



Predator palatability in two Neotropical species of Sepsidae (Diptera, Sciomyzoidea)

Palatabilidade de predadores em duas espécies neotropicais de Sepsidae (Diptera, Sciomyzoidea)

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Chemical defense consists of the usage of substances that can cause damage to the predator or repel their attacks. A few true fly (Diptera) species use chemical defenses and among the adult ones, these mechanisms have only been formally registered in the family Sepsidae. Some species of this family possess an abdominal gland (Dufour gland) that produces a substance with a characteristic and intense odor. This odor supposedly turns the sepsids unpalatable to their predators. However, there is no study testing this hypothesis with Neotropical species yet. Thus, the aim of this study is to verify if two neotropical species of Sepsidae (*Archiseopsis armata* and *Microseopsis armillata*) are unpalatable to invertebrate predators (jumping spiders, giant crab spiders, and mantises). The experiment consisted in offering specimens of sepsids (treatment group) and fruit flies (drosophilids; control group) to three species of predators. Furthermore, a study of the internal morphology of the two sepsid species has been performed to verify the presence of the Dufour gland. There has not been any significant predation difference between the sepsids and the control group, and the Dufour gland has not been found in both of them. This data suggests that both neotropical species of sepsids are not unpalatable.

Keywords: defense, fly, predation.

A defesa química consiste na utilização de substâncias que causam algum tipo de dano ao predador ou repelem seu ataque. Poucas espécies de moscas utilizam defesas químicas e, nos espécimes adultos, este mecanismo já foi formalmente registrado somente em espécimes da família Sepsidae. Algumas espécies dessa família possuem uma glândula no abdômen (glândula de Dufour) que produz uma substância com odor característico e intenso. Esse odor supostamente torna os sepsídeos impalatáveis para os predadores. Apesar disso, ainda não há nenhum estudo testando esta hipótese com a maioria das espécies. Desta forma, o objetivo do presente estudo é verificar se duas espécies neotropicais de Sepsidae (*Archiseopsis armata* e *Microseopsis armillata*) são impalatáveis para predadores invertebrados (aranha-saltadora, aranha-caranguejo e louva-a-deus). O experimento consistiu em oferecer espécimes de sepsídeos (grupo tratamento) e de drosofilídeos (grupo controle) aos predadores. Além disso, foi realizado um estudo da morfologia interna das duas espécies de sepsídeos para verificar a presença da glândula de Dufour. Não houve diferença significativa de predação entre os sepsídeos e o grupo controle e não foi encontrada a glândula de Dufour nas duas espécies. Estes dados sugerem que as duas espécies neotropicais de sepsídeos não são impalatáveis.

Palavras-chave: defesa, mosca, predação.

1. INTRODUCTION

Predation is one of the main selective pressures and, consequently, various aspects of behavior and morphology of the organisms evolved as an anti-predatory mechanism [1, 2]. Many defense mechanisms contribute significantly to avoid or reduce predation, among them, the chemical defenses, the use of noxious, irritants, or distasteful chemicals [3-6]. The chemical substances used in defense can be synthesized in the organism's body, mainly inside specialized glands, or

can be acquired through feeding [4, 6]. Some chemical compounds can attribute unpleasant taste/odor to its bearer, making it unpalatable, but some of these compounds can cause paralysis or even death [7-10].

Chemical defenses are widespread among the metazoans, in which they evolved independently many times in various lineages and, in terrestrial organisms, are quite common among insects [10]. However, the use of chemical defenses is little documented in Diptera species (true flies and mosquitoes), and taking only the adult phase into consideration, it has been recorded in one family of flies: Sepsidae or black scavenger flies [10]. Black scavenger flies are relatively small (body length 2 to 7 mm), usually black or dark brown colored (some species are reddish or orange) with an ant-like morphology [11, 12]. They are easily found in large quantities near feces or carcasses of medium to large-sized mammals in open and forested places [12, 13].

Certain studies have demonstrated that some species of Palearctic Sepsidae are unpalatable to spiders [14] and ants. Occasional observations also indicate that Palearctic species are unpalatable to a wasp species of *Vespula* genus and to predator flies of *Scathophaga* genus [15]. The unpalatability of sepsids seems to be caused by volatile chemical defenses produced by the so-called Dufour gland, which is attached to the rectum.

Sepsidae is composed of 38 genera and about 340 valid species [16], distributed through every biogeographical region, except the poles [12, 13]. Most studies and observations about Sepsidae palatability are based on species from the Old World of the *Sepsis* genus, especially *S. fulgens* (Meigen, 1826). The Dufour gland is absent in *Orygma*, *Ortalischema*, and *Toxopoda*, which are supposedly not unpalatable, indicating that the unpalatability is not widespread among the Sepsidae genera.

There have been registered 10 genera and 26 species in the Neotropical region [13], eight of which are exclusive of the Americas, which constitute a clade [17]. However, none of the Neotropical species have been used in palatability studies. Therefore, the aim of this study is to verify if two Neotropical species of Sepsidae, *Archiseptis armata* (Schiner, 1868) and *Microsepsis armillata* (Melander & Spuler, 1917), are unpalatable to certain kinds of predators.

2. MATERIAL AND METHOD

2.1 Acquisition of specimens and maintenance in laboratory

Sepsidae species used in this study were *Archiseptis armata* and *Microsepsis armillata*, which are relatively common and abundant, so they are easy to find in large quantities. They are widespread in the Americas, from the south of the USA (*M. armillata*) and Mexico (*A. armata*) to the southern part of South America [13]. The identification has been made utilizing the key to genera from Orezov (2010) [11] and the key to species from Silva (1993) [18]. The specimens have been collected in the garden of a residence and in the pasture areas in the campus of Universidade Federal Rural da Amazônia (UFRA), both located in the city of Belém, state of Pará, in the Brazilian Amazon. Most specimens in these places belong to one of the target species utilized in the present study.

The sepsids have been collected with an entomological net while they were flying near mammal (bovine and dog) feces and over a swine carcass. Then, they were transferred to small transparent plastic bags and transported to the laboratory in the research campus of Museu Paraense Emílio Goeldi (MPEG), Belém, Pará, Brazil, to be utilized in the experiments. Some specimens were killed by freezing, mounted on pinned card triangles, and deposited in the entomological collection of MPEG.

Specimens of the fruit fly (Diptera, Drosophilidae, *Drosophila* spp.), utilized as the control group, were collected with transparent plastic bags at MPEG, using rotten bananas and jackfruits as bait. Like many other species of true flies, fruit flies are not in the list of chemically protected species [10] and they have been widely utilized to feed caged predator animals [19-21].

The predator models used in this research were adult jumping spiders *Plexippus paykulli* (Audouin, 1826) (Araneae, Salticidae), third instar giant crab spider *Heteropoda venatoria* (Linnaeus, 1767) (Aranea, Sparassidae), and first instar nymphs of praying mantis *Stagmatoptera binotata* (Scudder, 1869) (Mantodea, Mantidae). The spiders were collected with transparent

plastic jars inside some residences in the urban area of Belém. The sepsids are rarely encountered inside the same residences where the spiders were collected, eliminating the possibility of the previous contact between these species. The previous contact between predator and prey was prevented with the praying mantises because all the nymphs used in the experiment were obtained from ootheca. All the predators were released at the same place when they have been collected after the experiments were carried out. The spiders and mantises were individually maintained in 250 ml plastic jars, containing grooves on the inner surface, which were made with sandpaper, to facilitate the adherence and locomotion of the predator specimens. Each jar had a 2cm diameter hole on its base, where food and water were inserted, which was closed by a piece of plastic sponge. The water was provided in small pieces of cotton and nymphs of *Schistocera nitens* (Thunberg, 1815) and *Orphulella concinulla* (Walker, 1870) grasshoppers were utilized as food, which were collected by sweeping vegetation with an entomological net in the research campus of MPEG. These two species have been utilized to feed caged specimens of tarantula spiders, whip spiders, scorpions, and lizards in MPEG laboratory, indicating that they are not unpalatably.

A glass test tube was used to transfer the flies (sepsids and drosophilids) from the sacs to the predator cage, avoiding contact with eventual physical damage to the flies.

2.2 Experiment

The jumping spiders and the praying mantis were divided into three groups of 15 individuals each. A group of each of the predator species received only drosophilids, the other received *A. armata* and the last one received *M. armillata*. The giant crab spiders were divided into two groups of 15 individuals. One received only drosophilids and the other received *A. armata*. Each predator specimen was only given one prey specimen (Figure 1).

Before the palatability test, the predators were left without food for 48 hours. Observations about predator-prey interactions were recorded during a period of 30 minutes after sepsids and drosophilids have been inserted in the predator cages. The experiment was conducted at room temperature (20 to 25 °C) in August to December 2016.

Both species of sepsids used in the study can be easily distinguished by their size since *A. armata* specimens are clearly bigger than *M. armillata* ones. Species confirmation of all sepsid specimens used in the study was carried out after the palatability tests under stereomicroscope through analysis of diagnostic characters on genital and/or fore-femoral ornamentation. Even specimens that were preyed upon were identified, because the predators, except for the praying mantises, usually did not damage the lower part of the abdomen where the terminalia is located, which is useful for identification. In the case of the praying mantises, the prey was removed from their raptorial legs with the help of a fine brush when they started to eat the abdomen. Thus, only male specimens of the two sepsid species were used in the experiment.

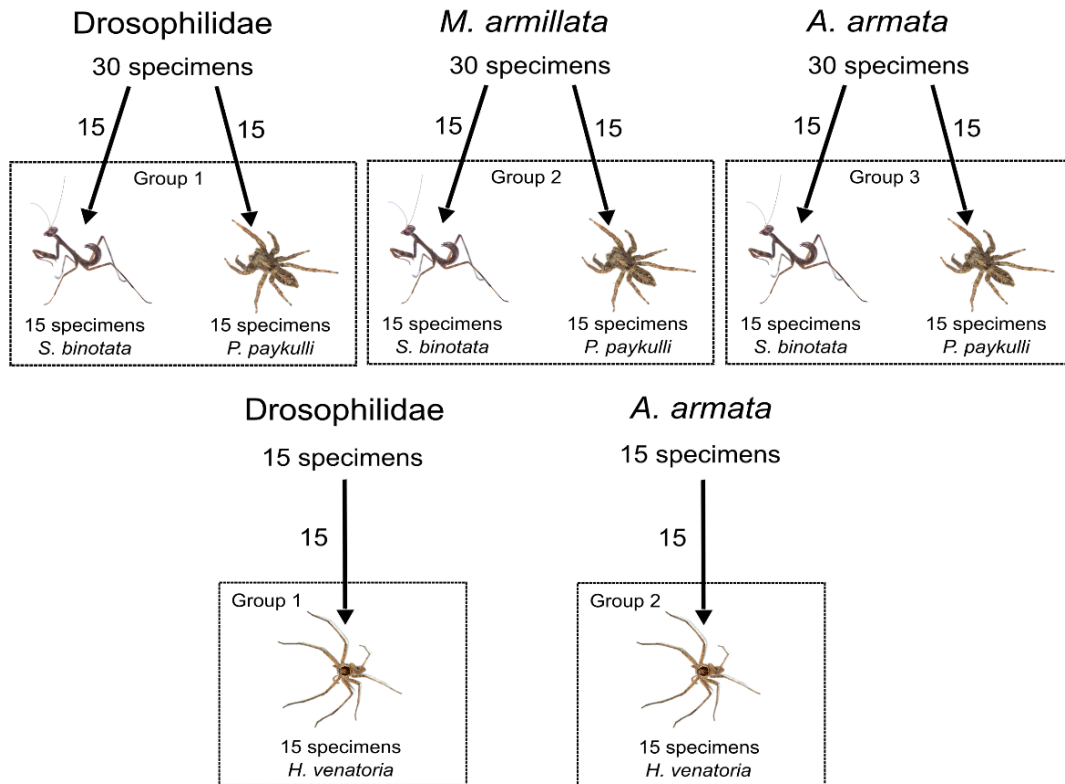


Figure 1: Schematic distribution of the specimens of Drosophilidae and Sepsidae (*Archiseopsis armata* and *Microseopsis armillata*) to model predators (giant crab spider (*Heteropoda venatoria*), jumping spider (*Plexippus paykulli*) and praying mantis (*Stagmatoptera binotata*) during the palatability test.

2.3 Data analysis

The registered behaviors of predators have been categorized and codified in numbers, starting with 0 (zero), where (0) is when the predator unsuccessfully attacked but stopped attacking soon after (unsuccessful attack), (1) when the predator successfully attacked and proceeded to consume the prey (successful attack); 2) when the predator does not react to the presence of the prey during the observation period (no reaction). The behavior (2) was removed from the analysis for a better evaluation of predation success. To evaluate the hypothesis that two Neotropical species of Sepsidae are unpalatable to certain kinds of predators, we used a Generalized Linear Model (GLM), using the quasibinomial family, since the residuals and the homogeneity of variances did not adjust in the binomial family. All statistical analyses were made on the R program, version 3.4.1 (R Core Team, 2017), and considered significant when $p < 0.05$. Finally, graphics were generated to demonstrate the predation of sepsids and the control group (drosophilids) for each type of predator.

2.4 Morphological analysis

In order to verify the presence of Dufour gland, 10 males and 10 females of *A. armata* and *M. armillata* (not used in the palatability experiments), were collected and killed by freezing. They were immediately transferred to petri dishes containing a drop of PBS (Phosphate buffered saline) mixed with glutaraldehyde 2%, where they were immersed. Later, the inner abdominal structures were dissected with micro styli and then, analyzed under a stereomicroscope to check for the presence of Dufour glands.

3. RESULTS

3.1 Palatability study

The behavioral categories of *S. binotata* toward *A. armata* and *M. armillata* were the following: “successful attack” and “no reaction”, and the first one was the most common (93,3%) (Figures 2 and 3). Regarding the drosophilids, three categories were observed: “successful attack” (86,7%), “unsuccessful attack” (6,6%), and “no reaction” (6,7%) (Figures 2 and 3).

Plexippus paykulli manifested three behavioral categories toward the *A. armata*: “successful attack” (73,3%), “unsuccessful attack” (6,7%), and “no reaction” (20%) (Figure 2). In relation to *M. armillata* and drosophilids, two categories were recorded: “successful attack” (80%) and “no reaction” (20%) (Figures 2 and 3). All *H. venatoria* specimens attacked and ate the *M. armillata* and fruit fly specimens (Figure 3).

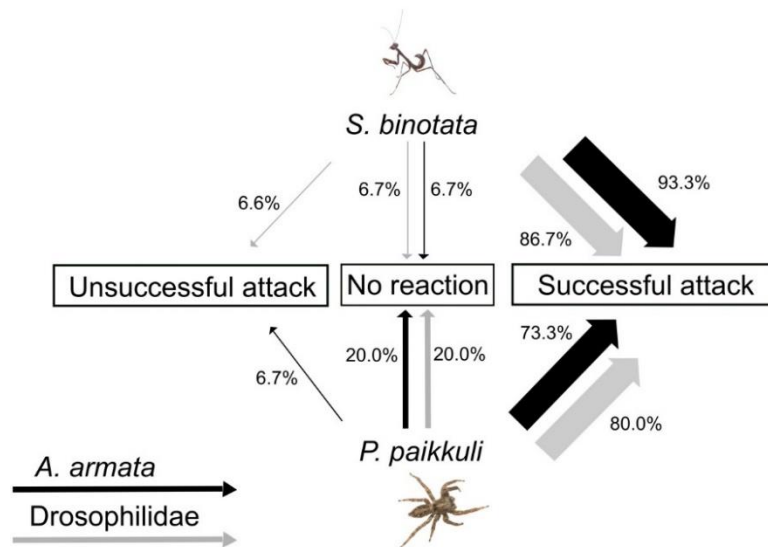


Figure 2: Fluxogram of the interaction between the predators (jumping spider (*Plexippus paykulli*) and praying mantis (*Stagmatoptera binotata*)) and *Drosophilidae* and the two species of *Sepsidae* (*Archisepsis armata*). Arrows indicate frequency. Black arrows indicate acts displayed by predators interacting with *Sepsidae*, and grey indicates acts displayed by predators with *Drosophilidae*.

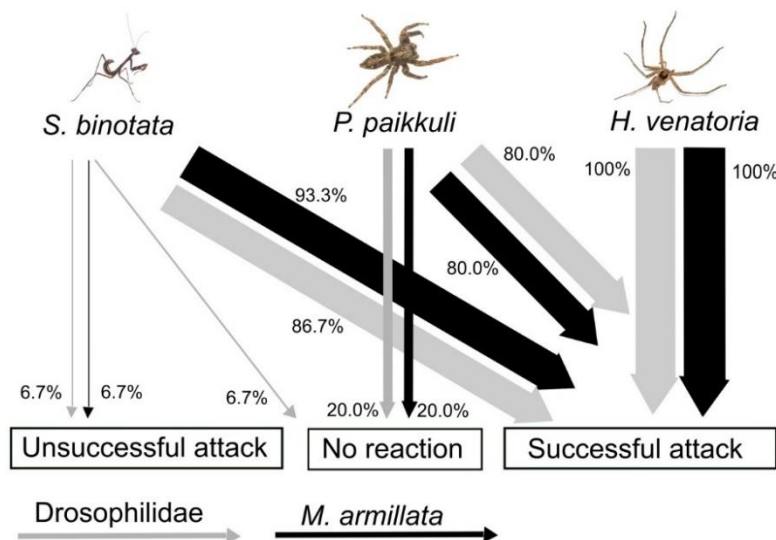


Figure 3: Fluxogram of the interaction between the predators (jumping spider (*Plexippus paykulli*), giant crab spider (*Heteropoda venatoria*) and praying mantis (*Stagmatoptera binotata*)), *Drosophilidae* and *Sepsidae* (*Microsepsis armillata*). Arrows indicate frequency. Black arrows indicate acts displayed by predators interacting with *Sepsidae*, and grey indicates acts displayed by predators with *Drosophilidae*.

According to the obtained data, there was no significant difference among the Drosophilidae and *A. armata* specimens consumed by *S. binotata* (Estimate = 1.423; df = 1; p = 0.116) and *P. paykulli* (Estimate = 1.429; df = 1; p = 0.119) (Figure 4), as well as among the Drosophilidae and *M. armillata* consumed by *S. binotata* (Estimate = 1.423; df = 1; p = 0.116), *P. paykulli* (Estimate = 1.272; df = 1; p = 0.152), and *H. venatoria* (Estimate = 0; df = 1; p = 1) (Figure 5). None of the predators demonstrated any repulsive behaviors upon contact with the sepsids.

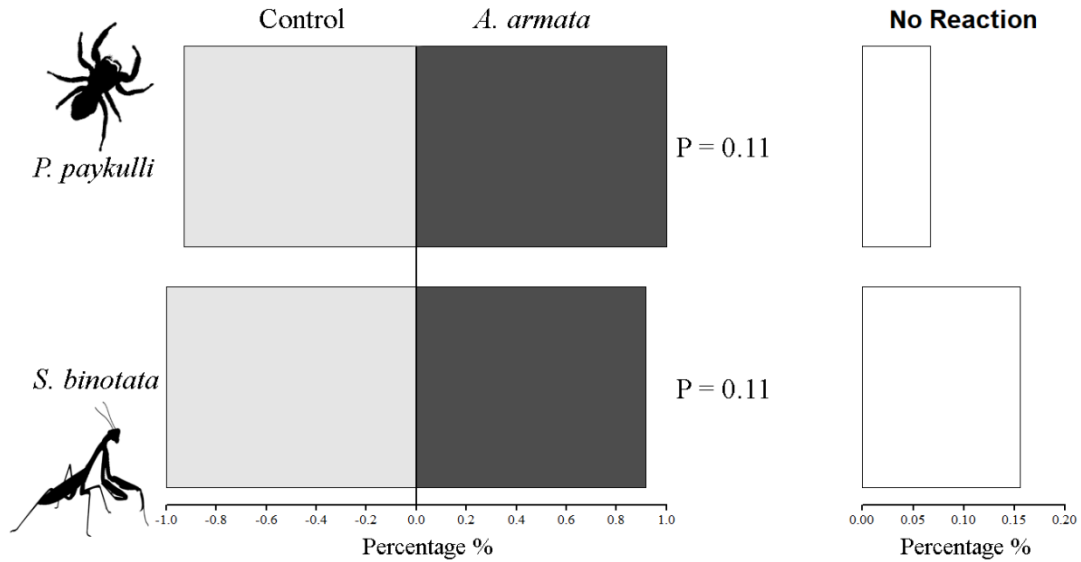


Figure 4: The percentage of control and sepsiid (*Archisepsis armata*) that were consumed by jumping spider and praying mantis.

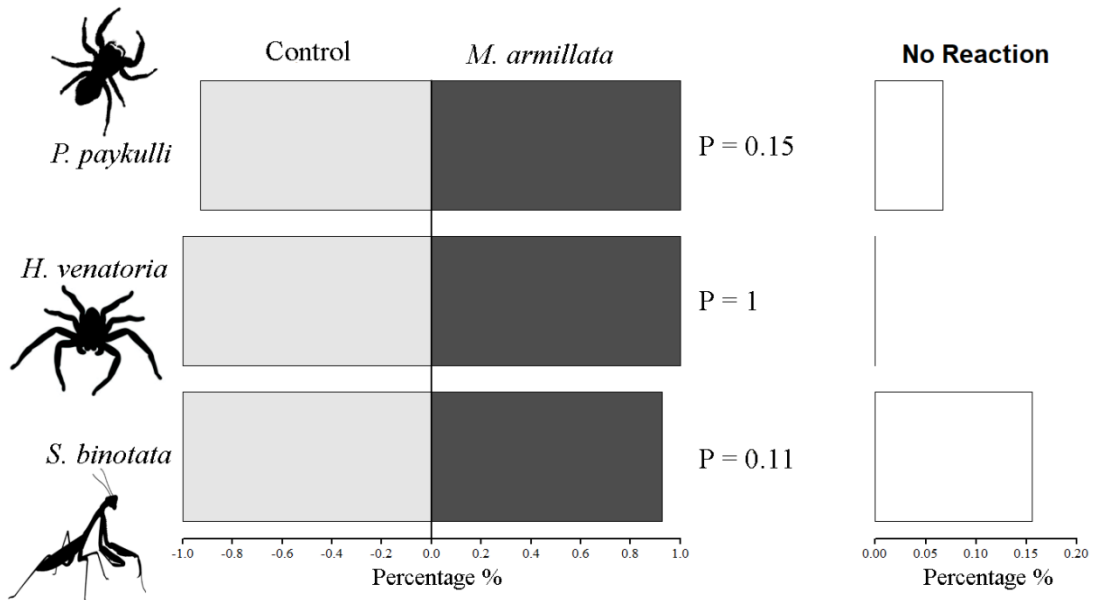


Figure 5: The percentage of control and sepsiid (*Microsepsis armillata*) that were consumed by jumping spider, giant crab spider, and praying mantis.

3.1 Morphological analysis

Concerning the two dissected species, we found no evidence of any structures akin to the Dufour gland, similar to that described for other species of Sepsidae.

4. DISCUSSION

The data presented in this study does not corroborate the hypothesis that *Archiseopsis armata* and *Microsepsis armillata* are unpalatable since preyed specimen rates from these species compared to those of fruit flies (control group) were not statistically significant for the three species of predators utilized (Figures 4 and 5).

The chemical defenses, as well as the other types of defenses, are not efficient against all kinds of predators since some of them developed mechanisms to overcome them and/or are not so sensitive to the chemical substances produced by a given prey. The praying mantises are generalist predators, in other words, they consume many kinds of prey, including species that are unpalatable to other predators, such as honeybees (*Apis mellifera* Linnaeus, 1758) [22], stink bugs of Pentatomidae family [23], and caterpillars of the monarch butterfly (*Danaus plexippus* Linnaeus, 1758) and of some moth species [24, 25]. However, some praying mantis species avoid to eat preys that use chemical substances as defense [26], such as ants, and some species even show innate aversion to these insects.

Despite consuming a great variety of prey, jumping spiders usually avoid chemically protected species [27, 28], including some Sepsidae species [14]. Although, there are no records of Salticidae feeding on sepsids in natural conditions, they are potential predators of these flies, since this is one of the most diversified and abundant spider families in many kinds of environments [29] where sepsids occur. There are few studies about predator-prey interaction in *H. venatoria*, but other studies not published yet (F. S. Carvalho-Filho personal communication) reveal that they avoid chemically protected prey.

Therefore, the possibility that the predator chemical resistance has interfered in the results of this study can be disregarded, since there was no significant difference in the predation rate of the Sepsidae and the control group, even in predators that are more sensitive to chemically defended species, such as jumping spiders and giant crab spiders.

However, studies that investigate the palatability of Neotropical Sepsidae to other potential predators (hemipteran, robber flies, ants, and wasps) need to be done, because wasps and ants have already been observed attacking some sepsids in Europe. Moreover, studies of palatability with vertebrate predators (*e.g.* amphibians, lizards, and birds) are also necessary since some species of birds have been observed feeding on sepsids in Europe [30].

Bristowe (1979) [14], in a classic study that aimed to investigate the palatability and predatory interactions between spiders and an Old World species of sepsid (*Sepsis fulgens*), used a non-standard number of specimens, which were offered to seven species of web-building spiders and four species wandering spiders, including one Salticidae. Despite some spiders have rejected certain sepsid specimens, many of them fed on or did not manifest any reaction. Based on his observation, Bristowe (1979) [14] has been concluded that the odor released by sepsids does not repel spider attacks. However, Bristowe (1979) [14] did not perform statistical analysis to verify if that difference was significant.

It must also take into account the scenario where the sepsid chemical defense was so strong that the predator does not even bother to attack. In this scenario, it is expected that the behavioral categories “unsuccessful attack” and/or “no reaction” would be more common. However, it was not observed for all types of predators utilized in the palatability experiment.

According to some authors, the sepsid substance that inhibits predator attacks is produced by an abdominal gland (Dufour gland) present in male and female specimens [31] and has a characteristic and perceptible odor, at least to human beings [30, 31]. This odor also possibly acts as a stimulus to the formation of hibernation swarms that can last for many weeks over vegetation, which can comprise of hundreds of individuals, and this has already been observed in a few species of *Sepsis*, especially *S. fulgens*, in Europe [30].

The Neotropical species of Sepsidae have not been observed forming aggregations as that observed in the Old World, but it is common to encounter temporary aggregation with many individuals close to carcasses and feces of large mammals, which act as a food source to adults, copula location and substrate for breeding immatures [11, 12, 30, 31]. The absence of hibernation swarms in the Neotropical species, coupled with the absence of attack inhibition in *A. armata* and *M. armillata*, suggest that the Dufour gland is lacking in these species. This fact has been confirmed by the analysis of internal morphology of the abdomen, which did not reveal a structure fitting the description [30] and picture [32] of this gland.

Despite the Dufour gland is considered to be a diagnostic feature of Sepsidae [30, 31, 33], its presence and morphology have not yet been properly studied along with the genera. It has already been registered in some species of *Sepsis*, *Themira*, and *Nemopoda* [32, 33, 34] and might be found in some species of *Meroplius* [33]. However, this gland has not been found in species of *Orygma*, *Ortalischema*, and *Toxopoda* [31].

According to the phylogenetic hypothesis of Zhao et al. (2013) [17], *Orygma* and *Ortalischema* (both lacking the gland), belong to a clade that is the sister group of the clade composed of the other Sepsidae genera. *Themira* and *Nemopoda* (which possess the gland) form a clade, which is the sister clade of the largest clade composed by the remaining genera. Inside this large clade, there are lineages with the gland (*Sepsis* and *Meroplius*) and lineages lacking it (*Archisepsis*, *Microsepsis*, and *Toxopoda*) (Figure 6). *Archisepsis* and *Microsepsis* belong to a clade composed of Neotropical genera, which in turn is the sister clade containing the Old World genera, including *Sepsis* and *Toxopoda* (Figure 6) [17]. As there are still many genera lacking information about the presence of Dufour gland, it is not yet possible to assess if the gland evolved in the ancestor of all Sepsidae and later was lost in some lineages or if it evolved independently in many genera and/or species.

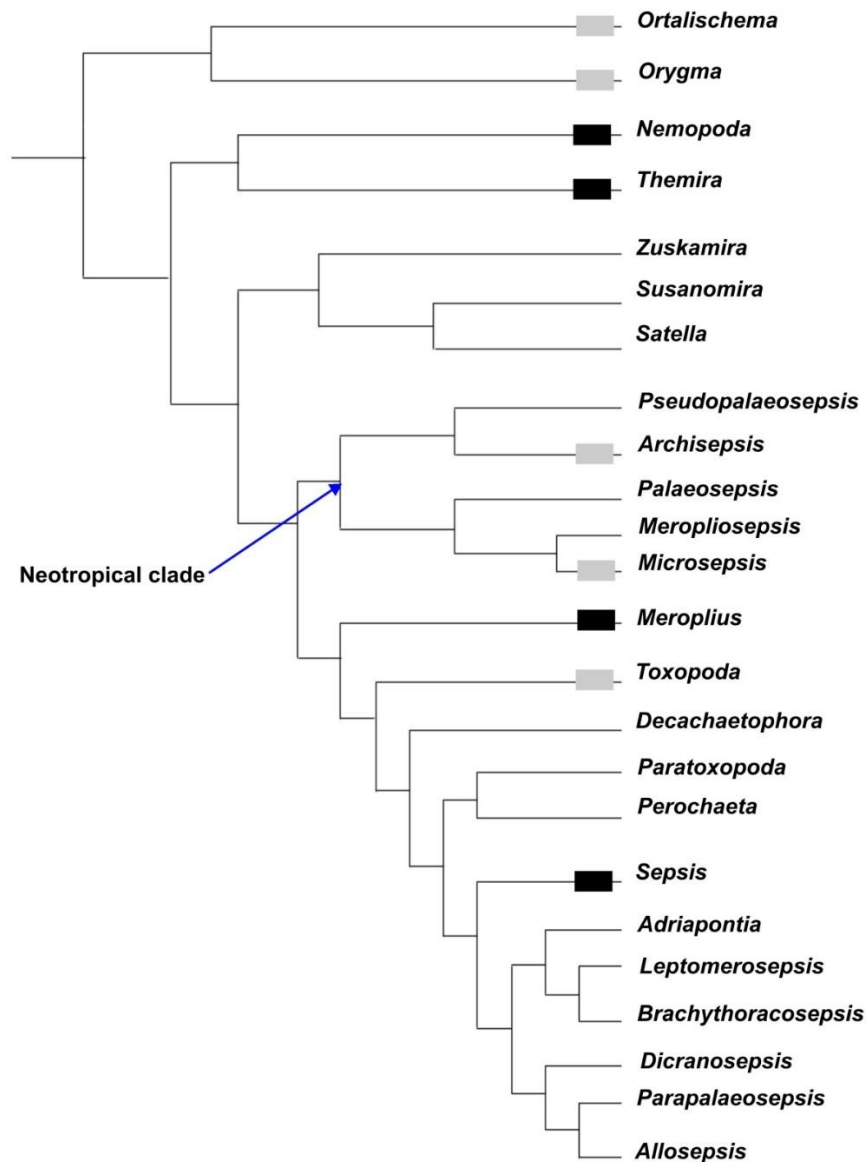


Figure 6: Phylogenetic hypothesis of Sepsidae genera (modified from Zhao et al. (2013)). The genera whose species have Dufour gland are highlighted with black box and those ones without Dufour gland are highlighted with grey box.

Archisepsis armata and *Microsepsis armillata* are widely distributed in the Americas [13] where they are easily found near feces of medium and large-sized mammals. Thus, these species may constitute an important food source to many vertebrate and invertebrate species. Despite that, the defense mechanism of these species, as observed in this study is not the unpalatability, as suggested for the species from Old World [31]. Most of Sepsidae species are morphologically similar to some ant species [12, 13, 31]. Ants are avoided by many predators due to their social behavior, chemical defenses, powerful jaws, and stings [35, 36-38]. For this reason, they are common models for the Batesian mimicry of many invertebrate species [35, 38], including the unpalatable species of Sepsidae (Carvalho-Filho, in preparation). Therefore, we believe that Neotropical sepsids are using batesian mimicry as a form of defense.

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