 4 out of the 14 families. In some genera, e.g., *Anaphe*

Table 3. Biological and ecological traits of venomous Lepidoptera.

Superfamily	Family	Wingspan (cm)	Stage	Seta	Native distribution	Hosts	Gregariousness	Outbreak	Major references
Zygaenoidea	Limacodidae	2–4	larva	spine, true seta	Africa, America, Asia, Australia	trees (broadleaved, occasionally conifers)	no	no	Lin et al. 2019; Cooley & Reardon 2022
	Megalopygidae	1–9	larva	spine	N C S America	trees (broadleaved)	no	no	Lambdin et al. 2000; Quintana et al. 2017
	Aididae	4–6	larva	spine	C S America	trees (Fabaceae, Myrtaceae, Rubiaceae)	no	no	Epstein 1995; Specht et al. 2005
	Somabrachyidae	4–5	larva, moth	spine, true seta	Africa	dry shrubs (fynbos), pine plantations	no	no	Epstein 1996
	Zygaenidae	2–4	larva, moth	modified seta, true seta	N America, Asia, Australia	herbaceous and woody (monocots and dicots)	early	yes	Tsutsumi 1959; Tarmann 2005
Papilionoidea	Nymphalidae	5–10	larva	spine	Asia, N C S America, Europe	herbaceous and woody (broadleaves)	no, early, late	local	Lambkin 2021; Galicia-Curiel et al. 2014
Noctuoidea	Notodontidae	2–12	larva, moth	true seta	Africa, Asia, Australia, Europe	trees (broad-leaved and conifers)	yes	yes	Battisti et al. 2017; Walker et al. 2023
	Erebidae	1–13	larva, moth	modified seta, true seta	Africa, N S America, Asia, Australia, Europe	herbaceous and woody	no, early, late	yes	Kawamoto et al. 1978; Balit et al. 2001
	Nolidae	1–3	larva	spine	Australia	trees (eucalypt)	late	yes	Southcott 1987; Derraik 2006
	Noctuidae	1–30	larva	spine	N America	trees (broadleaved)	no	no	Mullen & Zaspel 2019
Lasiocampoidea	Lasiocampidae	2–17	larva (+ cocoon)	modified seta	Africa, America, Asia, Australia, Europe	herbaceous and woody (broadleaves)	no, early, late	yes	Specht et al. 2006; Faucheux 2012
Bombycoidea	Eupterotidae	2–14	larva	true seta	Asia, Australia	trees (eucalypt)	yes	yes	Froggatt 1911; Sutantoyo & Dayrit 2015
	Anthelidae	2–16	larva (+ cocoon)	true seta	Australia and Australasia	trees (broad-leaves and conifers)	no	yes	Southcott 1978; Balit et al. 2004
	Saturniidae	3–30	larva, moth	spine, true seta	N C S America, Asia	trees (broadleaves)	no, early, late	yes	González et al. 2023; Villa-Ruano et al. 2023

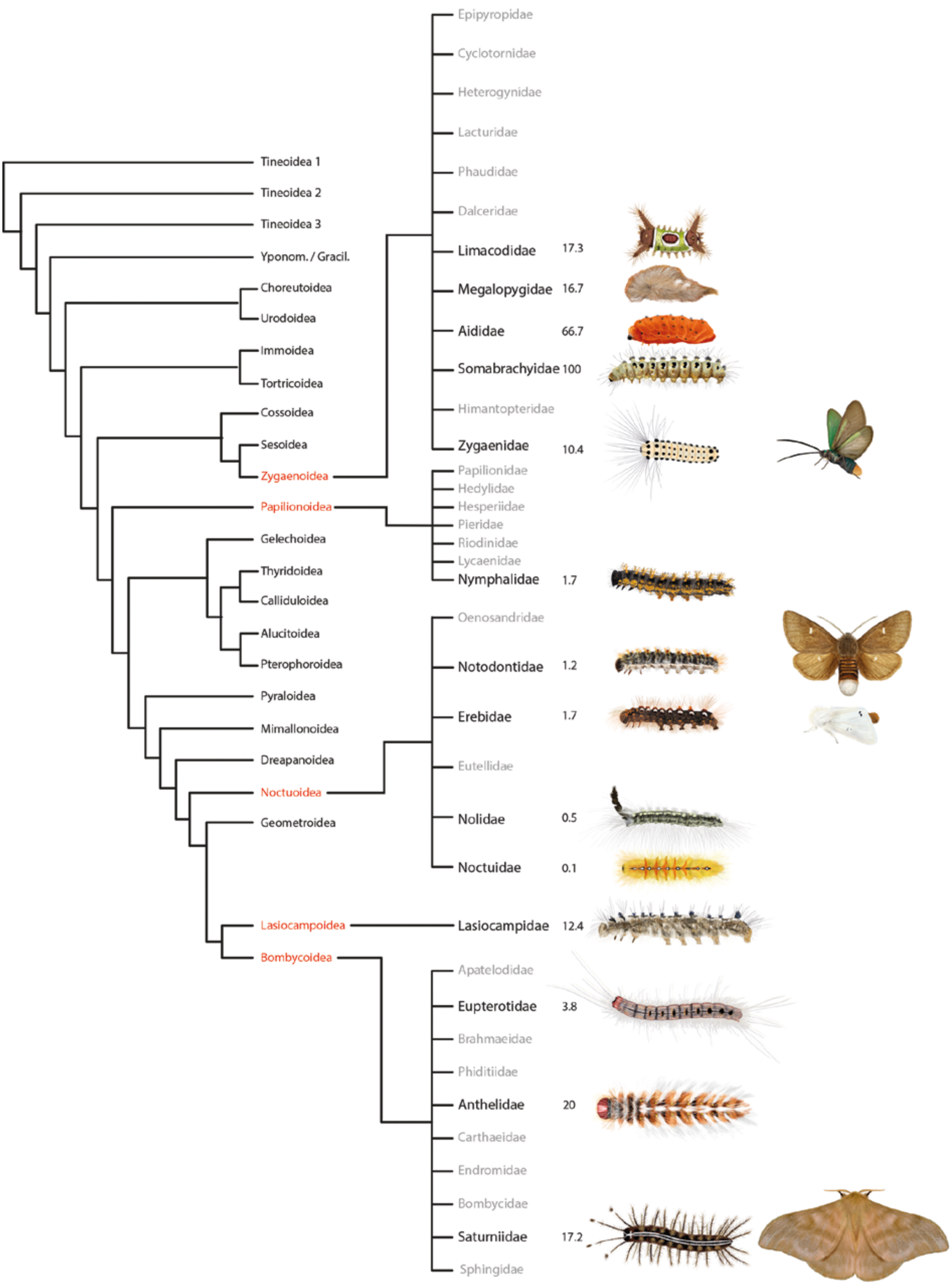

Fig. 2. Families of venomous Lepidoptera in the phylogeny of the order derived from van Nieukerken et al. (2011), Kawahara et al. (2019) and Mayer et al. (2021). The number after each family identifies the percentage of genera with venomous species. Examples of larvae and moths are presented whenever they occur.

(Notodontidae), venomous setae are only produced by female moths (Rotschild et al. 1970). While spines are restricted to the larvae, modified setae and true setae may be carried over to cocoons/pupae/adults and to the eggs/neonate larvae, indicating the dynamic and multifunctional nature of the defence.

Most of the venomous Lepidoptera are associated with mature, perennial communities of arboreal plants, irrespective of the biome, and very few are linked to herbaceous vegetation. This is not surprising as it is a common pattern in ditrysian Lepidoptera (Menken et al. 2010). There is a large variety of life habits, from solitary to strictly gregarious, both within and among families. The solitary species tend to produce more spines while gregariousness is often associated with true setae. The production of large egg masses is also associated with true setae produced by female moths. Gregarious species are known to produce population outbreaks more often than solitary species (Hunter 1991) but whether this is explained by the defensive setae remains unknown. Certainly, some gregarious and venomous Lepidoptera are among the most frequently outbreaking species (Koricheva et al. 2012).

4 Conclusions and future issues

There is a large gap in knowledge on venomous Lepidoptera between the medical and the natural history fields. The disparity can be explained by the different level of knowledge in the two fields and the difficulties using the same language to link natural history with clinical outcomes. This review may offer the human and animal health practitioners a tool to better understand the origin of the reactions observed and to improve the identification of the causing agent. It is clear that the gap between the two fields of science can be filled only through a holistic approach. Firstly, this involves understanding the ecological role of the defensive structures, then explaining their diversity and evolution, and secondly, assessing their undesired impacts on humans and domestic animals. The difficulties associated with such an approach can be addressed by using the latest technology available for both behavioural and molecular studies. The diversity of defensive structures that have evolved over millions of years in Lepidoptera is certainly worthy of exploration to infer the role they could play in the evolution and life history of the order and to find molecules of interest for medical applications.

Acknowledgements: Davide Nardi for data extraction from GBIF. National History Museum Paris, Paolo Paolucci for drawing Fig. 2. The analysis presented in this document has been generated in part during expertise work carried out on behalf of the French Agency for Food, Environmental and Occupational Health & Safety (ANSES). We acknowledge support from the Australian Research Council through Discovery Project DP200102867. This paper is dedicated to Prof. Luigi Masutti on the occasion of his 90th birthday.

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Manuscript received: September 23, 2023
Revisions requested: December 3, 2023
Revised version received: January 2, 2024
Manuscript accepted: January 11, 2024

The pdf version (Adobe JavaScript must be enabled) of this paper includes an electronic supplement:
Appendix 1