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Evolution of Secondary Sexual Characters in Pselaphinae (Coleoptera: Staphylinidae)

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EVOLUTION OF SECONDARY SEXUAL CHARACTERS IN PSELAPHINAE (COLEOPTERA: STAPHYLINIDAE)

A Dissertation
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Entomology

by
Laura María Vásquez Vélez
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ABSTRACT

Secondary sexual characters (SSC) are traits present only in one sex, commonly on males, and different from the reproductive organs. These characters have evolved mainly through the action of Sexual Selection, the differential mating success of organisms of the same species. Males use SSC to challenge other males for access to females, while females use these traits as signals to choose mates with overall good. SSC can manifest as horns, tusks, enlarged appendages, spines, coloration, and body size. Sexually dimorphic traits are present in all major groups of animals, including Insects. Sexual selection and secondary sexual traits have been proposed to be drivers for speciation on hypothetical bases, but empirical evidence has proven to be inconclusive.

To explore this hypothesis in species rich lineages, such as insects, it is necessary to identify the diversity and frequency of SSC within particular lineages. Pselaphinae beetles (Coleoptera: Staphylinidae) are a great example of high species richness and broad morphological variation in sexual traits. This group contains more than 10,470 described species distributed worldwide. They are predators of small invertebrates, and their large number of species contrasts with their small size, between 0.6 and 3.0 mm. The diversity and frequency of SSC in Pselaphinae was obtained from species descriptions, fauna catalogues, and databases. A total of 40 dimorphic body structures were identified in 218 species from 34 tribes. The SSC present in the largest number of species were modification of abdominal sternites, eyes, and mesotibiae. Differences on the quality and quantity of SSC were found among different tribes. To look at the evolution of SSC at the genus scale, in the genus *Batrisodes* were documented on a phylogenetic context. The basal process on antennomere XI showed most convergence among species of Nearctic and Palearctic regions. The ventral fovea on antennomere X, was the most constant across the genus. This research is an initial step towards the recollection of SSC in Pselaphinae, that can be used to study character evolution, character correlations with microhabitats, and character correlation with other characters.

DEDICATION

To my family, here, there, and beyond.

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CHAPTER ONE

LITERATURE RIVIEW

Sexual Selection and Secondary Sexual Characters

In organisms with sexual reproduction, secondary sexual characters are traits different from the reproductive organs and present in only one of the sexes (Darwin 1879; West-Eberhard 1979; Andersson 1994). Males more often than females present modifications in their external morphology, such as horns, tusks, enlarged appendages, spines, coloration, and body size. Additionally, visual, chemical, and sound production signals can differ between the two sexes. Such differences are in many cases the result of Sexual Selection acting differently on males and females of the same species (Darwin 1879; West-Eberhard 1979; Andersson 1994). Under sexual selection some individuals will mate more often than others of the same sex, thus secondary sexual traits can be used by males to compete against other males for access to females, defend territories, or search and attract mating partners. Meanwhile, females can choose their mates using males' sexual traits as signals of conspecificity, overall health, fecundity, and offspring qualities (West-Eberhard 1979).

Sexual selection theory has been traditionally explained by two mechanisms: male-male combat and female choice (Darwin 1879; Maynard-Smith 1978; Andersson 1994). Males can interact with each other in combat, using weapons or can initiate behavioral displays to signal aggression to other males and courtship to females. Whether they use weapons or displays, it is expected that these interactions continue if the chances of mating are greater than the cost of continuing fighting or signaling (West-Eberhard 1979, 1983).

The action of sexual selection can continue after mating has finished and male and female are decoupled. Sperm competition occurs within the female's reproductive canal; in there, sperm from two or more males may compete for the fertilization of her ova (Eberhard 1996; Weddel *et al.* 2002). Conversely, some females can discriminate among sperm from different males, choosing to use, keep or discard accordingly. This post-copulatory behavior is known as cryptic female choice (Eberhard 1996).

Several hypotheses have been proposed to explain how female choice has evolved and how it can influence the diversity of male' sexual traits. Fisher (1930), proposed that female choice is the result of a **self-reinforcement or runaway process**, requiring genetic variations in both the male's sexual trait and the female's preference for the trait. The secondary sexual characters will continue to vary according to females' preference; males carrying the favored trait will have higher mating success until the sexual trait is counter-selected by Natural Selection (Fisher 1930; West-Eberhard 1983). Conversely, **the sensory bias hypothesis** predicts that signalers use competition or courtship displays to exploit sensory responses already present in the receptor; usually these sensorial responses are also under selection pressure in other contexts than mating (West-Eberhard 1983). Secondary sexual characters like conspicuous ornaments and bright coloration might also work as **indicator mechanisms**, where males' traits reflect their good health and higher fitness, and females recognize these as cues for mate choosing (Andersson 1994; Balenger and Zuk 2014). Secondary sexual characters may also work as **species recognition mechanisms** used by females to identify partners of the same species, avoiding hybrid crosses; under this mechanism of female choice, secondary sexual traits and sexual selection could contribute to forming new species by reinforcement of prezygotic isolation (West-Eberhard 1984; Anderson 1994). Under **sexual conflict**, males and females have different fitness interests, female choice is the direct result of mating avoidance, selecting for males with sexual traits able of overcome female resistance to costly mating (Chapman *et al.* 2003). Female reluctancy to mating coevolves with exaggerated traits in males like grasping mechanisms, longer legs, or larger body size (Rowe *et al.* 1994; Chapman *et al.* 2003).

In the last two decades, however, research in these interactions has shown that there are more nuances around the combat for mates and mate choice (Wedell *et al.* 2002; Kelly 2018; Hare & Simmons 2019). Even though males produce much more gametes than females, sperm quantity is limited. Males must use strategies to assess the risk of mating without fathering any offspring; if the number of receptive females increases, a male will use less sperm per female, given his chances of multiple encounters with several females. Also, sperm production will decrease when the probability of sperm competition increases by the presence of other males. On the other hand, males will give more sperm to virgin females, but this will depend similarly on the number of competitive males. The ejaculate size that a male produces can depend on the female's age, because the chances of previous mating encounters in older females are higher (Weddel *et al.* 2002). Thus, males can exercise some degree of choosiness to secure multiple matings by sperm production optimization. The intensity of female's choice also depends on other factors in addition to male attractiveness (Eberhard 1996). In older females, choosiness would decrease when the time and energy costs associated with searching for partners are higher than the benefit of selecting a preferred mate; mating history as well as the quality and quantity of the sperm stored for future fertilizations are conditions for female choosiness, too. Females would mate with less attractive males if the risk of predation is elevated. And social cues are important for female choice, for example, when there are more males available for mating, choosiness would increase (Kelly 2018).

Secondary sexual characters in Vertebrates

Secondary sexual characters can be found in almost all groups of animals. In vertebrates, mammals show sexual size dimorphism in different lineages. Males may be bigger and heavier than females, can bear horns, tusks, or antlers; large body size and weapons are related to male-male combats to access to groups of females or harems. Male weapons usually present an allometric growth, where certain traits will increase disproportionately in size as overall body size increases (Pélabon *et al.* 2014); also, in primates, male and female genital area can change coloration during mating season (Andersson 1994). Likewise, change in coloration is common on lizards and serpents during mating periods; differences in body size may exist in some taxa, where males tend to be bigger than females and exhibit aggressive displays against other males (Andersson 1994). Male anurans have call repertories that present properties like call rate, call loudness, call pitch, etc.; since call properties can be related to male size or fitness, females use call properties to choose among different males (Andersson 1994). Nuptial coloration in fish males of some taxa has been proposed as the result of sexual selection by female choice, where females choose males with brighter color and are capable of differentiating between sympatric species (Andersson 1994; Martin and Mendelson 2014); yet in other taxa bright coloration is attributed to mimicry and aposematism (Andersson 1994). Birds show noteworthy examples of secondary sexual traits: males in many taxa present showy colors, plumage ornaments such as long tails, and complex songs (Andersson 1994). In general, polygynous taxa are more ornamented than monogamous ones (Møller and Pomiankowski 1993); these conspicuous colors and threat songs can function as part of the male repertoire to defend suitable breeding habitats from other males, while ornaments and displays attract females, leading to mate choice (Andersson 1994).

Secondary sexual characters in Insects

Insects are the largest group of animals in the world. Throughout all insect taxa there are examples of secondary sexual characters, represented as sexual size dimorphism, weapons, visual, acoustic, and chemical signals, nuptial gifts, or genitalia diversification. Understanding the origins of secondary sexual characters is a complex challenge, involving a species' ecological niche, behavior, and developmental genetics. While a great diversity of secondary sexual characters has been described and exploited for taxonomic purposes, our understanding of their function and evolution are less well understood. Nonetheless, there are diverse examples where the function of secondary sexual characters is well established.

Sexual size dimorphism

In many insects, females rather than males have larger body sizes, this is particularly common in species that mate in flight like some ants, or on water like water striders. In these cases, small size of males can be advantageous for movement energetics (Andersson 1994; Rowe *et al.* 1994). In scarab beetles (Scarabaeidae), large size in males is also related to large size of horns, which are projections on the head and/or prothorax, used as weapons in male-male combat for females and territories (Eberhard 1980; Emlen and Nijhout 2000). Yet, differences in larval diet affect directly the final body size in males of the same species; as a consequence, in the same population will be males with small, intermediate, and large body sizes. Thus, larger males tend to have advantage over their opponents during combats (Eberhard 1980; Emlen *et al.* 2005). Stag beetles (Lucanidae), offer another example of size sexual dimorphism and weaponry; with the exaggerated development of males' mandibles, often as long as the rest of their bodies, male beetles grab contenders and throw them away in territorial displays. As in scarab beetles, the final body size depends on larval feeding, and intraspecific variation occurs. Also, in some species, larger males do not have flying wings, while small males have developed wings and disperse easily (Eberhard 1980; Kawano 2006). According to Kawano (2006), large weapons may be a consequence of large body size as a sexually selected trait in scarab and stag beetles, among other taxa; since large size increases allometric effects in other characteristics, males would present large bodies accompanied by large weapons, thereby improving their winning chances.

Visual signals

Differences in coloration between males and females are common in butterflies (Lepidoptera), dragonflies, and damselflies (Odonata), where both sexes have highly developed vision. Males are usually more colorful in butterfly lineages where sex-dimorphic coloration is present, and coloration difference is greater among males of closely relates species than in females (Andersson 1994). In the species *Heliconius erato,* yellow wing pigmentation is the result of a UV-yellow-reflecting molecule. It has been observed that female butterflies in *H. erato* express two UV photoreceptors, while males only express one, as an example of sexual dimorphism in compound eyes structure. The extra UV photoreceptor in females has been suggested to aid females to distinguish among congeneric males (McCulloch *et al.* 2016). In Odonata, males of some taxa have distinctive pigmentation on the abdomen that aids in male-male competition for territories (Andersson 1994). Also, in some damselflies, females have several color morphs, with one resembling male coloration (ref.); nevertheless, males do not show preference for a particular female morph. In *Megalagrion* damselflies, female-limited dimorphism occurs among species that have different altitudinal distributions on the Hawaiian archipelago. Cooper *et al.* (2016) found that the observed dimorphism was mainly correlated to the different habitats males and females occupy, and female dimorphism was a consequence of clines in the degree of habitat difference. Bioluminescence is used as visual signal by adult fireflies (Lampyridae) to find mating partners. The flashing displays are initiated by males during flight in determined habitat areas, mainly at sunset or after dark; each firefly species has its own flight path and light emission pattern; females remain perched on nearby vegetation, and answer male signals with their own flashes after characteristic pauses. This flash and answer behavior usually results in mating when males locate receptive females (Andersson 1994; Matthews and Matthews 2010).

Acoustic signals

Acoustic signals as secondary characters are widespread in orthopterans and hemipterans. Female response is affected by the intensity of songs, thus choosing males that sing louder; also, females can prefer long and continuous songs over short songs (Andersson 1994). In periodical cicadas from the genus *Magicicada* (Hemiptera: Cicadidae), females and males form large groups where several species can concur, and form choruses. Cooley and Marshall (2005) observed male-female interaction of 13 and 17- years cicadas, finding that receptive females flick their wings in response to an individual chorusing male. Female response depends on particular changes in the frequency of the approaching male, which are species-specific and noticeable against the background chorus; after perceiving female's wing movement, a male gets closer and continues a sequence of courting calls until female accepts or rejects the pairing. Additionally, when a male has been accepted by a female, he can signal other approaching males to stay away from the mating pair, using buzzing sounds that apparently confound the intruder.

Chemical signals

Maybe the most widespread examples of secondary sexual characters in insects are those used in chemical communication. Pheromones detection demands tuned sensorial structures capable of identifying minimal amounts of chemical signals (Andersson 1994). Ramsey and collaborators (2015) observed the behavior of *Rhipicerus* beetles

(Rhipiceridae) and addressed the morphology and function of male antennae. In this genus, males present enlarged lamellate antennae, like those observed in some moths, suggesting that *Rhipicerus* males may use their antennae to detect trace quantities of odorant molecules associated to females. Then, the researchers examined factors that may influence molecule capture in male *Rhipicerus* beetles such as behavior, morphology, morphometry, and ultrastructure using SEM. They found sexual dimorphism at the ultrastructure level, where males presented around 10000 more sensilla placodea on antennal surface compared to females' antennae; these types of sensilla have been found to respond to scent associated with female conspecifics in other insects. In some cases, pheromones may be produced from food sources and may be used in parental investment, impacting female choice (Eisner and Meinwald 1995; Eisner *et al.* 1996). For example, in the moth *Utetheisa ornatrix* (Lepidoptera: Erebidae), larvae feed on toxic plants of the genus *Crotalaria* (Fabaceae) that contain pyrrolizidine alkaloids. Adult moths start courtship when female moths use a sex attractant to lure males during dusk; when a male finds a female, he first flies around her and pushes his abdomen against her; at the end of his abdomen the male displays coremata, a pair of modified groups of scales that are associated with glandular openings. After one or more pushes, the female opens her wings and exposes the abdomen for mating; the male then transfers his spermatophore. Females mate with more than one male. In a series of rearing and behavioral experiments, Eisner and Meinwald (1995) observed that dissected coremata from experimental males contained the pheromone hydroxydanaidal, and that this was produced using, as chemical basis, the pyrrolizidine alkaloids from their nutritious plants. Additionally, eggs fathered by males with alkaloid-rich pheromones, were avoided by predators such as ladybeetles and lacewing larvae. The authors found that larger males produced spermatophores with more alkaloid content; females then use the pheromone signal to assess alkaloid load in males' spermatophores, and favor sperm from larger males to fertilize her eggs. Similarly, in the beetle *Neopyrochroa flabellata* (Pyrochroidae), males ingest the chemical cantharidin and store it in their large accessory glands. During courtship, males release a cantharidin-rich secretion from the cephalic gland, a deep transversal frontal cleft, internally pilose; females approach to males and sample the cephalic gland (Eisner *et al.* 1996a). Eisner and collaborators (1996ab) observed that females mated with males that were fed with cantharidin and with males that did not receive cantharidin diets, but with the substance added to their cephalic gland; males that lacked cantharidin were not accepted by females. After mating, females laid eggs that were unpalatable to predators. Researchers realized that eggs fertilized by cantharidin-fed males contained the substance as well, offering protection against predation. Thus, when females approach the cephalic gland during courtship, males offer a signal of the cantharidin load they have in their large accessory glands. During mating, males transfer part of the substance to the females through the spermatophore, using cantharidin as a nuptial gift.

Genitalia

Among many insect groups, finding closely related species in which external morphology is generally invariable can be rather common, where genitalia morphology is the only way species can be differentiated. For instance, the genus of scarab beetles

Phyllophaga (Scarabaeidae) contains species that look very similar externally. Nonetheless, this group presents highly variable, species-specific genitalia in both males and females. Richmond and collaborators (2016) contrasted the evolution of variation in genitalia structures from males and females against phylogenetic relationships in some *Phyllophaga* species. They observed mating structures from males and females dissected during copula; the results suggested that the specificity of male and female genitalia was advantageous as a mechanical mechanism to keep the couple engaged during copula, while the male is hanging upside down, and only male and female genitalia are keeping them attached. The authors discussed that the stabilizing interaction of male-female genitalia can be beneficial for efficient sperm transfer, and/or dislodging prevention from predators. They did not find evidence for coevolution between male and female genitalia. Eberhard (1985; 1996; 2010) proposed genitalia diversification as a result of sexual selection by cryptic female choice, and by a runaway mechanism; for females, male genitalia alone may not be the best indicator of the male's fitness; yet, male genitalia can induce female response aiding the reproductive process; if the response in the female changes male's reproductive success, male genitalia act as a signal to the female, then natural selection may act on both improvement of male's signaling and female's reception of the signal, although the signal by itself has no influence on the individual's fitness (Eberhard 1985). On the other hand, an alternative hypothesis states that genitalia diversification has also been considered a consequence of sexual conflict (Rowe *et al*. 1994; Chapman *et al.* 2003), where males and females' interests regarding courtship, mating, and fertilization are not the same, rendering both sexes in a continuous coevolutionary arms race to dominate reproductive processes (Rowe *et al.* 1994; Hosken and Stockley 2004; Eberhard 2010).

Evolution of secondary sexual characters

The above diversity of sexual selection strategies illustrates the importance of understanding not only the morphological differences themselves, but also of having a strong foundation of phylogenetic relationships, data on the natural history, and behavior of the lineages. To establish evolutionary drivers of intersexual differences, all these factors may be interacting. Furthermore, taking a broader phylogenetic perspective can reveal factors that may not be apparent in studying the sexual differences in individual species. In particular, variation in the species natural histories may covary with variation in prevalence of secondary sexual characters, and lineages which contain both dimorphic and monomorphic species offer particularly useful systems to illustrate this. For example, Dombroskie and Sperling (2013), constructed a preliminary phylogeny for the tribe Archipini (Lepidoptera: Tortricidae: Tortricinae). They mapped secondary sexual characters, number of host plants, and geographic distributions into the resulting phylogenetic tree. They found species that lack secondary sexual characters had fewer host plant species and had colonized the New World. Thus, a historical view of the secondary sexual characters can be also correlated to environmental variation and distribution patterns of related species in a group. Chatzimanolis (2005) studied the evolution of coloration and secondary sexual characters in the genus *Nordus* (Staphylinidae), in a phylogenetic context, using morphological characters; males of different species present modifications on abdominal sterna VII, VIII, and IX. Abdominal sternum VIII present three basic forms in its hind margin: it can be medially emarginated, can bear a single medial lobe, or it can have two medial lobes separated by an emargination. In this phylogenic hypothesis for *Nordus* species, the ancestral character seems to be the medial emargination, shared by the outgroups and the basal species of *Nordus*; most of the remaining species present variations of the hind margin with two medial lobes with an emargination between them; and finally, a single clade of three species exhibit one medial lobe. In relation to coloration evolution, aposematic coloration (golden-orange) seem to have evolved in the ancestor of *Nordus.* It was suggested that color differences in the same species are related to different elevations in which morph inhabits, with golden-orange morphs inhabiting lowlands, whereas brown to black morphs are found at elevations higher than 900 m. (Chatzimanolis 2005).

Secondary sexual characters, Sexual Selection and Speciation

Sexual traits incorporate sources of variation that over evolutionary time can be translated into species diversification. The importance of sexual selection as a unique driver for speciation has been explored theoretically by several authors (Lande 1981; West-Eberhard 1984). Under certain genetical models, species can be formed by sexual selection following runaway processes (Lande 1981). Potentially, sexual selection can lead to speciation because it acts directly on characters used in mate recognition (Panhuis *et al.* 2001; Ritchie 2007). Although empirical evidence is difficult to assess due to the time scales in which species can form, and to uncertainty regarding the action of other evolutionary processes, such as natural selection, that may also result in new species (West-

Eberhard 1983; Panhuis *et al.* 2001; Ritchie 2007), there have been efforts to find correlations between sexual selection and speciation for different animal taxa. In Passerine birds, Barraclough and collaborators (1995), using a published phylogeny at tribal rank, found that taxa with greater proportions of sexually dichromatic species contained more species overall than sister groups where monochromatism was in larger proportion, supporting their hypothesis that under sexual selection by female choice for male traits, higher proportions of sexual dimorphism within a clade are correlated with higher number of species. Nonetheless, the methodological approach used by Barraclough *et al* (1995) has been criticized and found to have equivocal results after replication, Janicke *et al.* (2018), used a meta-analysis of publications using the Bateman gradients as measure of the intensity of sexual selection throughout the animal kingdom. They found that when males are under more intense sexual selection (i.e. fitness benefits gained by additional mating), the species richness within the family level is higher. To explore this hypothesis in other species rich lineages, such as insects, it is necessary to identify the diversity and frequency of secondary sexual characters within particular lineages. It is critical to consider the evolutionary relationships among taxa within the group of interest (Barraclough *et al.* 1995; Janicke *et al.* 2018), expecting that sister taxa will have similar ages and comparable evolutionary time to assess whether clades with more species actually present secondary sexual characters in higher diversity and frequency.

From the examples exposed above, it is noticeable that beetles (Coleoptera) in general, express extensive diversity in the presence of secondary sexual characters. Among these, the subfamily Pselaphinae (Staphylinidae) is a great example of high species richness and broad morphological variation in sexual traits. This diversity contrasts with the currently inadequate knowledge of natural history of the group.

The following chapters explore the manifestation and evolution of secondary sexual characters in the diverse group of Pselaphinae beetles (Coleoptera: Staphylinidae). In Chapter 2, the incidence of secondary sexual characters in all major lineages of Pselaphinae is documented, in the context of their presence in different parts of the male body. The diversity of secondary sexual traits is compared among different tribes to assess the potential correlation between highly sexual dimorphic taxa and species richness; a compilation of the ubiquity of sexual traits in highly diverse lineages can represent a first step towards the recognition of correlations between processes such as speciation and sexually selected traits in males. Chapter 3 deals with the evolution of secondary sexual characters at the genus scale, looking at their manifestations in the Holarctic genus *Batrisodes* Reitter, with special attention to North American species. The documentation of the secondary sexual characters in Nearctic *Batrisodes* in an evolutionary context is here used to identify whether these characters are highly convergent within the lineage, what characters are more constant across the genus, which tend to be lost or gained more frequently, and to recognize secondary sexual characters present in the most diverse clades. The phylogenetic relationships within this group are reconstructed to elucidate the distribution of taxon diversity at the level of species groups, and to explore whether certain secondary sexual characters are related to species numbers.

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CHAPTER TWO

EVOLUTION OF SECONDARY SEXUAL CHARACTERS IN PSELAPHINAE (COLEOPTERA: STAPHYLINIDAE).

INTRODUCTION

The subfamily Pselaphinae (Staphylinidae) is a diverse group of beetles with more than 10,470 described species in 1,278 genera, distributed worldwide (Newton 2018; Thayer 2005; Parker 2016). Adults and larvae are predators of small invertebrates like annelids, mites, Collembola, and larvae of other insects (Chandler 2001). Their great number of species contrasts with their small size, between 0.6 and 3.0 mm in length, and with the lack of information about their natural history (Chandler 2001, Parker 2016). However, some biological generalities for the group have emerged throughout years of specimen collection and taxonomic descriptions. Some species exhibit interesting ecological relationships with social insects, especially with ants; the association between beetles and ants varies from loose interactions towards colony members such as brood predation, to complete integration where adult beetles are accepted and fed by the ants through trophallaxis (Parker & Grimaldi 2014; Parker 2016). Several lineages within Pselaphinae contain taxa with different degrees of association to the colony life, but only in the Supertribe Clavigeritae are all the species myrmecophiles (Parker 2016). Species associated with caves are also common within the subfamily, with the most extreme examples in the Supertribes Batrisitae and Goniaceritae, where troglobitic species have evolved several times (Chandler 2001; Chandler & Reddell 2001, 2009). Such specializations could be the result of the general preference pselaphines have for dark and humid places like leaf and wood litter, decaying wood, riparian edges, lake shores, and under rocks. Even so, information about their behavior as adults has been observed only in a few opportunities (Schomann *et al.* 2008). Likewise, larval stages have been studied in few species (De Marzo 1988; Carlton and Leschen 2008), and fewer still have examined pupal chamber and cocoon construction (De Marzo 1988b).

Newton and Thayer (1995) downgraded Pselaphidae to a subfamily of Staphylinidae, based on morphological similarities with the Omaliinae group of subfamilies. Later, Chandler (2001) changed the internal classification of Pselaphinae, rendering six supertribes, 37 tribes, and 38 subtribes. The largest supertribe is Goniaceritae, with 3,061 described species in 266 genera, grouped in 14 tribes, with a worldwide distribution. Euplectitae follows in species richness with 2,633 species, 416 genera, eight tribes, distributed globally. Most Batrisitae are distributed around the tropics, with some genera represented in the Holarctic region; there are three tribes that include 1,948 species and 228 genera. The fourth supertribe in numbers of species is Pselaphitae with 1,632 species, 206 genera, contained in 11 tribes and present in all biogeographical regions. Clavigeritae groups 367 described species in 108 genera contained in three tribes. Lastly, the supertribe Faronitae, considered to be the sister group to all other pselaphine supertribes (Newton and Thayer 1992; Chandler 2001), contains 330 species, and 27 genera, distributed in the temperate regions (Newton *et al*. 2001; Chandler 2001; Newton 2018).

Pselaphinae species diversity is matched by a vast amount of morphological variations in its species, particularly related to sexual dimorphism, and secondary sexual characters in males. Taxonomically, such traits are often used to describe new species and differentiate closely related taxa. However, the important role of these morphological traits for taxonomic species delimitation contrasts with the lack of information about their function during intraspecific interactions, their evolution, and their frequency in different lineages. Some secondary sexual traits found in Pselaphinae include modifications of the abdominal sternites (Cuccodoro *et al.* 2012), spurs on the mesotibiae, changes in the metaventrite (Baňař and Hlaváč 2014), different size and shape of male antennomeres (Kurbatov and Cuccudoro 2015), and in some dramatic cases, marked depressions on the head vertex (Yin and Li 2015).

Sexual traits as those mentioned above may incorporate sources of variation that under evolutionary time can be translated into species diversification. Through sexually selected traits, new species can emerge when these characteristics are associated with mate search, attraction, and recognition systems (Panhuis *et al.* 2001). The importance of secondary sexual characters and sexual selection as drivers for speciation has been explored theoretically by several authors (Lande 1981; West-Eberhard 1984). Empirically, this prediction has proved difficult to test, yet in highly diverse groups such Passerine birds, a correlation between species richness and sexual dimorphism has being found (Barraclough *et al.* 1995; Janicke *et al.* 2018). Pselaphine beetles offer a great possibility to identify relationships between species diversity and secondary sexual characters. A great array of taxonomic publications describes and illustrates the external morphology males and females, allowing comparison between sexes; also, sexual traits can be found in multiple body parts on the same species, which helps to find differences among different lineages in different hierarchies; finally, most sexual traits are discrete, facilitating their quantification to assess their frequency throughout the different lineages. Thus, a synthesis of these data could provide a valuable perspective on the group's diversity.

This chapter seeks to document the incidence of sexual secondary characters in males of all major lineages of Pselaphinae, reports their specific manifestations on different parts of the body, illustrate their diversity, and discuss the potential correlation between highly sexual dimorphic taxa and species richness.

MATERIALS AND METHODS

The exploration of secondary sexual characters in Pselaphinae was based on the super tribes Batrisitae, Clavigeritae, Euplectitae, Goniaceritae, and Pselaphitae, or higher Pselaphinae (*sensu* Parker 2016). The supertribe Faronitae, being the sister taxa to all other pselaphinae lineages, and being considered to carry mostly plesiomorphic characteristics (Chandler 2001), was used as a morphological reference to compare the remaining supertribes. Through the revision of faunistic catalogues, databases and taxonomic descriptions, information about supertribe and tribe names was recorded using catalogues from the Palearctic region (Löbl & Löbl 2015), Neotropical region (Navarrete-Heredia *et al.* 2002; Asenjo *et al.* 2019), Nearctic (Chandler 1997; Chandler *2001*), and Australia (Chandler 2001); for other biogeographic regions individual species descriptions and local catalogues were used. Because, in many circumstances, there was no difference between the quantity and quality of sexual traits among species in the same genus, each tribe was represented with at least two genera (when possible), and the Staphyliniformia World Catalogue Database (Newton 2018) was used to corroborate the current validity of generic and specific names. All these information sources rendered a list of taxonomic publications where genera and species were described. To be considered for the list of sexual secondary characters in Pselaphinae, the species descriptions must have information about morphological differences between males and females; species descriptions were disregarded when only one of the sexes was described; although most sexual characters reported here are present only in male specimens (reduction in eyes size is presented in females rather than males), the description of female morphology allowed comparation and certainty of actual sex dimorphism. The secondary sexual characters were recorded in a presence/absence matrix; for each selected species, a value of one (1 = presence) was given to body parts bearing the secondary sexual characters. The body part selection was based on their recurrence in taxonomic descriptions: every time that a structure was described as different between male and female specimens, it was included in the secondary sexual character matrix. The male body parts used were grouped in six categories: 1) Antennae, including antennal flagellum (length), scape/pedicel, and flagellum segments (segments III to IX); 2) Head: Head capsule, mouth parts, and eyes; 3) Thorax: elytra, pronotum, and metaventrites; 4) Abdomen: abdominal terga and abdominal sterna; 5) Legs: coxae, trochanters, femora, tibiae, and tarsi of pro-, meso-, and metathoracic legs; and 6) flight and size dimorphisms: wing dimorphism, leg size dimorphism, and body size dimorphism. Line drawings were made using Adobe Illustrator (version 2019) and correspond to the body morphology in Faronitae (illustrations A and B, or otherwise expressed on the Figure label), and to the same structure, sexually modified in higher pselaphines as examples of the observed variation during the construction of this synthesis.

A linear regression analysis was used to assess the relationship between the number of described species worldwide for each Pselaphinae tribe and the total number of morphological variations for species within each tribe recorded in this study. The test statistic *t* was used to evaluate if there is a relationship between variables. The coefficient of determination r^2 was used to establish the strength of relationship between the two variables.

RESULTS

A total of 34 tribes, 106 genera, and 218 species were included to construct the matrix of secondary sexual characters (herein SSC). This species number is not yet adequate to conclude any ecological and biogeographical correlations since species descriptions and taxa catalogues are highly biased towards the Holarctic and Australasian regions. Nonetheless, it was possible to include several tribes, genera, and species that are endemic to certain less-studied biogeographical regions such the Neotropical and Afrotropical regions. This information was retrieved from 95 publications, dating from 1894 to 2019. Overall, the secondary sexual characters found in the largest number of species were the modification of male abdominal sterna, eye size reduction in females, male mesotibiae, and metasternum modifications (Fig. 1).

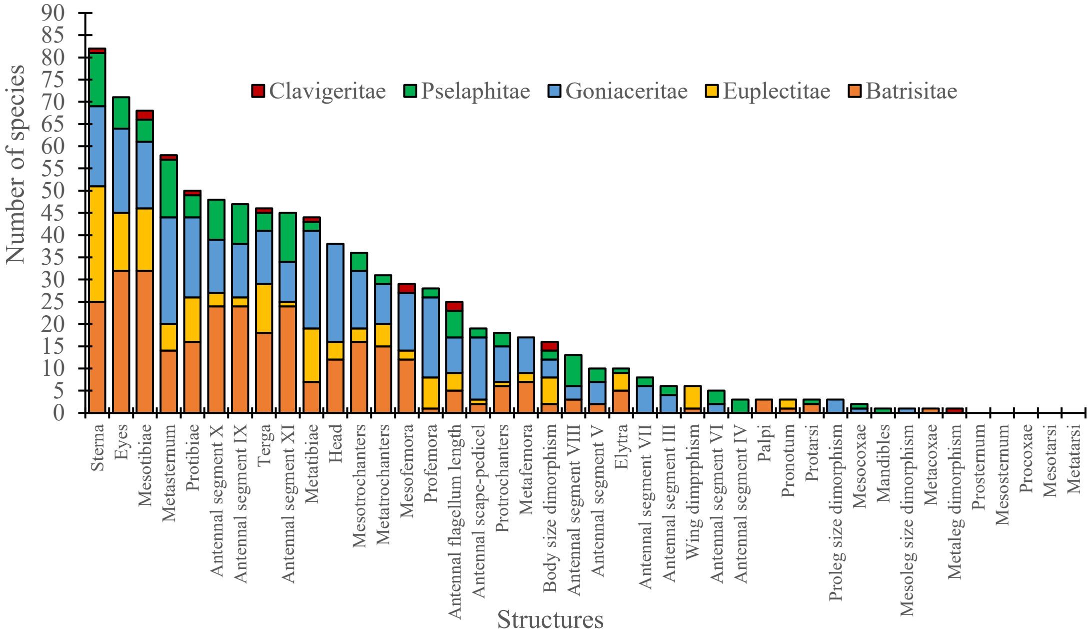


Figure 1. Number of species expressing secondary sexual characters on body structures of males from Higher Pselaphinae.

Antennal SSC

Most Pselaphines have 11-segmented antennae (figure 1A), except for the clavigerites (figure 1B), which present fusion of the terminal antennal segments, and some species of neotropical Goniacerini, some Bythinoplectini, and Cyathigerini species. Antennal sexual dimorphism was found in 22 tribes (table 1). Most secondary sexual characters (SSC) were found on antennomeres IX, X, and XI in 47, 47 and 44 species respectively, mostly in the tribes Batrisini (24, 23, and 23 species in seven genera) and Brachyglutini (10, 12, and 9 species in three genera). Flagellum length was the SSC most common among the tribes with dimorphism on the antennae, for a total of 12 tribes, 19 genera and 26 species. The tribe Bythinini had the most species with SSC in the scape-pedicel category, with 11 species from one genus. In general, the antennomeres III to VII changed the least, being dimorphic only in the tribes Arhytodini and Ctenistini, additionally, antennomere V changed in Batrisini and Brachyglutini; antennomere VII was also variable in the tribes Brachyglutini, Cyathigerini, Iniocyphini and Goniacerini.

Male scape and pedicel variation were observed in size related to flagellomere size; the scape can present dorso-ventral expansions, lateral asymmetry, be laterally swollen or ventrally flattened; an individual spine, tooth or tubercle can also be present. Antennal club, when present, was formed by the four or three apical antennomeres; intermediate antennomeres (III to VI, and sometimes VII) variation was limited to shape: transverse versus elongate, or size: same size or increasing in diameter distally. When variable, antennomere VII can show lateral asymmetry, have lateral excavations, differentiated setae, or being modified together with antennomere VIII. Antennomere IX can show lateral asymmetry, lateral excavations, denticles, lateral expansion, apophyses, specialized setae, or it can be bilobed; in many cases this antennomere marks the beginning of the antennal club. In the antennomere X (Figure 1C and D), variation was commonly encountered in its larger size compared to basal antennomeres, and its variations in shape; it can be also characterized by the presence of ventrolateral excavations, projections, tubercles, and be asymmetrically flattened. Finally, dimorphism in antennomere XI (Figure 2C and 2D) was related to its size, being in most cases the largest, and its lateral symmetry; other common variations were the presence of a single basolateral tooth, pore or tubercle, ventral or lateral excavations, and its surface bearing small tubercles.

Table 1. Antennal secondary sexual characters (SSC) in Pselaphinae tribes

Supertribe	**No.**	**Tribe (number of species)**	**Flagellum length**	**Scape-pedicel**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**total SSC**
BATRISITAE	1	Amauropini (5)										1	1	**2**
	2	Batrisini (65)	5	2			2			3	24	23	23	**82**
CLAVIGERITAE	3	Clavigerini (3)	2											**2**
EUPLECTITAE	4	Bythinoplectini (6)		1								2		**3**
	5	Euplectini (6)									1	1	1	**3**
	6	Jubini (1)	1											**1**
	7	Trichonychini (20)	3								1			**4**
	8	Trogastrini (2)	2	1										**3**
GONIACERITAE	9	Brachyglutini (22)	5	2	2		5	1	3	2	12	10	9	**51**
	10	Bythinini (14)	1	11						1				**13**
	11	Cyathigerini (3)			2			1	2					**5**
	12	Iniocyphini (3)							1					**1**
	13	Goniacerini (4)							1	1				**2**
	14	Proterini (3)										2		**2**
	15	Tychini (10)	2											**2**
PSELAPHITAE	16	Arhytodini (7)	1		1	2	2	2	1	2	1			**12**
	17	Ctenistini (4)	2		1	1	1	1	1	3	3	3	3	**19**
	18	Hybocephalini (3)									1	1	2	**4**
	19	Odontalgini (3)	2											**2**
	20	Schistodactylini (2)	1											**1**
	21	Tmesiphorini (3)								1	1	2	2	**6**
	22	Tyrini (6)		2						1	3	2	3	**11**
Total number of species with SSC			**27**	**19**	**6**	**3**	**10**	**5**	**9**	**14**	**47**	**47**	**44**	

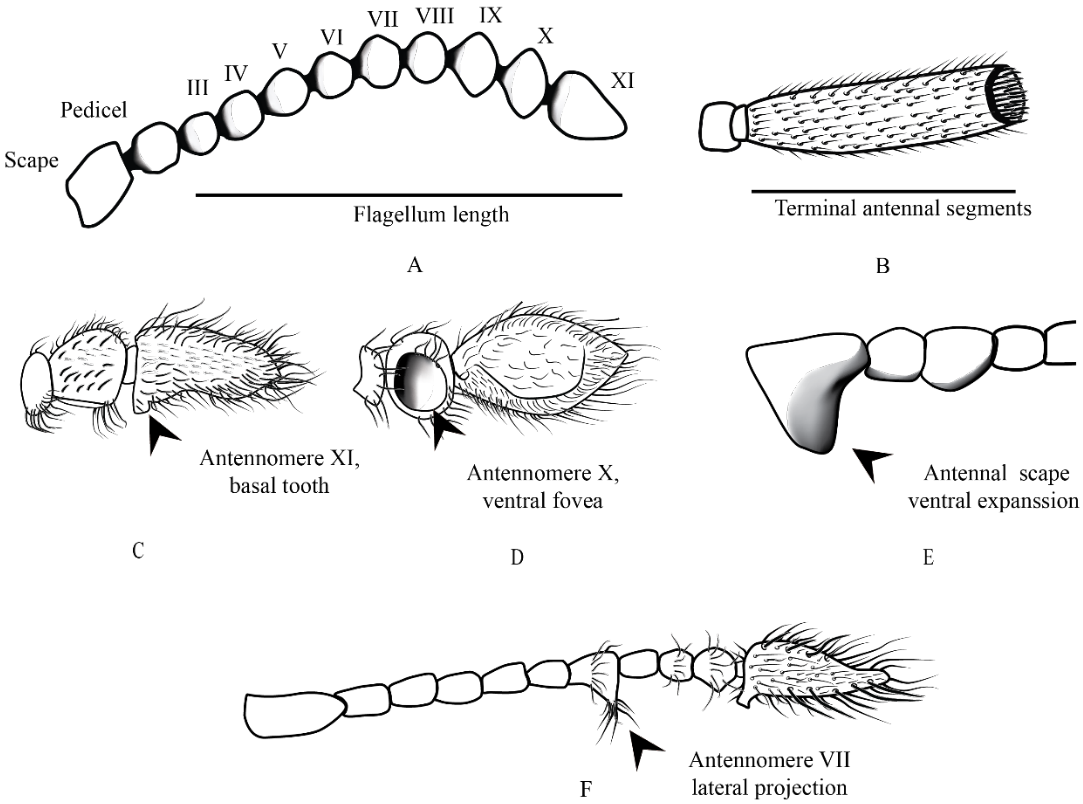


Figure 2. Antennae in Pselaphinae: A. Faronitae; B. Clavigeritae; C. male *Batrisodes riparius* (Batrisini) terminal antennomeres in lateral view; D. male *B. riparius* ventral view; E. Male *Batrisodes nigricans* frontal view; F. Male *Batrisodes schaumi*.

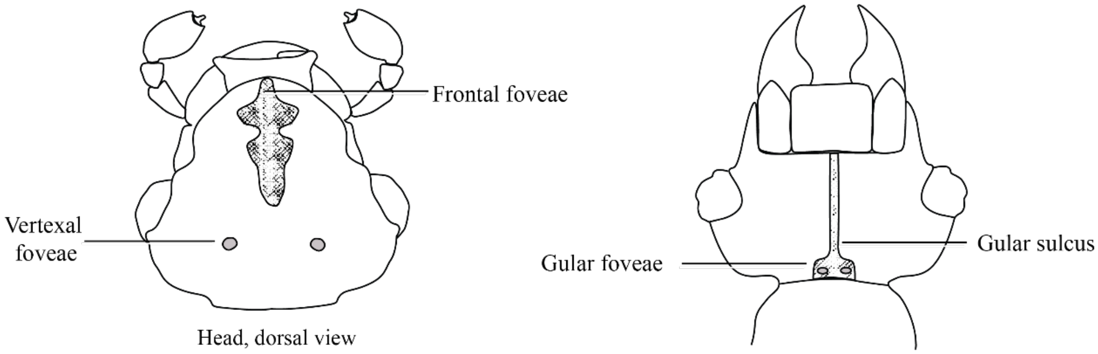
Head capsule, mouth parts, and eyes SSC

Sexual dimorphism in the head and head structures was found in 20 tribes (Table 2). Sexual variation on the eyes was the prevalent trait in 72 species and 34 genera; 32 of these species belonged to the tribe Batrisini. Overall, eye dimorphism was shared by 14 of the 20 tribes in this category. Head capsule variation was found in 38 species, with most species in Batrisini (six of 25 genera) and Brachyglutini (two of four genera). Sexual dimorphism in maxillary palpi was found only in three species from two genera in the tribe Batrisini, and only one species in the tribe Arhytodini showed variation in the mandibles.

Table 2. Head capsule and head structures SSC in Pselaphinae tribes.

Supertribe	**No.**	**Tribe (number of species)**	**Head capsule**	**Mandibles**	**Palpi**	**Eyes**	**total SSC**
BATRISITAE	1	Batrisini (65)	12		3	32	**47**
EUPLECTITAE	2	Bythinoplectini (6)	2			3	**5**
	3	Dimerini (1)	1				**1**
	4	Euplectini (6)				1	**1**
	5	Jubini (1)				1	**1**
	6	Trichonychini (20)				8	**8**
GONIACERITAE	7	Arnyllini (1)				1	**1**
	8	Brachyglutini (22)	11			4	**11**
	9	Bythinini (14)	6			6	**12**
	19	Cyathigerini (3)				1	**1**
	11	Goniacerini (3)				1	**1**
	12	Iniocyophini (3)	3				**3**
	13	Proterini (3)				1	**1**
	14	Tychini (10)	1			6	**7**
	15	Valdini (1)	1				**1**
PSELAPHITAE	16	Arhytodini (7)		1		1	**2**
	17	Ctenistini (4)				1	**1**
	18	Odontalgini (3)				1	**1**
	19	Tmesiphorini (3)				2	**2**
	20	Tyrini (6)				2	**2**
Total number of species with SSC in head capsule, mouth parts, and eyes			**38**	**1**	**3**	**72**	

Head variation can be summarized as dorsal (Figure 3A), ventral (Figure 3B), frontal (Figure 3C), and lateral variation (Figure 3D). Dorsal variation consisted of modifications of the occiput region, vertexal region, vertexal sulcus and foveae, such as longitudinal excavations, swelling, transversal excavations behind the anterior margin of the eyes, and antennal tubercles. Ventral variation was limited to the widening of the gular fovea and gular carina. Frontal dimorphism was represented by the presence of a transversal sulcus between the frontal region and the clypeus, clypeal tubercles, clypeal projections, specialized setae, and enlargement of the clypeal carinae. Lateral variation was found as extensions of the transversal frontal excavations below the antennal insertions, also lateral spines or projections behind the eyes, and convexity in the genal region.

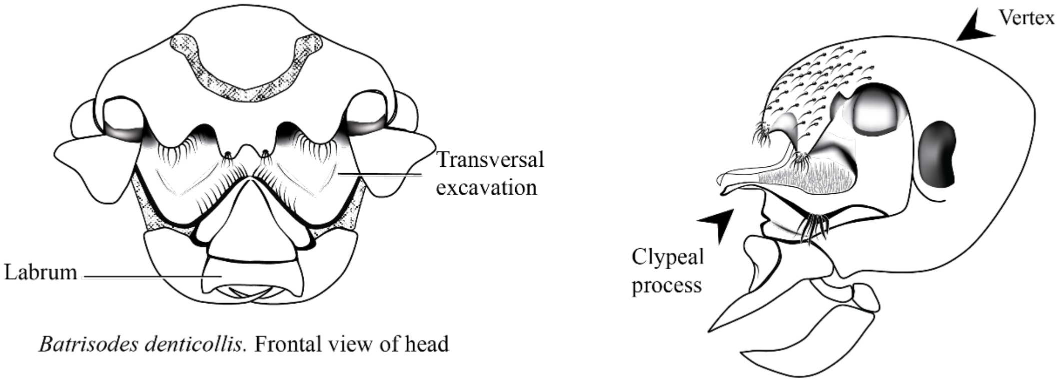


Head, dorsal view

A

Head, ventral view

B



Batrisodes denticollis. Frontal view of head

C

Batrisodes sinuatifrons. Lateral view of head

D

Figure 3. Head in Pselaphinae. A. Faronitae dorsal view; B. Faronitae ventral view; C. Male *Batrisodes denticollis* (Batrisini) transversal excavation on fronto-clypeal region, in frontal view; D. Male *Batrisodes sinuatifrons* (Batrisini) transversal excavation in fronto-clypeal region, in lateral view.

Thoracic SSC

Secondary sexual traits on the thorax were found in 17 tribes (table 3). Male metasternum was variable in 58 species and 27 genera from 16 tribes, with most species in the tribes Brachyglutini (three of four genera), Batrisini (six of 21 genera), and Trichonychini (one of nine genera). Elytra dimorphism was common in the tribes Batrisini, Thaumastocephalini, Bythinoplectini, Trichonychini, and Ctenistini. Only the tribes Thaumastocephalini (1 species) and Bythinoplectini (2 species) presented sexual characters in the pronotum.

Table 3. Thoracic SSC in Pselaphinae tribes.

Supertribe	No.	Tribe (number of species)	Elytra	Pronotum	Metasternum	Total SSC
BATRISITAE	1	Batrisini (65)	4		13	**17**
	2	Thaumastocephalini (8)	1	1	1	**3**
CLAVIGERITAE	3	Tiracerini			1	**1**
EUPLECTITAE	4	Bythinoplectini (6)	1	2		**3**
	5	Trichonychini (20)	3		6	**9**
GONIACERITAE	6	Brachyglutini (22)			19	**19**
	7	Cyathigerini (3)			3	**3**
	8	Speleobamini (2)			2	**2**
	9	Tychini (10)			1	**1**
PSELAPHITAE	10	Arhyodini (8)			2	**2**
	11	Ctenistini (4)	1		1	**2**
	12	Hybocephalini (3)			1	**1**
	13	Odontalgini (3)			1	**1**
	14	Phalepsini (1)			1	**1**
	15	Pselaphini (4)			3	**3**
	16	Schistodactylini (2)			1	**1**
	17	Tmesiphorini (3)			1	**1**
	18	Tyrini (6)			2	**2**
Total number of species with SSC in Thorax			**10**	**3**	**59**	

Metasternum enlargement between the metacoxae was common, together with the longitudinal sulcus and its variable depths and widenings; these regions could be covered by differentiated setae; lamellae and ctenidia can be also present on the posterior margin of metasternum; also metasternal tubercles could be present and directed towards anterior, ventral, or posterior body regions (Figure 4C). Pronotal dimorphism was found mostly in size, shape, and pronotal sulci and foveae intensity and definition between males and females. Likewise, elytra differences were limited to their size and proportions between the two sexes.

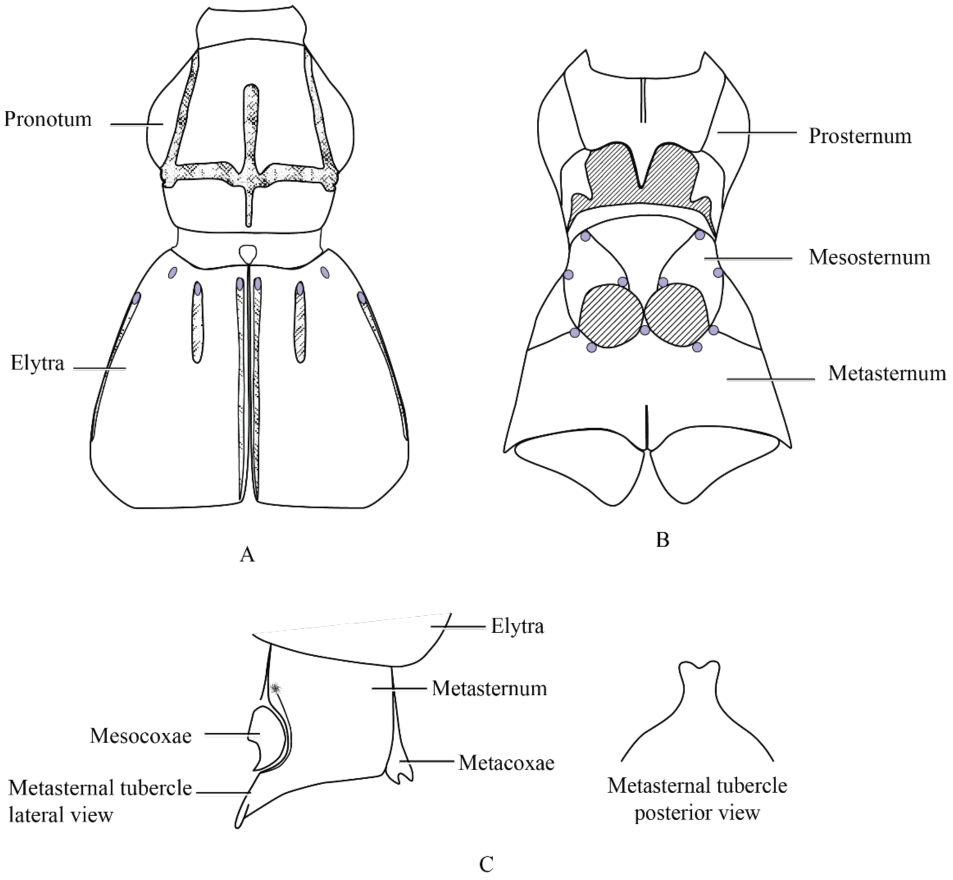


Figure 4. Thoracic structures: Faronitae A. Dorsal view; B. Ventral view. Speleobamini C. Metasternal tubercle in male of *Prespelea myersae* (modified from Caterino and Vasquez-Velez 2017).

Abdomen SSC

Abdominal sexual dimorphism was seen in 23 tribes (table 4). Most SSC were found on abdominal sterna in 82 species in 48 genera from 21 tribes, while dimorphic characters in the abdominal terga were observed in 45 species in 21 genera from 10 tribes. The tribes that included more genera with sexual dimorphism in the abdominal sterna and terga were Batrisini, with nine and five genera, respectively, then Trichonychini with six and four genera, and Brachyglutini with four and two genera, respectively.

Sexual dimorphism on the abdominal sterna was characterized by the presence of a flattened surface on some segments or throughout the abdominal length; some segments could be completely concave or with central or longitudinal depressions. Tubercles, protuberances, and convex sternite surface were also present (Figure 5C). Abdominal sterna could be modified on their margins, either by projecting posteriorly or with showing emarginations. Frequently, abdominal sternites were covered by dense hairs, thick setae, or small denticles. Abdominal terga was exemplified by modification of segments IV and V (visible segments 1 and 2) mainly; protuberances, impressions, longitudinal and transversal carinae were found to be in the median region of the tergites; these modifications were frequently bearing tuft of long hairs, short hairs covering the surface or small spines (Figure 5D and E).

Table 4. Abdominal SSC in Pselaphinae tribes.

Supertribe	**No.**	**Tribe (number of species)**	**Tergites**	**Sternites**	**Total SSC**
BATRISITAE	1	Batrisini (65)	18	25	**43**
CLAVIGERITAE	2	Collilodionini (1)		1	**1**
	3	Tiracerini (1)	1		**1**
EUPLECTITAE	4	Dimerini (1)		1	**1**
	5	Euplectini (7)		6	**6**
	6	Jubini (1)	1	1	**2**
	7	Mayetiini (3)		3	**3**
	8	Metopiasini (1)		1	**1**
	9	Trichonychini (20)	10	14	**24**
GONIACERITAE	10	Brachyglutini (22)	8	9	**17**
	11	Cyathigerini (3)	1	2	**3**
	12	Imirini (1)		1	**1**
	13	Iniocyphini (3)		2	**2**
	14	Proterini (3)	1		**1**
	15	Tychini (10)	2	3	**5**
	16	Valdini (1)		1	**1**
PSELAPHITAE	17	Arhyodini (8)		4	**4**
	18	Hybocephalini (3)		1	**1**
	19	Odontalgini (3)		1	**1**
	20	Pselaphini (4)	2	3	**5**
	21	Schistodactylini (2)		1	**1**
	22	Tmesiphorini (3)		1	**1**
	23	Tyrini (6)	1	1	**2**
Total number of species with SSC in Abdomen			**45**	**82**	

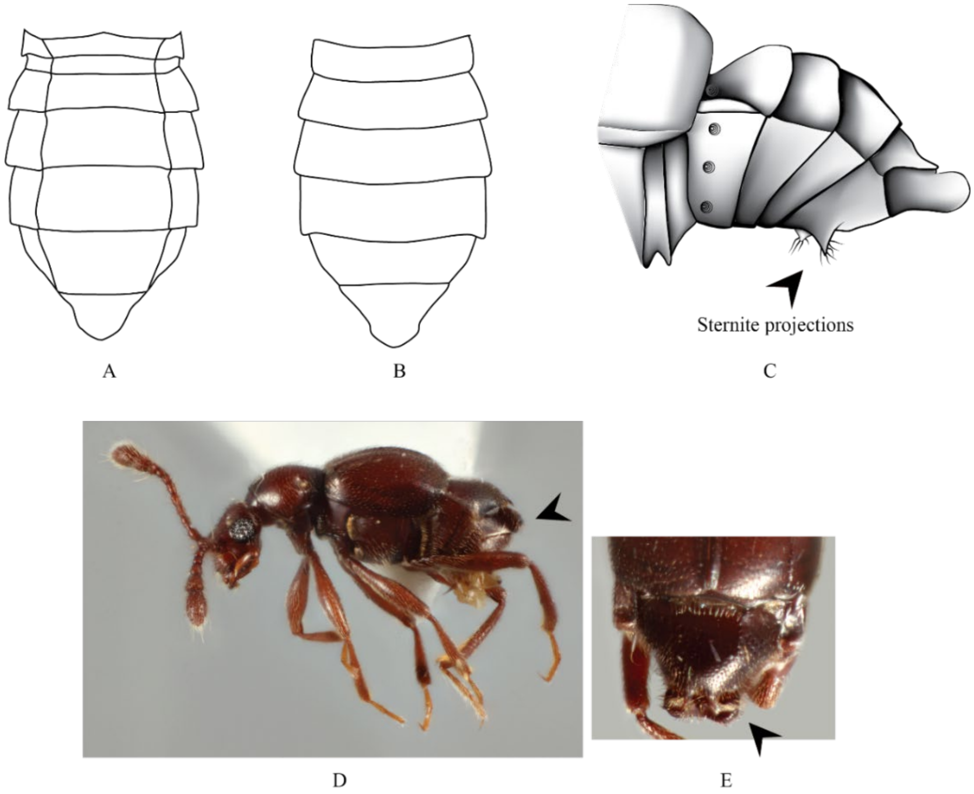


Figure 5. Abdomen: Faronitae A. Dorsal, B. Ventral; Batrisini C. Male *Batrisodes cryptotexanus* modification of abdominal sterna, lateral view; Brachyglutini D. Male *Brachygluta ulkei* modification of abdominal terga, lateral view; E. male *B. ulkei,* dorsal view.

Leg SSC

Secondary sexual traits on legs were observed in 21 tribes (Table 5). In general, tibial segments presented higher variation; mesotibial dimorphism was present 67 species in 32 genera, being the most variable segment on legs, followed by protibial variation in 49 species in 21 genera, and metatibial dimorphism in 43 species in 18 genera. The SSC at the mesotibiae were found in 28 species of Batrisini (12 of 25 genera), 11 from Trichonychini (three of six genera), and 10 Brachyglutini (two of four genera). The tribes

Trichonychini and Bythinini had nine species each where protibial dimorphism was present, followed by the tribes Batrisini and Thaumastocephalini, with eight species each. Metatibial sexual dimorphism was found in 10 species of Bythinini (one of three genera), and 10 species of Brachyglutini (three of four genera). The leg segments that varied the least among tribes were the mesocoxae, variable only in one species of Brachyglutini and one of Schistodactylini, and the metacoxae were dimorphic in just one species in the tribe Batrisini.

The variation recorded on the protrochanters was mainly the presence of a single spine on ventral surface or a long digitiform apophysis; the spine could be sharp, acute, or small resembling a tubercle. Profemora were found to get thick around their middle, and to bear a tubercle near their bases. Protibiae could have on their surface a single tooth on the mesial region, a medioapical spur, and short denticles or spines; protibial surface could also be covered by short and dense pubescence, bear a transverse sulcus on the mesal margin, or be swollen in the middle. Protarsi could present variations on the second segment as being bilobed or bearing a small denticle. Dimorphism on the mesocoxae was a limited to a small tooth. Mesotrochanter variations were on the ventral and posterior margins, represented by a single spine, tooth or apophysis, in most cases these were short, round, blunt, apically curved, or long and stout; in addition, short setae or long bristles could be present. Mesofemora were found to vary in their thickness more than other leg segments; most modifications along their surface were a single protusion, spine, tooth, or carinae, commonly located on the ventro-basal, or postero-median margins (Figure 6); only in Clavigerini, a small spine was observed just beyond the midpoint. Mesotibial modifications were found more frequently on the preapical and apical portions of the segment, and near to the base in a few instances; these modifications included a single tooth, spur, or denticle, and acute mucro; short pubescence could be covering any of these projections. In several cases these leg segments were curved inwards. On the hind legs, metacoxae were covered in setae and elongated posteriorly. Metatrochanters showed dimorphisms on the posterior and ventral margins, bearing one short tooth, spur or denticle; a longer and apically curved apophysis, scoop-like apical hook or a very oblique tooth could be present, and sometimes the whole segments were densely covered with long hairs. Metafemora presented variations on their base, in the anterior side with an excavation coated with a setiferous patch, and the posterior side could be sinuated, or have a carina covered with a tuft of hair, a small protuberance, and an angular projection. The ventral margin could bear spines near the apex or be flattened and glabrous. Finally, on the metatibiae, the most common modifications were at their apex on the mesal margin; these consisted in a flange with three spines, solitary spurs of different lengths and thickness, trichomes, and dense combs of setae.

Table 5. Leg SSC in Pselaphinae tribes. cx = coxae, trch = trochanters, fmr = femora, tb = tibiae, and trs = tarsi.

Supertribe	**No.**	**Tribe (number of species)**	**Pro-leg**				**Meso-leg**				**Meta-leg**				**Total SSC**
			trch	**fmr**	**tb**	**trs**	**cx**	**trch**	**fmr**	**tb**	**cx**	**trch**	**fmr**	**tb**	
BATRISITAE	1	Amuropini (6)						1	3	3				3	**10**
	2	Batrisini (65)	5	1	8	2		14	9	28	1	14	7	4	**93**
	3	Thaumastocephalini (8)	1		8			1		1					**11**
CLAVIGERITAE	4	Clavigerini (3)							2	2					**4**
	5	Tiracerini (1)			1					1				1	**3**
EUPLECTITAE	6	Dimerini (1)										1	1	1	**3**
	7	Euplectini (7)		1	1			2	1	3		2	1	2	**13**
	8	Mayetiini (3)										1			**1**
	9	Trichonychini (20)	1	6	9			1	1	11		1		9	**39**
	10	Trogastrini (2)								1					**1**
GONIACERITAE	11	Brachyglutini (22)	6	8	4		1	10	8	10		6		10	**63**
	12	Bythinini (14)		8	9			1	1			1	6	10	**36**
	13	Cyathigerini (3)			3					3					**6**
	14	Goniacerini (3)		1		1			4				1		**7**
	15	Iniocyphini (3)		1				1	1				1	1	**5**
	16	Proterini (3)	2		2			1		2					**7**
	17	Speleobamini (2)										2			**2**
	18	Tychini (10)			1					2					**3**
PSELAPHITAE	19	Arhyodini (8)			3					4		1			**8**
	20	Odontalgini (3)	1												**1**
	21	Schistodactylini (2)			1		1							1	**3**
	22	Tmesiphorini (3)		1		1									**2**
	23	Tyrini (6)	2	1	2			3		1		1		1	**11**
Total number of species with SSC in Legs			**18**	**28**	**49**	**4**	**2**	**35**	**31**	**68**	**1**	**31**	**18**	**43**	

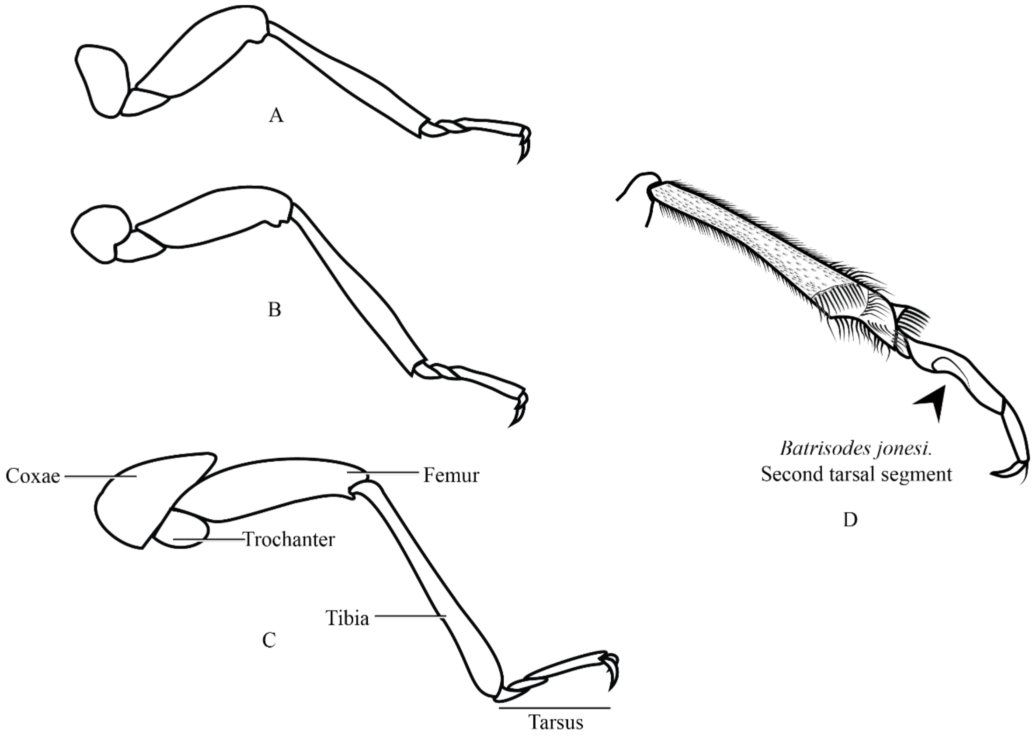


Figure 6. Legs in Pselaphinae. A. Prothoracic leg; B. Mesothoracic leg; C. Metathoracic leg with leg parts; D. Sexual dimorphism in a Batrisini species.

Wing and size dimorphism

Wing dimorphism was present in six species from the tribes Batrisini, Bythinoplectini, Jubini, and Trichonychini (table 6). Body size dimorphism was found in 15 species from the tribes Amauropini, Thaumastocephalini, Clavigerini, Euplectini, Trichonychini, Bythinini, Tychini, Ctenistini, and Odontalgini. Only eight species showed size dimorphism in any of the legs, with six species in the tribe Brachyglutini.

Table 6. Wing and Size dimorphism in Pselaphinae tribes

Supertribe	**No.**	**Tribe (number of species)**	**Wing dimorphism**	**Size dimorphism**				**Total SSC**
				Pro-leg	**Meso-leg**	**Meta-leg**	**Body**	
BATRISITAE	1	Amuropini (6)					1	**1**
	2	Batrisini (65)	1					**1**
	3	Thaumastocephalini (8)					1	**1**
CLAVIGERITAE	4	Clavigerini (3)					2	**2**
EUPLECTITAE	5	Bythinoplectini (6)	2					**2**
	6	Euplectini (7)					1	**1**
	7	Jubini (1)	1					**1**
	8	Trichonychini (20)	2		1		5	**8**
GONIACERITAE	9	Brachyglutini (22)		3	3	1		**7**
	10	Bythinini (14)					1	**1**
	11	Tychini (10)					2	**2**
PSELAPHITAE	12	Ctenistini (4)					1	**1**
	13	Odontalgini (3)					1	**1**
Total number of species with wing and size dimorphism			**6**	**3**	**4**	**1**	**15**	

The correlation between the number of described species worldwide in Pselaphinae tribes and the sum of SSC recorded for each tribe in this study (Fig. 7) was significantly positive (r^2=0.86, 32 d.f., *p*-value< 0.00001). The tribes Batrisini, Brachyglutini, Trichonychini, Tyrini, and Bythinini showed the largest amount of secondary sexual traits. Also, these four tribes contain most of the described species of Pselaphinae worldwide.

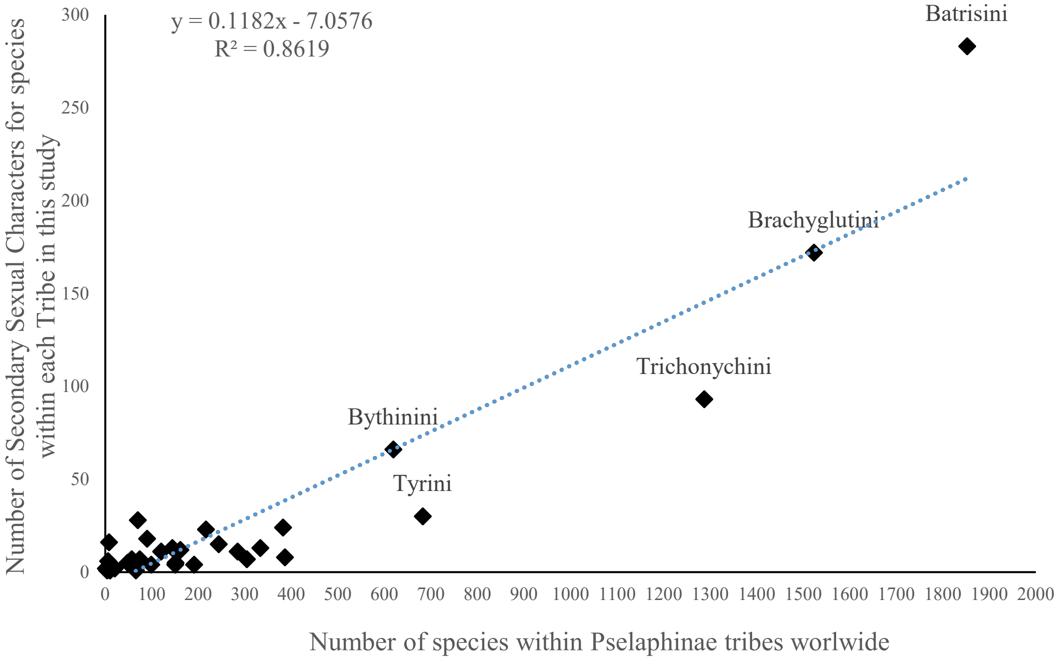


Figure 7. Relation between number of species worldwide and number of Secondary Sexual Characters in Pselaphinae tribes.

DISCUSSION

Secondary Sexual Characters are widespread through all major lineages within Pselaphinae. Several authors agree on the tendency of these characters to change at the intrageneric level (Park 1947, De Marzo 1989, Chandler 2001), and in some cases intraspecific levels (Besuchet and Kurbatov 2007). At the tribal level it is difficult to trace a relationship from ancestral to derivate states for SSC. Nonetheless, characters in the abdominal sterna, eyes, and mesotibiae are frequent in all tribes, with at least half of the genera carrying them (Appendix A). It is important to mention that in the supertribe Faronitae (i.e. Park and Carlton 2014), several genera present sexual dimorphism of the abdominal sterna, which could suggest that sexual dimorphism on male abdomen could be an ancestral condition for secondary sexual characters in Pselaphinae. Sexual dimorphism on the abdominal ventrites is also present in other Staphylinidae lineages; for instance, in the neotropical genus *Nordus* Blackwelder (Staphylininae: Staphylinini), males present modification on the segments VII, VIII, and IX of the abdominal sterna (Chatzimanolis 2005); and in some species of the genus *Bryoporus* Kraatz (Staphylinidae: Tachyporinae) males present groups of setae medially on the apical margin of the eight abdominal sternite (Campbell 1993). As with many other morphological characters, SSC in Pselaphinae seem to have been gained and lost in different tribes during the evolution of the group (Chandler 2001). For example, in batrisines and brachyglutines, antennal dimorphism at the apical four to three antennomeres shows some similarities among members of the two tribes: the presence of solitary foveae, depressions, or concavities, as well as spines, lateral projections, or teeth; frequently associated to modified setae or hairs. In contrast, in the tribes Euplectini, Trichonychini, and Bythinoplectini (from Euplectitae), four of the genera included in this study, present secondary sexual traits of the apical antennomeres, limited to changes in the shape and degree of symmetry in relation to the rest of the antennae.

When compared to other subfamilies in Staphylinidae, Pselaphines have characteristic compact bodies, reinforced by the internal projections of the foveae on their integument (Nomura 1991; Chandler 2001); as consequence, the abdominal flexibility common to other staphylinid groups is limited in pselaphines (Newton and Thayer 1995). Likewise, Pselaphines are the only ones among other Omaliinae-group members to present secondary sexual characters, other than wing dimorphism (Thayer 1992) or modification of the abdominal sternites. From the few cases where copulatory behavior in staphylinids has been documented (Peschke 1987; Betz 1999; Drugmand 1992; Alcock 1991; Alcock and Forsyth 1988; Forsyth and Alcock 1990), it is common to find that males and females flex their abdomens upwards before and during copula, and from side to side as a signal of rejection from female to male. In *Aleochara curtula* (Staphylinidae: Aleocharinae), males can grab females' terminalia with their clasp-like genitalia while bending the abdomen (Peschke 1987). In *Eusphalerum* (Omaliinae), the male would be on top of the female with his prolegs around the articulation between the pronotum and the elytra, his mesolegs would rest upon the mesopleural region, and the metalegs would be at the apex of the female's elytra or on her abdomen for at least one hour. The copula lasts only a few seconds, and starts when the male arches his body and touches the last segments of the female's abdomen with his own, the female moves side to side several times, and when stops the male makes pressure with the aedeagus on the females last sternites, the apex of the median lobe enters the female's genital tract, while the parameres keep resting on the female's sternites (Drugmand 1992). Male abdominal morphology in higher Pselaphinae suggests that flexing this part of the body before or during mating could be difficult, contrary to the observed in other Staphylinidae. In the genus *Plagiophorus* Motschusky (Goniaceritae: Cyathigerini), the abdomen is composite, with tergal and sternal segments IV to VII fused in both sexes; males have a large concavity on the abdominal composite sternum, and in some species the antennal clubs are concave ventrally as well. Sugaya (2005) observed in a pair of *Plagiophorus amygdalinus* Sugaya, that during copula while the male mounts the female, their abdomens fit when the large concavity on the male's composite sternite receives the female’s composite tergite, and keeps the couple connected during their interaction. This observation suggests a possible function of the SSC in the abdominal sternum; if copulatory behavior requires immobilization of the female’s body, it could be possible that Pselaphinae males have to use, beside abdominal modifications, other body parts to hold onto their mates; for example, male legs would be important to maintain female’s position before intromission of the male’s genitalia. If this were the case, it would be expected for males mesolegs to show modifications such as spines or protuberances along the leg segments. The copulatory behavior described above could explain, in part, the ubiquity of sexual secondary characters on abdominal sterna (Fig. 10) and legs (Table 5) found in the present study.

Pselaphinae beetles have shown a high reliance on their olfactory system to find a capture prey; maxillary palps, antennae, and leg segments are important during feeding behavior for males and females (Schomann *et al.* 2008). More than other body parts, antennae are covered in different types of sensilla, that allow the beetles to distinguish the direction of chemical cues in their environment. Schomann and collaborators (2008), studying prey capture behavior in six different species of European pselaphines, found that apical antennomeres have a higher concentration of olfactory sensilla, which were used during prey search by movement of the antennae. Although there were not differences reported between male and female antennae, it was observed that ommatidia number and size of the cornea were lower in the female compared to the male of *Bryaxis puncticollis* (Goniaceritae: Bythinini). Given the importance of the olfactory system for feeding behavior in Pselaphines, it is expected that this system would be formed by the same anatomical elements in males and females. However, the morphological differences found on the male antennae of different lineages, suggest that males could use these antennal modifications to attract females by exploiting their already tuned olfactory system (West-Eberhard 1984; Andersson 1994). As reported here, males of several species in the tribe Batrisini present enlargement of the two terminal antennomeres (i.e. Fig. 2C and D). For instance, De Marzo and Vit (1983), studied the internal morphology of the male antennae in several species of palearctic *Batrisodes* and *Batrisus.* Within each antennomere there is a glandular reservoir that changes in shape and size according to the species; in antennomere XI, the glandular unit is connected to the external surface through a series of small channels that lead to a tubercle at the base of the antennomere; in the antennomere X, the glandular reservoir is connected to separated glandular channels that lead to a larger surface on the exterior. In the females, these two antennomeres are simple, containing a few, small, and isolated glandular units, among many units of the olfactory system (De Marzo and Vit 1983; De Marzo and Vovlas 1989). Nonetheless, sexual dimorphism on antennomeres and head capsule (Fig. 10) seem to be less common than abdominal or legs dimorphism. Head capsule dimorphism appears to absent in the Supertribes Pselaphitae and Clavigeritae; in this monophyletic group, antennal dimorphism is limited to differences in the flagellum length, where some antennomeres are larger in males compared to females. In the “Tyrini group” of tribes (Ctenistini, Hybocephalini, Odontalgini, Tmesiphorini, and Tyrini), males do not show modifications in cephalic capsule, as the other Pselaphitae groups, but many species within this related tribes have asymmetric antennomeres, and different flagellum lengths. Secondary sexual characters on the head capsule are present in the two most diverse tribes Batrisini and Brachyglutini, and in their closely related respective tribes, Trogastrini and Bythinini. No hypotheses have been proposed for their function, although their evolution could be related to the protection of the cephalic appendages (Coulon 1989).

Another aspect of Pselaphinae natural history is that phenotypic plasticity seems to occur in different lineages; for instance, species with dimorphic males have been found in the tribes Batrisini (Nomura 1991), Bythinini (Besuchet and Kurbatov 2007), Bythinoplectini (Coulon 1989), Hybocephalini (Yin *et al.* 2020), among others. Dimorphic forms are characterized, in most cases, by brachypterous and macropterous males, with females being commonly brachypterous as well. The reduction on wings has been seen accompanied by a reduction or atrophy of the eyes' size (Batrisini, Nomura 1991; and Bythinoplectini, Coulon 1989). In other cases, major males would show secondary sexual characters, while minor males would be similar to females (Bythinini; Coulon 1989). If phenotypic plasticity is widespread in Pselaphinae, during evolutionary time, these morphological differences can impact lineage diversification by acting together with either natural selection, for example different microhabitat preferences in the two male phenotypes, or sexual selection, if there is divergence on female choice that benefits differential reproductive success in both male forms (West-Eberhard 2003).

Phylogenetic relationships within Pselaphinae continue to be evaluated constantly through morphological and molecular characters (Parker and Grimaldi 2014; Parker 2016; Yin *et al.* 2017; Yin *et al.* 2019). Figure 8 shows the current phylogenetic hypothesis about the relationships within higher Pselaphinae. Batrisini and Brachyglutini are currently the tribes with more described species worldwide with 1,852 and 1,523 species, respectively; also, these had larger numbers of SSC recorded in the present study. Under this phylogenetic hypothesis both Batrisini and Brachyglutini are sister taxa to tribes with significantly lower number of species worldwide: Batrisini with Trogastrini (150 species), and Metopiasini (66 species) + Jubini (151 species); and Brachyglutini with Bythinini (619 species) + the Trichonychine genus *Oropodes*. Differences in species diversity and presence of sexual dimorphisms between sister clades can indicate that the process or processes promoting species diversity have impacted differently each sister clade; if after the ancestral lineage split, the resulting sister groups were exposed to different environments, from ecological shifts at the local scale, to new geographical distributions, the distinct selective pressures would affect diversification and extinction rates of the resulting lineages (Barraclough *et al.* 1998). However, because of the limited sampling of secondary sexual characters in many of the Pselaphinae tribes included here, assessing the relationship between secondary sexual characters and species richness, can be biased by several factors. First, species descriptions can vary on the detail level which is used to delimit a species; for example, some authors may focus more in describing genitalia characteristics rather than external morphology, because in many cases these are the only structures with different morphology in closely related species. Second, some species descriptions are vague when indicating the qualities of the secondary sexual characters present in the species, commenting only which structures show dimorphism, without recording further details. Thus, any sexually dimorphic structure present in the species will not be recorded in works such this, unless specimens of said species can be observed directly.

In the last decade, several fossil specimens from Burmese amber (around 99 Ma) have been recovered and described: *Boreotethys arctopteryx* Parker 2016*, B. grimaldii* Parker 2016, and *Cretobythus excavatus* Yin, Parker, and Cai 2018 from the tribe Bythinini; *Cretobrachygluta laurasiensis* Yin, Kurbatov, Cuccodoro, and Cai 2019 from the tribe Brachyglutini; and *Protrichonyx rafifrons* Parker 2016, *Priscaplectus carinatus* Yin, Chandler, and Cai 2019, and *P. grandiceps* Yin Chandler, and Cai 2019, all left as *incertae sedis* but within the supertribe Euplectitae. From these, *Cretobrachygluta* and *Priscaplectus* spp. show evidence of secondary sexual characters. *Cretobrachygluta* shows protuberances on mesotrochanters, apical spine on mesotibiae, and the abdominal tergite VIII with an apical notch (Yin *et al.* 2019); while *Priscaplectus carinatus* showed modification on the vertex region, and *P. grandiceps* presented protuberances on the metatrochanters (Yin *et al.* 2019). Therefore, these findings suggest that secondary sexual characters in the Higher Pselaphinae lineage had already evolved around the Cretaceous.

The origin and evolution of secondary sexual characters in any animal group are difficult to figure out. In the particular case of pselaphine beetles, it seems that the innovations that have been suggested to explain the evolution of myrmecophiles in the group (Parker and Grimaldi 2014; Parker 2016), are the same that helped the different lineages within Higher Pselaphinae to evolve many of the sexual modifications observed in males. The transition from the highly flexible abdomen in staphylinids to the strengthening of the body in pselaphines, worked as a preadaptation to inquiline life, environmental protection, and as a selective pressure to use modifications on the body appendages to ensure mating success. In other words, a compact body may have increased survival by protecting against environmental conditions and predators, but at the same time limited abdomen mobility, and forced the use of legs and abdominal ventrites to hold onto the females during copula. Under these conditions, the great diversity of Pselaphinae beetles is probably the consequence of first natural selection, and then maybe reinforced by sexual selection. These hypotheses could be tested by comparing mating displays among higher Pselaphinae and their sister group Faronitae. Looking at morphological and putative behavioral differences between these two groups can elucidate whether males have distinct ways to approach females or not, and how SSC are used during these interactions.

This study is an attempt to explore the diversity of forms that have helped taxonomists to discriminate between related genera and species. These characters are remarkably valuable for the taxonomy of the hyperdiverse Pselaphinae. Because these characters are unique on each species, their use to classify higher taxa is reduced. Nevertheless, their great variation is also intriguing because they may represent an important part of the evolutionary history that took Pselaphines to be so diverse. To record all the diversity of secondary sexual characters in this group is a monumental task, since the current study includes roughly 2% of all the species of Pselaphinae. Behavioral observations and phylogenetic analyses to compare the evolution of these traits are pivotal to understand how these characters are used, and how they correlate with other aspects of Pselaphinae evolution.

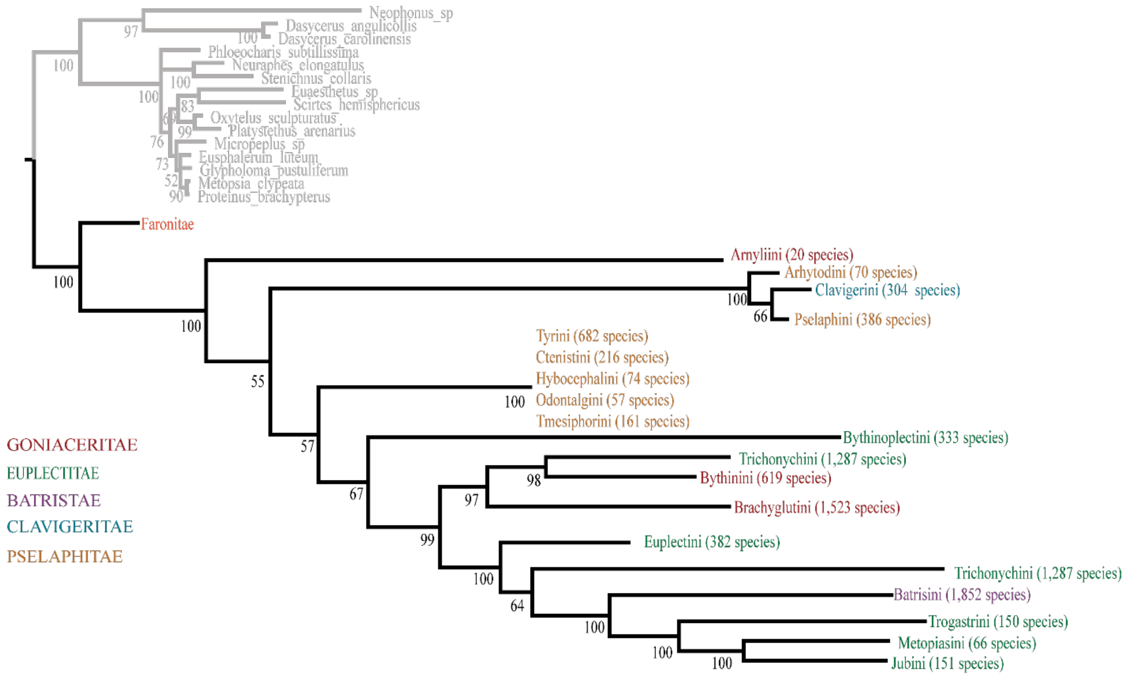


Figure 8. Phylogenetic relationships within higher Pselaphinae among tribes (modified from Parker 2016).

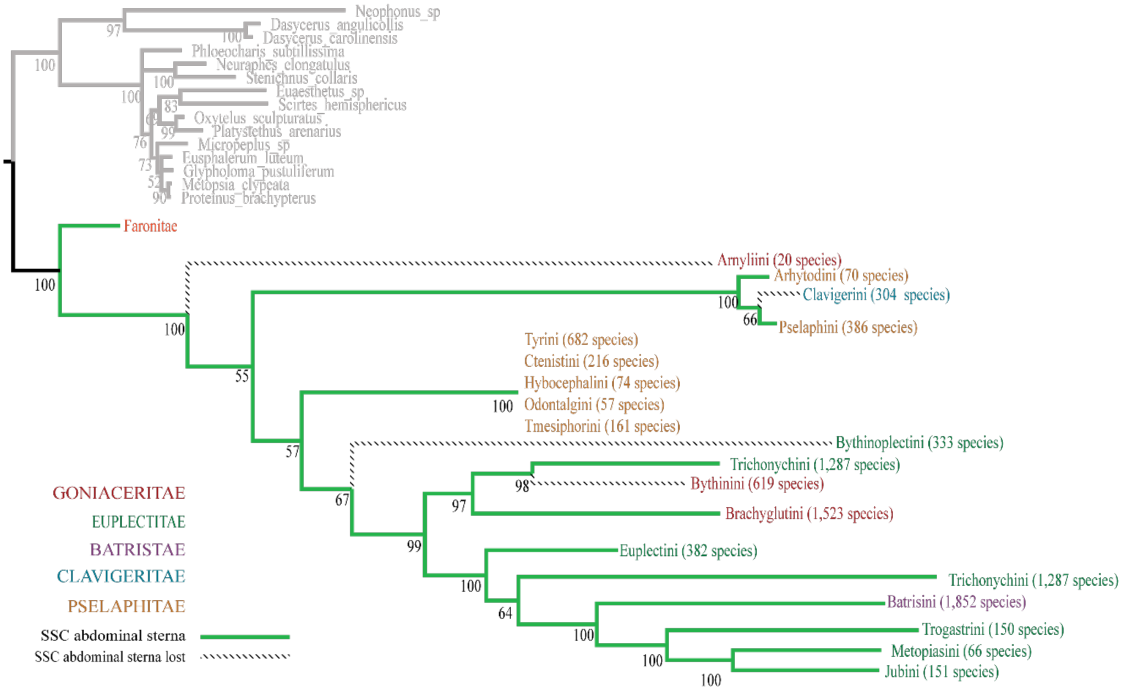


Figure 9. Distribution of Secondary Sexual Characters on abdominal sterna throughout Higher Pselaphinae tribes.

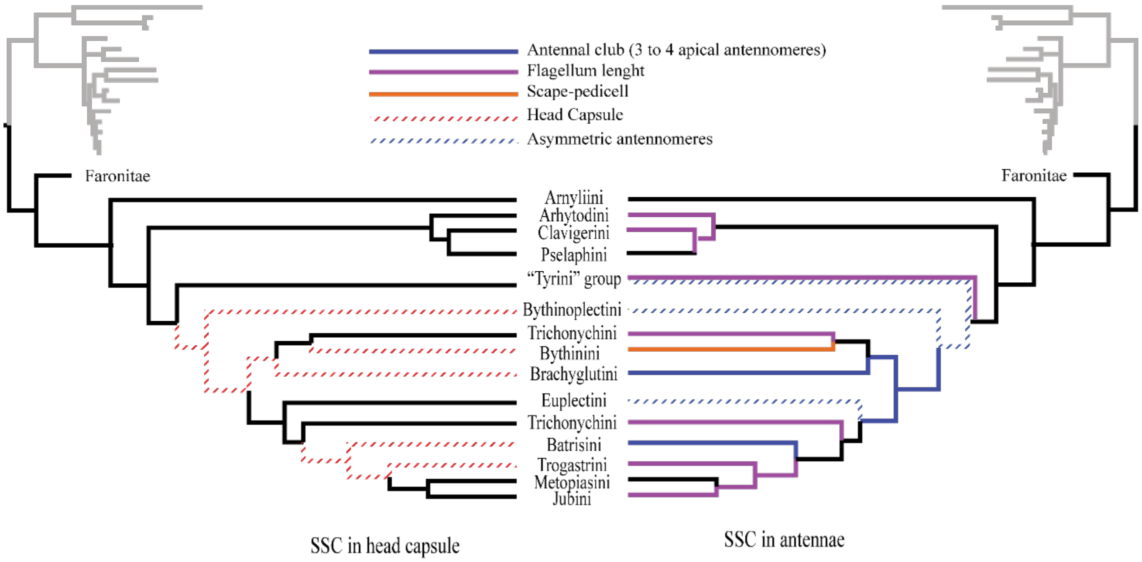


Figure 10. Distribution of Secondary Sexual Characters on head capsule (left) and antennae (right) throughout Higher Pselaphinae tribes.

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CHAPTER THREE

EVOLUTION OF SECONDARY SEXUAL CHARACTERS IN *BATRISODES* REITTER, 1882 (STAPHYLINIDAE: PSELAPHINAE) FROM NORTH AMERICA, NORTH OF MEXICO

INTRODUCTION

The genus *Batrisodes* comprises around 160 species distributed in the Holarctic region (Newton & Chandler 1989; Chandler *et al.* 2009; Yin & Li 2013; Newton 2018), there are 64 species described for the Palearctic region with 19 species from Europe, and 44 species from Asia (Yin & Li 2013; Yin *et al.* 2015; Newton 2018). In North America, the genus includes 85 species, and one subspecies, divided in seven subgenera, and one species *B. juvencus* Brendel 1865, is not assigned to any subgenus (86 described species total) (Ferro & Carlton 2014). The subgenera *Babnormodes* Park 1951 (33 species), *Declivodes* Park 1951 (4 species), *Elytrodes* Park 1951 (1 species), *Excavodes* Park 1951 (20 species), *Pubimodes* Park 1951 (5 species), and *Spifemodes* Park 1953 (1 species), are present in the central and eastern regions; while *Empinodes* Park 1953 (19 species), is restricted to the western region (Grigarick and Schuster 1962; Newton & Chandler 1989; Chandler 1997).

As with most pselaphines, *Batrisodes* species are frequent in leaf litter, rotten wood, beneath loose bark, and inside tree holes; many species visit or live inside ant nests (Park 1947; Yin *et al.* 2015), while others live in caves (Park 1947; Park 1951; Park 1958; Park 1960; Chandler *et al.* 2009). There are 21 described species of *Batrisodes* collected with four different genera of ants, without a species-specific relationship (Park 1947; Chandler

1997). *Babnormodes* and *Excavodes* are the subgenera with larger numbers of cave inhabitants; of the described species known only from cave interior and cave entrance, 70% belong to *Babnormodes,* and 35% to *Excavodes* (Chandler *et al.* 2009). The preference for humid and dark places could have been a characteristic that took *Batrisodes* species to colonize habitats such as caves and nests, where they can act as predators or scavengers on mites, earthworms, and ant brood (Park 1947).

Batrisodes subgenera were proposed by Park (1951, 1953, 1960) to accommodate different species groups from North America and to differentiate these from Palearctic species. Park (1951) divided the genus into two groups of species for the Nearctic, based on genitalia morphology, metatibial spur presence, and male secondary sexual characters. One group of species was assigned to the subgenus *Batriasymmodes*, where males have complex genitalia with basal bulb, internal musculature, and articulate styles, and the metatibiae lack of an apical spur. Most other North American species were classified into five subgenera, where the aedeagus is reduced and sclerotized, lacking a basal bulb, internal musculature, or styles, and the apical spur on the metatibiae is present. The different subgenera are based on male secondary sexual characters, number of elytral foveae, presence of pubescence on the vertexal foveae, and integumental texture. The subgenus *Babnormodes* includes species where males have a ventral incision on the second segment of the mesotarsi; in *Excavodes* males present a transversal excavation between the antennae; males in the subgenus *Pubimodes* also bear the transversal excavation between the antennal insertions, and the vertexal foveae in both female and males are densely pubescent; the subgenus *Elytrodes* is characterized by having only two elytral basal foveae;

lastly, in the subgenus *Declivodes*, the male and female integument is rugose, plus males have antennomere X bearing a small ventral fovea. Later (1953), Park created other two subgenera, largely based on aedeagal structure, representing an alleged intermediate complexity between *Batriasymmodes* species group and the remaining subgenera: *Empinodes* comprises the western North American species, and *Spifemodes* with only one eastern species. All these subgenera contain species where males have modifications on antennomeres I, VII, IX, X, and XI. Finally, Park (1960) considered the differences in aedeagal morphology and the absence of metatibial spur were enough to elevated *Batriasymmodes* to the genus level.

Secondary sexual characters may play important roles in prezygotic isolation between closely related taxa and facilitate the formation of new species through sexual selection, when these characteristics are associated with mate search, attraction, and recognition systems (Panhuis *et al.* 2001). The importance of secondary sexual characters and sexual selection as drivers for speciation has been explored theoretically by several authors (Lande 1981; West-Eberhard 1984). Empirically, this prediction has proved difficult to test. Yet in highly diverse groups such Passerine birds, a correlation between species richness and sexual dimorphism has being found (Barraclough *et al.* 1995; Janicke *et al.* 2018).

Species-rich lineages such *Batrisodes* offer the possibility to evaluate the correlation between secondary sexual characters and species diversification at a finer scale; the most dramatic and diverse secondary sexual character are present in two of the seven subgenera, which are also the most species rich; these contain species with distributions ranging from widely distributed to cave-related endemic species. Meanwhile, one subgenus is restricted to western North America, and its species are relatively uniform in their external morphology, including secondary sexual traits. In an evolutionary context, it is feasible to compare closely related taxa (sister clades) in relation to their number of species and prevalence of sexual secondary characters. Also, it is possible to assess whether a distinct sexual trait is frequently found in a particular species-rich clade, or if a combination of several sexual characteristics corresponds with more species diversity. Even more, surveying such traits and looking at their frequency throughout the group and its current distribution, can help to identify prevalent secondary sexual traits in specific geographical regions (i.e. Palearctic vs. Nearctic or eastern vs. western Nearctic); also, looking at *Batrisodes* species relationships can help to identify whether ecological shifts (cave dwellers vs. leaf litter inhabitants) have influenced the frequency of sexually dimorphic conditions. This chapter constitutes the first attempt at constructing a morphological data set for *Batrisodes* phylogeny, including taxa from the Nearctic and Palearctic regions, and the first phylogenetic analysis of the genus *Batrisodes*. The aim of this chapter is to document the secondary sexual characters in Nearctic *Batrisodes* in an evolutionary context to identify: a) whether these characters are highly convergent within the lineage, b) what characters are more constant across the genus, c) which tend to be lost or gained more frequently, and d) recognize secondary sexual characters present in the most diverse clades.

MATERIALS AND METHODS

Specimens

The specimens used for phylogenetic analysis and observation of secondary sexual characters come from museum loans from the following institutions and personal collections:

CNC - Canadian National Collection of Insects, Ottawa, Canada (Dr. Anthony E. Davies).

CUAC—Clemson University Arthropod Collection, Clemson, U.S.A. (Dr. M. Ferro).

FMNH—Field Museum, Chicago, U.S.A. (Dr. M.K. Thayer, Ms. C.A. Maier).

LSAM—Louisiana State Arthropod Museum, Louisiana State University, Baton Rouge, Louisiana, U.S.A. (Ms. V.M. Bayless, Dr. C. Carlton).

MHNG—Museum of Natural History (Museum d'Histoire naturelle) Geneva, Switzerland. (Dr. G. Cuccodoro).

UNHC Chandler—Donald S. Chandler collection, Department of Zoology, University of New Hampshire, Durham, U.S.A. (Dr. D.S. Chandler).

Phylogenetic analysis

To assess the relationships among *Batrisodes* species and the evolution of secondary characters in the genus for North America, a matrix of 96 taxa and 81 morphological characters was constructed in Mesquite 3.61 (Maddison and Maddison 2019). The most parsimonious cladograms and character optimizations were identified in a comprehensive search strategy using the parsimony ratchet (Nixon 1999) as implemented in TNT (Goloboff *et al*. 2008; spawned from ASADO ver. 1.61 [Nixon 2004]), based on the following commands: (1) ratchet settings – 200 iterations per replication, 4% up-/down-weighted; (2) drift settings - 100 iteration per replication; (3) tree fusion settings – 10 rounds, 200 MB max RAM; (4) general settings – 1000 tree hold; (5) analysis – ratchet, drift, sectorial search, tree fusion, TBR-max; and (6) xmult settings – 3 hits, 5 consensus.

Taxa

Table 1. Taxa included in phylogenetic analysis of secondary sexual character evolution for the genus *Batrisodes*. 1 – 6: Pselaphinae genera and species of tribes outside Batrisitae; 7 – 19: species within Batrisitae from the tribes Amauropini (7 -9), and Batrisini (10 - 96); 31 – 96: *Batrisodes* species for North America, north of Mexico. Subgeneric names are only given to the focal Nearctic species.

Taxa	**Distribution**
1. *Sonoma* sp. Casey, 1886	Nearctic
2. *Conoplectus* sp. Brendel, 1888	Nearctic and Mexico
3. *Machaerodes carinatus* (Brendel), 1865	USA (OH, PA, WV, VA, NC, GA, TN)
4. *Reichenbachia* sp. Leach, 1826	Worldwide
5. *Tmesiphorus costalis* LeConte, 1849	Canada (ON), USA (IA, IL, IN, OH to PA, NJ, MD, FL, AL, MS, KY, MO, AR, LA, SC, TX, OK, KS)
6. *Upoluna batrisoides* (Motschulsky), 1857	USA (AR, FL, IL, IN, KS, KY, LA, MO, OH, OK, PA, NY, SC, TN, TX)
7. *Arianops* sp. Brendel, 1893	USA (GA, NC, PA, AL, SC, AR, TN, VA, TX, OK
8. *Pseudoamaurops mullerianus* (Ravasini), 1923	Albania
9. *Amaurops sulcatulus* Dodero, 1919	Italy (Sicily)
10. *Arthmius* sp. LeConte, 1849	Neotropical; Southeastern USA
11. *Texamaurops redelli* Barr and Steeves, 1963	USA (TX)
12. *Batriasymmodes* sp. Park, 1951	USA (PA, NC, SC, FL, AL, IN, OH, MD, GA, MO, IL, IN, NY, NJ, DE, DC, VA, WV, LA)
13. *Batrisus formicarius* Aubé, 1833	Europe (AU, BH, BU, CR, CZ, FR, GE, GR, HU, IT, LT, NL, PL, RO, SK, SL, SP, SZ, UK, YU), Turkey (European)
14. *Batrisus sibiricus* Sharp, 1874	Russia (Siberia, Far East), Korea (N, S), China (Beijing, Shanghai, Sichuan)
15. *Batrisus ormayi* Reitter, 1885	Romania
16. *Ambicocerus celisi* Leleup, 1973	Ghana
17. *Atheropterus alticola* Jeannel, 1952	République démocratique du Congo (Zaire)
18. *Batriscenellus insulicola* Nomura, 1991	Ryukyu Is. (Okinoerabu)
19. *Batrisocenus clavatus* Raffray, 1894	Malaysia

20. *Batrisodes sulcaticeps* Besuchet, 1981	Europe (BH, BU, GR, HU, RO)
21. *Batrisodes tichomirovae* Löeb, 1973	Rusia (Far East)
22. *Batrisodes pogonatus* Saulcy, 1874	Greece
23. *Batrisodes buqueti* (Aubé), 1833	Europe (AU, BH, BU, CR, CZ, FR, GE, GR, IT, NL, PL, RO, SK, SL, SP, SZ, UK, YU), Russia (southern European part), Turkey
24. *Batrisodes venustus* (Reichenbach), 1816	Europe (AU, BH, BU, BY, CR, CZ, DE, FI, FR, GB, GE, HU, IT, LA, LT, MC, NL, NR, PT, PL, RO, SK, SL, SP, SV, SZ, UK), Russia (European)
25. *Batrisodes delaporti* (Aubé), 1833	Europe (AU, BH, BU, BY, CR, CZ, FR, GB, GE, GR, HU, IT, MC, NL, PL, RO, SK, SL, SP, SV, SZ, UK, YU)
26. *Batrisodes oculatus* (Aubé), 1833	Europe (AU, BE, BU, CR, CZ, FR, GB, GE, GR, HU, IT, MC, NL, SL, SP, SZ, UK, YU, Russia (European), Turkey
27. *Batrisodes adnexus* (Hampe), 1863	Europe (AU, CR, CZ, DE, FI, FR, GB, GE, HU, IT, PL, RO, SK, SL, SV, SZ, UK, YU), Russia (northern European part)
28. *Batrisodes circassicus* Reitter, 1887	Russia (Caucasus)
29. *Batrisodes grossus* Jiang, Ri-Xin, and Yin, 2017	China (Yunnan)
30. *Batrisodes simianshanus* Jiang, Ri-Xin, and Yin, 2017	China (Chongqing)
31. *Batrisodes (Babnormodes) antennatus* Schaeffer, 1906	USA (NC, PA, TN, VA)
32. *B. (Babnormodes) barri* Park, 1958	USA (TN)
33. *B. (Babnormodes) cavicornis* (Casey), 1897	USA (IL, IN, OH, PA, KY)
34. *B. (Babnormodes) clypeospecus* Park, 1960	USA (TN)
35. *B. (Babnormodes) dentifrons* Chandler and Reddell, 2009	USA (TX)
36. *B. (Babnormodes) fanti* Chandler and Reddell, 2009	USA (TX)
37. *B. (Babnormodes) femeniclypeus* Chandler and Reddell, 2001	USA (TX)
38. *B. (Babnormodes) ferulifer* Park, 1960	USA (TN)
39. *B. (Babnormodes) foveicornis* (Casey), 1887	USA (IA, IN, OH, NY, TN, KY, LA)
40. *B. (Babnormodes) gemmoides* Park, 1960	USA (TN)
41. *B. (Babnormodes) gemmus* Park, 1956	USA (TN)
42. *B. (Babnormodes) gravesi*, Chandler and Reddell, 2001	USA (TX)
43. *B. (Babnormodes) hairstoni* Park, 1947	USA (IN)
44. *B. (Babnormodes) henroti* Park, 1956	USA (KY)
45. *B. (Babnormodes) hubrichti* Park, 1958	USA (KY)

46. *B. (Babnormodes) jocuvestus* Park, 1960	USA (AL)
47. *B. (Babnormodes) jonesi* Park, 1951	USA (AL)
48. *B. (Babnormodes) pannosus* Park, 1960	USA (TN)
49. *B. (Babnormodes) profundus* Park, 1956	USA (AL)
50. *B. (Babnormodes) punctifrons* (Casey), 1887	USA (OH, PA, NY, NH, MA, WV, MD)
51. *B. (Babnormodes) riparius* (Say), 1824	Canada (NB, ON, QC), USA (GA, KY, IL, IN, MI, MO, NC, NJ, NY, OH, OK, PA)
52. *B. (Babnormodes) schaefferi* Park, 1947	USA (NC, VA, SC, GA)
53. *B. (Babnormodes) specus* Park, 1951	USA (OH, AL, TN)
54. *B. (Babnormodes) spretoides* Ferro and Carlton, 2014	USA (TN)
55. *B. (Babnormodes) spretus* (LeConte), 1849	USA (DC, GA, IA, IL, IN, KY, VT, MA, ME, MO, NC, NY, OH, PA, TN, VA, WV)
56. *B. (Babnormodes) tumoris* Park, 1960	USA (AL)
57. *B. (Babnormodes) uncicornis* (Casey), 1897	USA (AL, FL, GA, LA, MA, MS, NC, NJ, NY, PA, RI, SC, TN, TX, VA)
58. *B. (Babnormodes) valentinei* Park, 1951	USA (AL, TN)
59. *B. (Babnormodes) wartoni* Chandler and Reddell, 2001	USA (TX)
60. *Batrisodes (Declivodes) bistriatus* (LeConte), 1849	USA (CT, DC, MD, NJ, PA)
61. *B. (Declivodes) cartwrighti* Sanderson, 1940	USA (SC)
62. *B. (Declivodes) declivis* Casey, 1908	USA (IA, IL)
63. *B. (Declivodes) fossicauda* (Casey), 1897	USA (IA, PA, NY, CT, LA)
64. *Batrisodes (Elytrodes) ionae* (LeConte), 1849	Canada (ON), USA (IN, PA, NJ, MD, DC, VA, GA, AL, MS, KY, MO, KS)
65. *Batrisodes (Empinodes) albonicus* (Aubé), 1833	Canada (BC), USA (AK, CA, OR, WA)
66. *B. (Empinodes) aphaenogastri* Fall, 1912	USA (ID)
67. *B. (Empinodes) cicatricosus* (Brendel), 1890	USA (CA)
68. *B. (Empinodes) denticauda* (Casey), 1893	Canada (BC), USA (WA, OR, CA)
69. *B. (Empinodes) indistinctus* Grigarick and Schuster, 1962	USA (CA)
70. *B. (Empinodes) lustrans* Casey, 1908	USA (CA)
71. *B. (Empinodes) medocino* (Casey), 1886	USA (CA)
72. *B. (Empinodes) opacus* Grigarick and Schuster, 1962	USA (CA)
73. *B. (Empinodes) yanaorum* Chandler, 2003	USA (CA)
74. *B. (Empinodes) zephyrinus* (Casey), 1886	USA (NV, CA)
75. *Batrisodes (Excavodes) auerbachi* Park, 1956	USA (GA, NC, TN)
76. *B. (Excavodes) beyeri* Schaeffer, 1906	USA (NC, TN)

77. *B. (Excavodes) cavernosus* Park, 1951	USA (AL)
78. *B. (Excavodes) clypeonotus* (Brendel), 1893	USA (AL, MO, AR, LA, SC, TX, OK)
79. *B. (Excavodes) cryptotexanus* Chandler and Reddell, 2001	USA (TX)
80. *B. (Excavodes) dorothae* Ferro and Carlton, 2014	USA (LA, SC)
81. *B. (Excavodes) frontalis* (LeConte), 1849	Canada (AB, MB, NB, ON, QC), USA (CO, IA, ID, IL, KS, LA, ME, MN, MO, OH, PA, WI)
82. *B. (Excavodes) furcatus* (Brendel), 1890	Canada (QC), USA (AL, IA, IL, IN, KY, MA, ME, MI, MN, NH, NY, OK, RI, TN)
83. *B. (Excavodes) grubbsi* Chandler, 1992	USA (TX)
84. *B. (Excavodes) lineaticollis* (Aubé), 1833	Canada (BC, NB, NL, NS, ON, QC), USA (CO, FL, IL, IN, MA, ME, MI, MN, NH, SC, TX, VT, WA, WI, etc.)
85. *B. (Excavodes) reyesi* Chandler, 1992	USA (TX)
86. *B. (Excavodes) scabriceps* (LeConte), 1849	Canada (NB, ON, QC), USA (WI, IL, IN, MI to NY, CT, NC, MS, TN, AR, OK)
87. *B. (Excavodes) sinuatifrons* (Brendel), 1893	Canada (ON), USA (MS, TN, AR, LA)
88. *B. (Excavodes) temporalis* (Casey), 1897	USA (PA, MD, FL)
89. *B. (Excavodes) texanus* Chandler, 1992	USA (TX)
90. *B. (Excavodes) venyivi* Chandler, 1992	USA (TX)
91. *B. (Excavodes) virginiae* (Casey), 1884	USA (MI, NC, SC, TN, VA, WV)
92. *Batrisodes (Pubimodes) denticollis* (Casey), 1884	USA (IA, IL, OH, PA, NY, NJ, MD, DC, VA, NC, SC, GA, TN, KY, MO, AR, OK)
93. *B. Pubimodes (nigricans)* (LeConte), 1849	USA (SC, GA)
94. *B. Pubimodes (schmitti)* (Casey), 1897	USA (IN, OH, PA, VA, NC, SC, AL, MS, TN, KY)
95. *B. Pubimodes (striatus)* Park, 1947	Canada (ON, QC), USA (MN, WI, IL, IN, MI to NH, GA, KY, MO, KS, NE)
96. *Batrisodes (Spifemodes) schaumi* (Aubé), 1844	USA (AL, FL, GA, IL, IN, KY, LA, MI, MO, MS, NC, NJ, NY, OH, PA, SC, TN, VA)

Morphological Characters

Characters pertaining to the external morphology were examined using a Leica M80 stereomicroscope (magnifications 7.5-60X). The morphological terminology is used in accordance with Park (1947) and Chandler (2001). Character photographs were taken with a camera Canon EOS 6D with 65 mm lens and a Passport Portable Imaging system by Visionary Digital and edited with Adobe Photoshop 2020. Line drawings were prepared with a drawing tube attached to the stereomicroscope. The initial sketches were scanned and redrawn using Adobe Illustrator 2020.

Characters (* = Secondary Sexual Characters)

1. Pronotal disc with processes: state 0 = present, state 1 = absent.
2. Antennal scape apex: state 0 = circular, state 1 = emarginate.
3. Antennal pedicel: state 0 = similar to scape, state 1 = barrel shaped or globose, state 2 = elongate.
4. Antennomeres III to VI: state 0 = oblong, state 1 = round transverse, state 2 = cylindrical.
5. Vertexal foveae: state 0 = absent, state 1 = present.
6. Lateral pronotal foveae: state 0 = absent, state 1 = present.
7. Median pronotal foveae: state 0 = absent, state 1 = present-typical, state 2 = present-foveoid depression.
8. Procoxal foveae: state 0 = absent, state 1 = present.
9. Elytral sutural foveae/stria: state 0 = absent, state 1 = present.
10. Elytral basal foveae: state 0 = absent, state 1 = 2-3, state 2 = 1.
11. Elytral subhumeral foveae: state 0 = absent, state 1 = present.
12. Metacoxae: state 0 = contiguous, state 1 = narrowly separate, state 2 = distant.
13. Tarsal claws: state 0 = equal, state 1 = unequal, state 2 = single.
14. First abdominal segment: state 0 = simple, state 1 = yes, state 2 = modified.
15. Paramedian pronotal carinae: state 0 = absent, state 1 = present.

16. Vertexal foveae pubescent: state 0 = absent, state 1 = present (Fig. 3B).

17. Fronto-clypleal region complete*: state 0 = present (Fig. 1A), state 1 = absent.

18. Eyes: state 0 = present, state 1 = absent.

19. Antennal tubercles: state 0 = absent, state 1 = present.

20. Fronto-clypeus constricted*: state 0 = absent, state 1 = present (Fig. 4B).

21. Fronto-clypeus interrupted*: state 0 = absent, state 1 = present (Fig. 3C and D).

22. Dorsal margin of frontal slope acute*: state 0 = absent, state 1 = present (Fig. 3C).

23. Dorsal margin of frontal slope rounded*: state 0 = absent, state 1 = present (Fig. 3D).

24. Dorsal margin of frontal slope sinuate*: state 0 = absent, state 1 = present (Fig. 3A and B).

25. Anterior margin of head concave*: state 0 = absent, state 1 = present.

26. Paired tufts of hairs on dorsal margin*: state 0 = absent, state 1 = present (Fig. 3B, D, and E).

27. Clypeal carina sinuate*: state 0 = absent, state 1 = present (Fig. 3A, E, and F).

28. Clypeal carina with tufts of hairs*: state 0 = absent, state 1 = present (Fig. 3E and F).

29. Clypeus with medial process round*: state 0 = absent, state 1 = present (Fig. 3A).

30. Clypeus with medial process acute*: state 0 = absent, state 1 = present (Fig. 3C to F).

31. Long tufts of hairs on clypeal process*: state 0 = absent, state 1 = present (Fig. 3E and F).

32. Transverse excavation glabrous*: state 0 = absent, state 1 = present (Fig. 4).

33. Transverse excavation covered by short pubescence*: state 0 = absent, state 1 = present (Fig. 3D).

34. Fronto-clypeal slope continuous between antennal insertions: state 0 = absent, state 1 = present (Fig 3E).
35. Anterior margin of head projecting forward*: state 0 = absent, state 1 = present (Fig. 4C).
36. Anterior margin of head flat*: state 0 = absent, state 1 = present.
37. Vertexal lateral carinae: state 0 = absent, state 1 = present.
38. Vertexal medial carina: state 0 = absent, state 1 = present.
39. Glabrous depression on dorsal portion of fronto-clypeal region*: state 0 = absent, state 1 = present (Fig. 4E and F).
40. Head integument in male: state 0 = dull, state 1 = polished.
41. Head integument in female: state 0 = dull, state 1 = polished.
42. Frontal slope vertical in females: state 0 = absent, state 1 = present.
43. Eye dimorphism in males and females: state 0 = absent, state 1 = present.
44. Antennomeres II to XI with modifications*: state 0 = absent (Fig. 5A and B), state 1 = present.
45. Scape expanded dorso-ventrally*: state 0 = absent, state 1 = present (Fig. 5 C).
46. Shape of antennomere IX*: state 0 = subquadrate, state 1 = trapezoid/triangular.
47. Antennomere X enlarged*: state 0 = absent (Fig. 5A), state 1 = present (Fig. 5B).
48. Antennomere X with ventral foveae*: state 0 = absent, state 1 = present (Fig. 5D and E).
49. Antennomere X with ventral pore*: state 0 = absent, state 1 = present (Fig. 5G).
50. Antennomere X ventrally concave*: state 0 = absent, state 1 = present (Fig. 5F and H).

51. Antennomere XI with basal process (tooth, pore, small fovea) *: state 0 = absent, state 1 = present (Fig. 5F, 6A to D).
52. Antennomere XI twice as wide as antennomere X: state 0 = absent, state 1 = present.
53. Antennomere XI ventrally concave: state 0 = absent, state 1 = present.
54. Pronotal laterobasal foveae pubescent: state 0 = absent; state 1 = present.
55. Pronotal median sulcus: state 0 = present; state 1 = absent.
56. Pronotal lateral stria: state 0 = present; state 1 = absent.
57. Pronotal basolateral spines: state 0 = present, state 1 = absent.
58. Basal elytral foveae discal, medial and sutural: state 0 = equidistant, state 1 = medial closer to sutural.
59. Paratergites after first visible tergite: state 0 = present, state 1 = absent.
60. Metatibial apical spur: state 0 = absent; state 1 = present.
61. Mesotibial basal spine*: state 0 = absent, state 1 = present
62. Mesotibial apical elongation*: state 0 = absent, state 1 = present.
63. Mesotrochanter ventral spine*: state 0 = absent, state 1 = present.
64. Mesofemur mesal spine or tooth on ventral margin*: state 0 = absent, state 1 = present (Fig. 7A).
65. Mesotibial mesal spine*: state 0 = absent, state 1= present (Fig. 7B).
66. Mesofemur basal spine on ventral margin*: state 0 = absent, state 1 = present (Fig. 7B).
67. Second mesotarsal segment compressed laterally*: state 0 = absent, state 1 = present.
68. Second mesotarsal segment ventrally incised pubescent*: state 0 = absent, state 1 = present.

69. Second mesotarsal segment ventrally incised glabrous*: state 0 = absent, state 1 = present (Fig. 7C).
70. Protrochanter triangular, with small ventral tooth*: state 0 = absent, state 1 = present.
71. Mesotrochanter ventral blunt projection*: state 0 = absent, state 1 = present (Fig. 7B).
72. Protibia sinuate at apical half: state 0 = absent, state 1 = present (Fig. 7E).
73. Profemur abruptly enlarged after first quarter: state 0 = absent, state 1 = present (Fig. 7D).
74. Profemur base covered by short and uniform group of hairs: state 0 = absent, state 1 = present.
75. Last visible abdominal sternite with small concavity*: state 0 = absent, state 1 = present
76. Depression on last abdominal sternite round*: state 0 = absent, state 1 = present.
77. Posterior corners of last visible abdominal sternite extended apically*: state 0 = absent, state 1 = present.
78. Last visible abdominal sternite with large concavity*: state 0 = absent, state 1 = present.
79. Depression on last abdominal sternite elongate*: state 0 = absent, state 1 = present.
80. Male genitalia: state 0 = asymmetric, state 1 = symmetric.

Habitat (based on the morphology of the genus, associated to these habitats): state 0 = leaf litter/ants' nests, state 1 = cave related.

Evolution of the secondary sexual characters in *Batrisodes*

To assess the change of secondary sexual traits across the species of *Batrisodes*, the number of steps (length), consistency index (*ci*), and retention index (*ri*) of each character, were visually compared and redrawn onto the resulting topologies from the phylogenetic analyses. Once identified, the characters with higher values of the consistency and retention indexes were contrasted with other characters, that showed lower values of the parsimony statistics. Additionally, secondary sexual characters were compared to known ecological traits for *Batrisodes* species.

RESULTS

Phylogenetic relationships

The cladistic analysis of 96 taxa (including an outgroup of seven species), 80 morphological characters, and one ecological character resulted in 33 equally parsimonious trees, with a length of 535 steps, consistency index (CI) of 0.16, and retention index (RI) of 0.67. The resulting majority rule consensus cladogram is shown in Figure 1. Under this phylogenetic hypothesis, the genus *Batrisodes* in the Nearctic region does not form a monophyletic group. Node 1 on the cladogram corresponds to the supertribe Batrisitae, with node 2 including the species *Batriscenellus insulicola* Nomura, and the remaining taxa in this analysis including species of Batrisini and Amauropini from the Palearctic and Nearctic regions. Node 3 includes a polyphyletic group where the position of *Declivodes* in relation to other *Batrisodes* subgenera is not resolved (node 4); nodes 5 contains species in the tribe Amauropini as sister group to *Texamaurops reddelli* plus a large clade including the subgenus *Excavodes* (paraphyletic), *Pubimodes* and species of Palearctic *Batrisodes*. Finally, node 6 consists of Palearctic *Batrisodes, Batrisus*, and the remaining *Batrisodes* subgenera *Empinodes, Elytrodes, Spifemodes*, and *Babnormodes* (as well as two species of *B. Excavodes*).

A second cladistic analysis was performed including only the genera and species of Batrisitae of the new world for a total of 77 taxa and 80 morphological characters and one ecological character (Fig. 2). Nearctic *Batrisodes* species form a monophyletic group; the subgenus *Elytrodes* with its unique species *B. (Elytrodes) ionae* resulted as the sister group to all other *Batrisodes* lineages. The subgenus *Empinodes* was resolved as monophyletic, and as sister group to *Declivodes, Spifemodes, Excavodes,* and *Babnormodes.* The last of these was paraphyletic in relation to the species *B. (Excavodes) venyivi* and *B. (Excavodes) cavernosus.* Similarly, *Excavodes* was paraphyletic in relation to *Pubimodes*, and the species *Texamaurops reddelli* Barr and Steeves was recovered as its sister taxon.

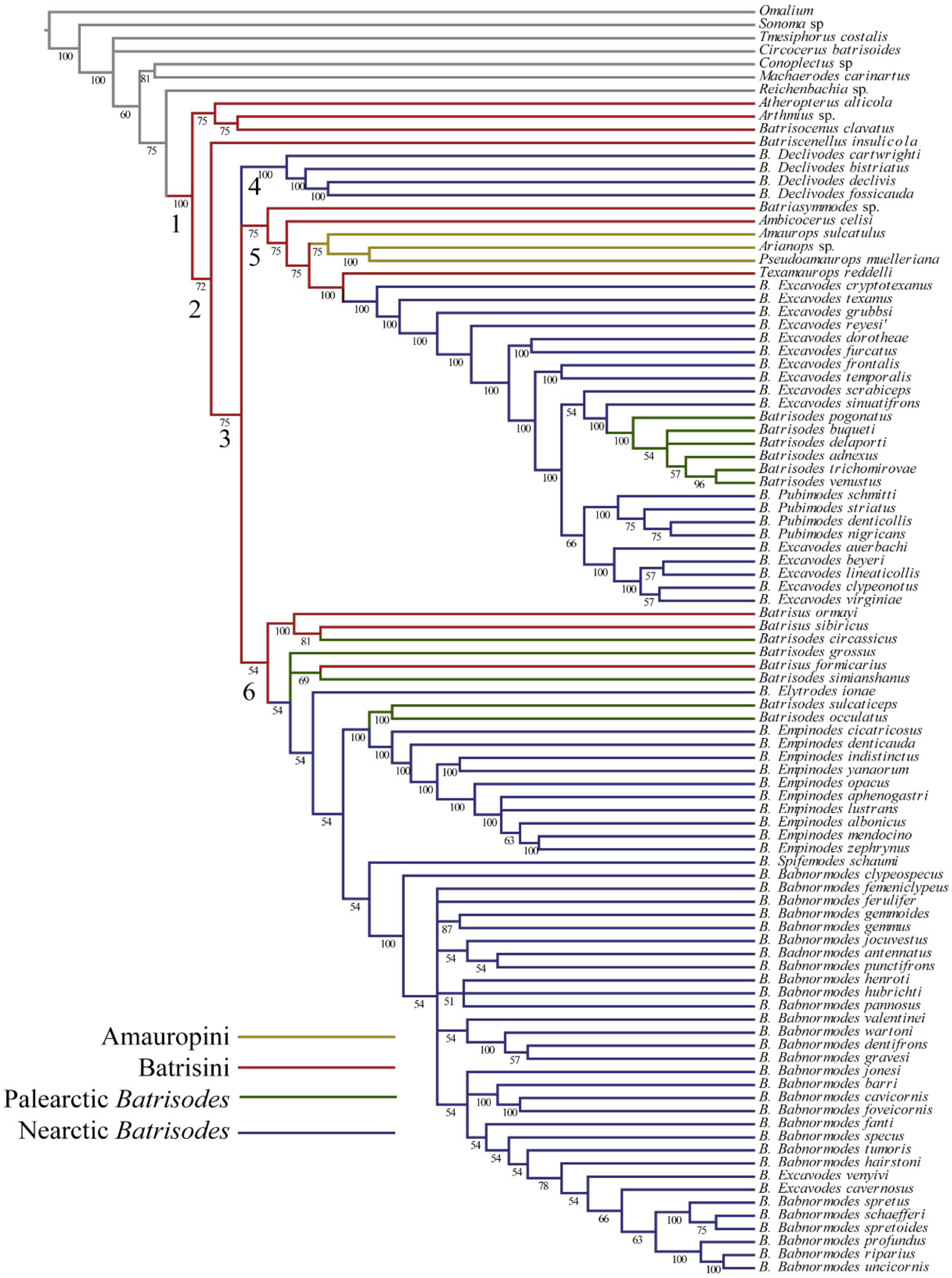


Figure 1. Relationships among Holarctic species of *Batrisodes.* Majority rule consensus of 33 equally parsimonious trees with length of 535 steps. Numbers on top of each node represent the consensus frequency; numbers below the nodes refer to different groupings obtained in this analysis.

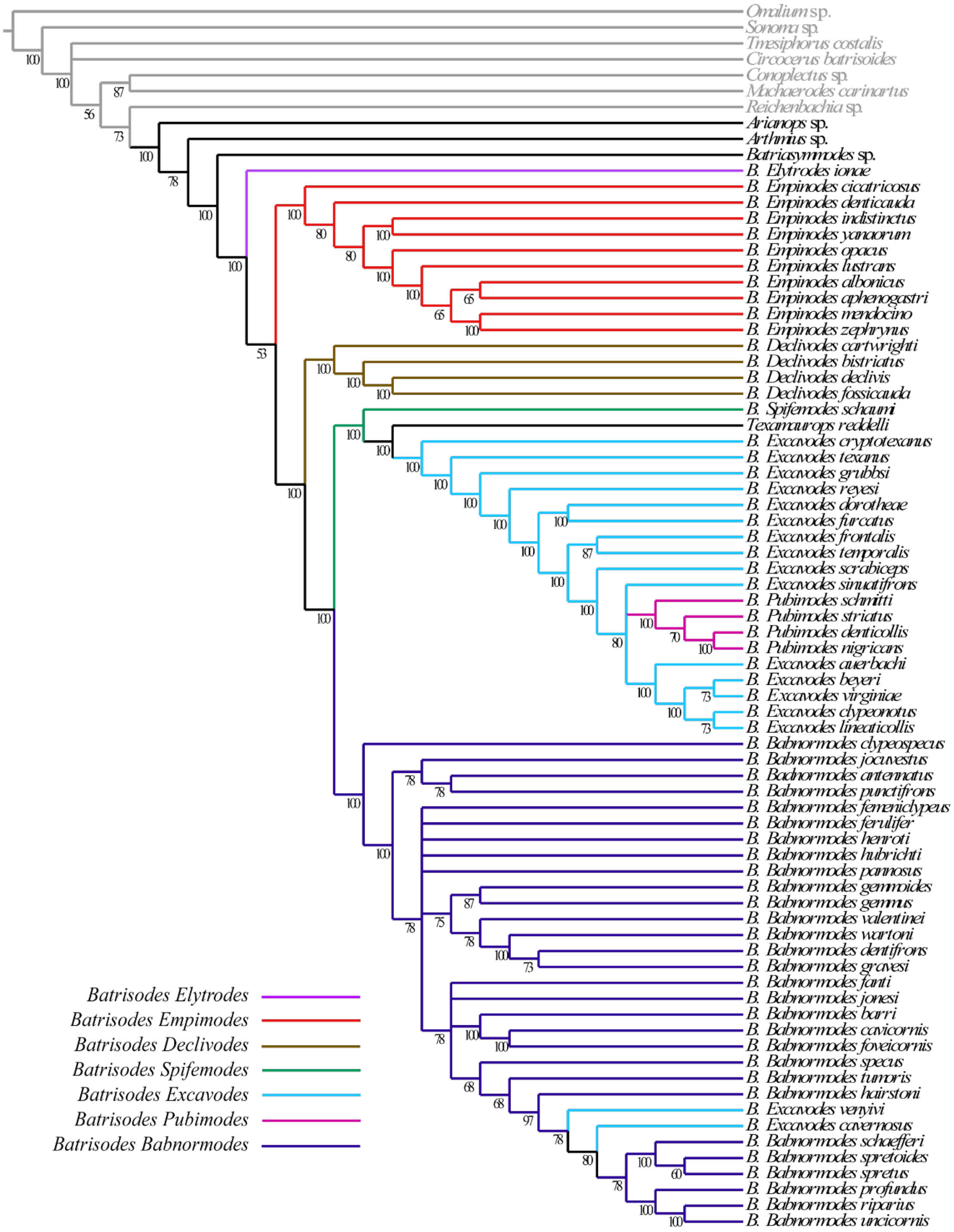


Figure 2. Relationships among Nearctic species of *Batrisodes.* Majority rule consensus of 43 equally parsimonious trees with length of 429 steps; consistency index (CI) = 0.19, and retention index (RI) = 0.68

Secondary sexual characters in *Batrisodes* Reitter

A total of 41 secondary sexual characters were identified and included in the character matrix. In *Batrisodes* one of the structures that varied the most was the fronto clypeal region (Figs. 2 and 3). In the subgenus *Babnormodes,* alone, variation of this region of the head presented at least four different conditions. A complete fronto-clypeal region (Fig. 3A) is also found in the subgenera *Declivodes*, *Empinodes, Elytrodes,* and *Spifemodes*. This characteristic is also common to other genera of Batrisitae such *Amaurops*, *Arthmius,* some *Batriasymmodes* species and *Texamaurops.* Fronto-clypeal region constricted (Fig. 3B) is a condition present only in four species within - *Babnormodes,* in two of these species this character was a synapomorphy. The transversal excavation on the fronto-clypeal region (Fig. 3) is found in some Palearctic species of *Batrisodes,* some species *Babnormodes* (ex., Fig. 3C and D), and in all the species of *Excavodes,* and *Pubimodes.* In these two subgenera, it can be observed some combinations of characters around the transversal excavation; for instance, many of the species in *Excavodes* and all *Pubimodes* present a couple of hairs tufts on the dorsal margin of the fronto-clypeal region (Fig. 4B) frequently on digitiform protuberances; only in *Excavodes* these are surrounded by a concave and glabrous area (Fig. 4E and F), but seem to be secondarily lost in *B. (Excavodes) frontalis* and *B. (Excavodes) lineaticollis*. In addition to these character combinations, the clypeal process can have on its dorsal surface two groups of long hairs directed in opposite directions (Fig. 4E); these are present in most *Excavodes* species and are secondarily lost in *B. (Excavodes) dorothae* and *B. (Excavodes) sinuatifrons*. The transversal excavation on the fronto-clypeal region (ex. Fig. 3D), covered by short pubescence seems to be convergent in the troglobite species of *Babnormodes* and *Excavodes*.

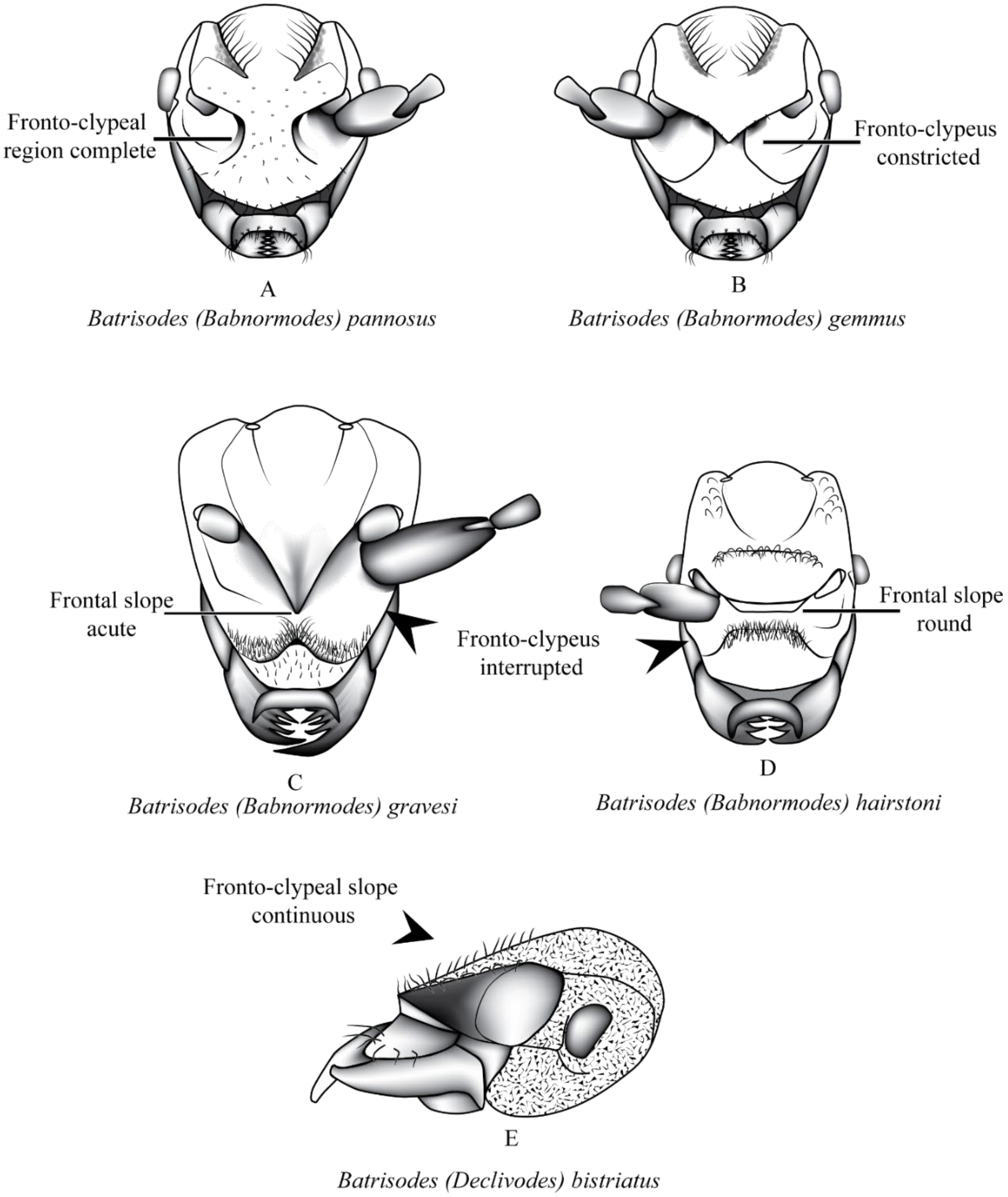
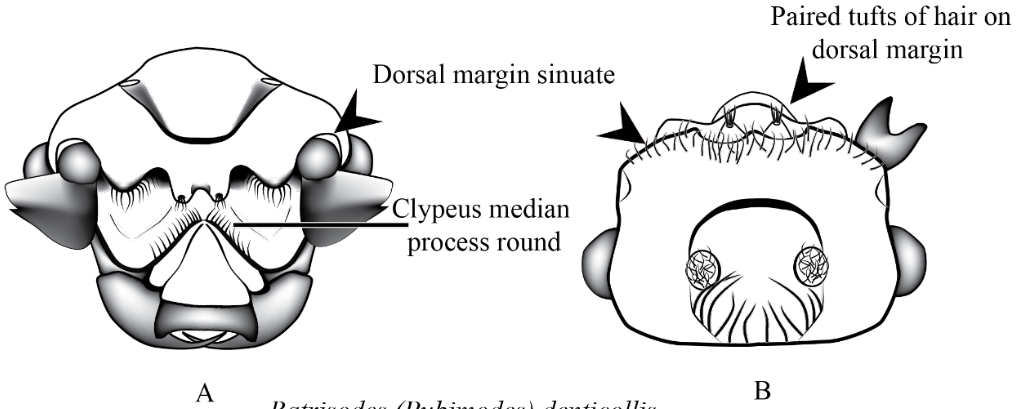
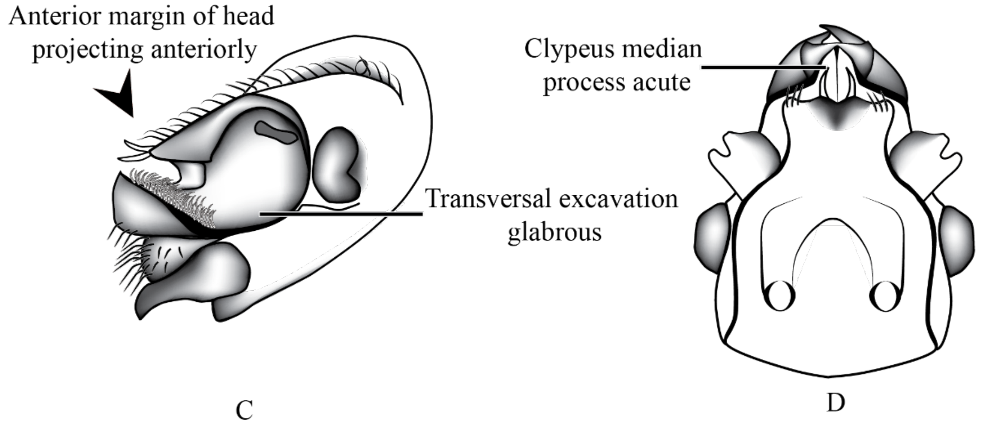


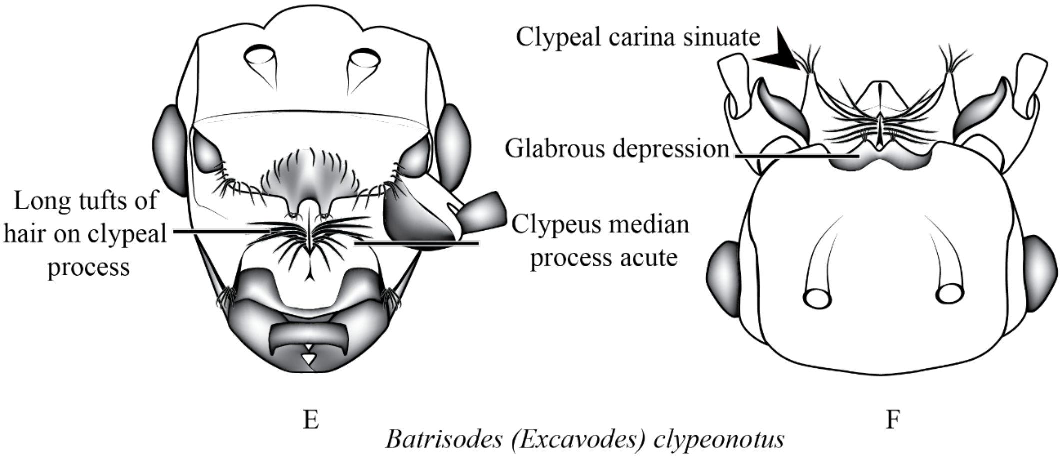
Figure 3. Variation of the fronto-clypeal region in males of *Batrisodes.*



Batrisodes (Pubimodes) denticollis



Batrisodes (Excavodes) dorotheae



Batrisodes (Excavodes) clypeonotus

Figure 4. Head variation on males of *Batrisodes.*

Antennal variation can be divided in two conditions for the scape and seven conditions for the three apical antennomeres (Figs. 5 and 6). Normal antennae (Fig. 5A and B) are found in all females of *Batrisodes* and males of some species of the subgenera *Excavodes* and *Babnormodes*; when this condition is present, the scape is elongate and cylindrical, antennomeres II to VIII are similar in shape and size, and antennomeres IX, X, and XI increase in size progressively. The scape can be expanded dorso-ventrally in species of *Excavodes* and *Pubimodes* (Fig. 5C) and can be concave on the interior face. Other common variations in *Batrisodes* (*sensu lato*) are the presence of a fovea or a pore on antennomere X (Fig. 5D, E, F, and G), and a pore or a tooth on antennomere XI (Figs. 5F and G and Fig. 6).

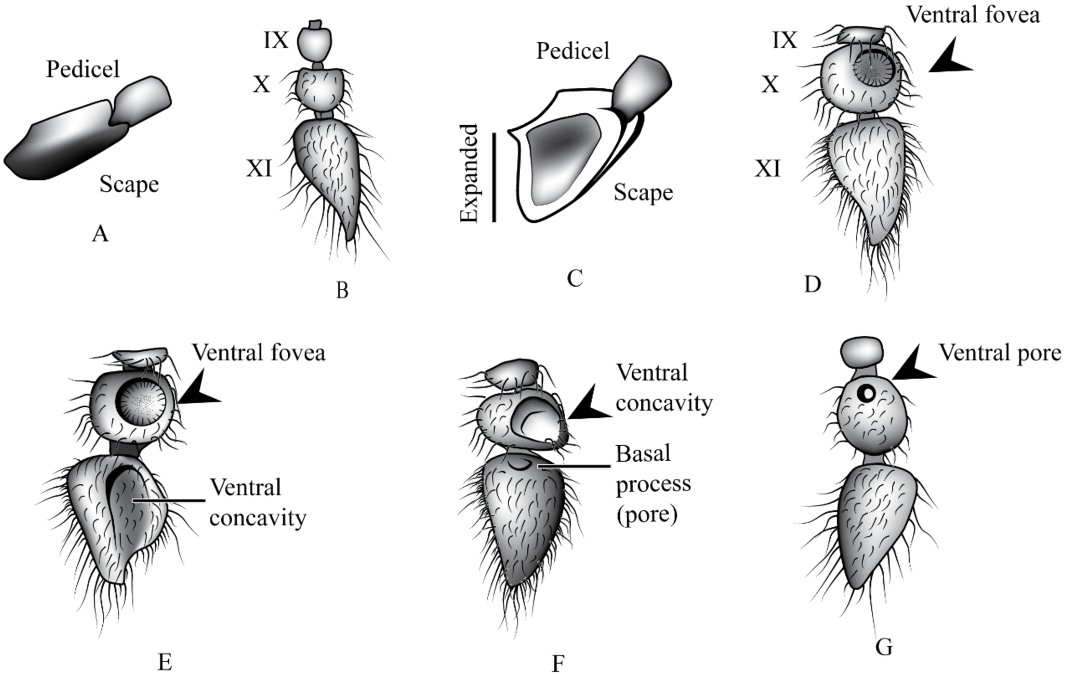


Figure 5. Antennal variation on scape, pedicel, and apical three antennomeres. A. Male scape and pedicel in *Batrisodes (Babnormodes) hubrichti;* B. Male apical antennomeres in *B. (Babnormodes) hibrichti;* C. Male scape and pedicel in *B. (Excavodes) dorothae*; D.

Male apical antennomeres in *B. (Babnormodes) specus;* E. Male *B. (Babnormodes) foveicornis;* F. Male *B. (Babnormodes) jonesi;* G. Male *B. (Excavodes) lineaticollis.*

In *Babnormodes*, three species present the condition depicted in Figure 6A: *B. (Babnormodes) profundus, B. (Babnormodes) riparius,* and *B. (Babnormodes) uncicornis* this character is a synapomorphy. When flexed inwards, the ventro-basal tooth in antennomere XI reaches the ventral concavity in antennomere X. The terminal antennomeres in males of *Empinodes* are similar in all the species included in this study, where antennomere X lacks any ventral processes and antennomere XI carries a conspicuous ventral tooth (Fig. 6B). In the subgenus *Declivodes*, the antennomere X is not enlarged, although it carries a ventral fovea (Fig. 6C), condition that is observed also in some troglobitic species in *Babnormodes* and *Excavodes.*

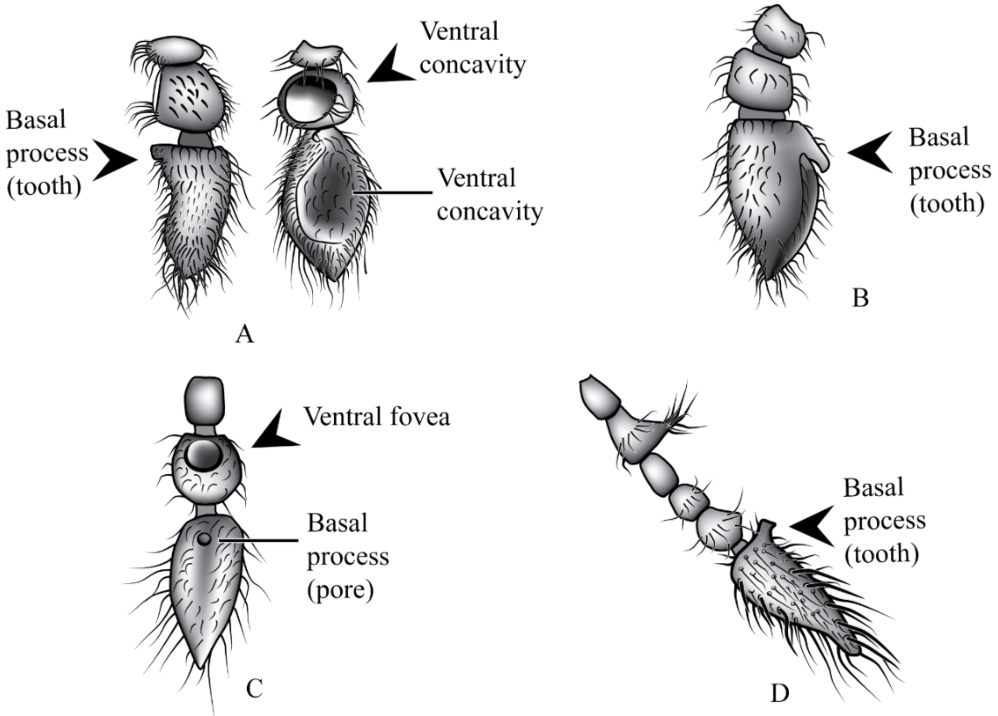


Figure 6. A. Male lateral (left) and ventral (right) sides of apical antennomeres in *B.*

(Babnormodes) riparius; B. Male *B. (Empinodes) denticauda*; C. Male *B. (Declivodes) bistriatus*; D. Male antennomere VI to XI in *B. (Spifemodes) schaumi.*

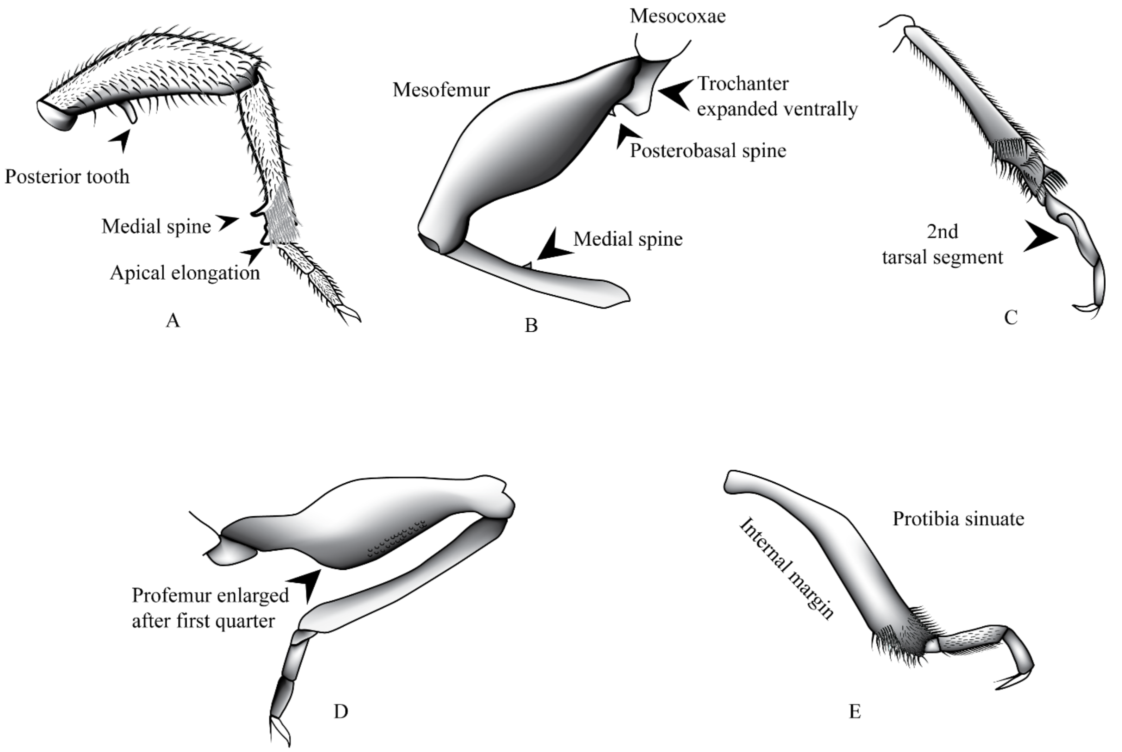


Figure 7. Leg variation in males of *Batrisodes.* A. Mesoleg in *Batrisodes (Spifemodes) schaumi,* anterior view, left leg; B. Mesoleg in *B. (Empinodes) albonicus,* posterior view, left leg; C. Mesotibia and mesotarsi in *B. (Babnormodes) jonesi,* anterior view, left leg; D. Proleg in *B. (Declivodes) cartwrighti,* anterior view, left leg.; E. Protibia in *B. (Bab.) jonesi*, anterior view, left leg.

Evolution of secondary sexual characters

All the morphological characters used in the parsimony analysis were binary (Table 2), therefore the length (L, number of steps on the tree), consistency index (*ci*), and retention index (*ri*), of the secondary sexual characters were used to identify the SSC that presented the best fit to the topologies in Figs. 1 and 2. In general, the *ci* values of individual characters were low for both Holarctic and Nearctic data sets, suggesting high homoplasy on the tree topologies. However, *ri* values were relatively high (above 0.5 in many cases), indicating that certain proportion of each character was contributing as synapomorphies along the cladograms. Characters in bold in table 2 were mapped and compared in the topologies presented in figures 8 to 13.

Table 2. Length (L), Consistency index (ci), and Retention index (ri) of secondary sexual characters for Holarctic and Nearctic data sets. Characters in bold are used to illustrate their changes in the cladograms from Figs. 8 to 13.

SSC	Secondary sexual character	Holarctic			Nearctic		
		L	ci	ri	L	ci	ri
17	**Fronto-clypleal region complete**	**5**	**0.2**	**0.89**	**5**	**0.2**	**0.87**
21	**Fronto-clypeus interrupted**	**5**	**0.2**	**0.89**	**5**	**0.2**	**0.87**
23	Dorsal margin of frontal slope rounded	5	0.2	0.33	5	0.2	0.33
24	Dorsal margin of frontal slope sinuate	5	0.2	0.84	5	0.2	0.8
26	Paired tufts of hairs on dorsal margin	5	0.2	0.77	4	0.25	0.76
27	Clypeal carina sinuate	4	025	0.88	4	0.25	0.85
28	Clypeal carina with tufts of hairs	6	0.16	0.66	5	0.2	0.71
29	Clypeus with medial process round	12	0.08	0.38	11	0.09	0.14
30	Clypeus with medial process acute	8	0.12	0.61	8	0.12	0.41
31	Long tufts of hairs on clypeal process	7	0.14	0.68	5	0.2	0.73
32	**Transverse excavation glabrous**	**4**	**0.25**	**0.85**	**4**	**0.25**	**0.78**
33	**Transverse excavation covered by short pubescence**	**7**	**0.14**	**0.68**	**6**	**0.16**	**0.72**
35	Anterior margin of head projecting forward	6	0.16	0.7	3	0.33	0.85
39	Glabrous depression on dorsal portion of fronto-clypeal region	5	0.2	0.69	3	0.33	0.8

44	**Antennomeres II to XI with modifications**	**8**	**0.12**	**0.76**	**5**	**0.2**	**0.82**
45	Scape expanded dorso-ventrally	12	0.08	0.71	7	0.14	0.6
46	**Shape of antennomere IX**	**8**	**0.12**	**0.76**	**7**	**0.14**	**0.76**
47	**Antennomere X enlarged**	**12**	**0.08**	**0.71**	**9**	**0.11**	**0.72**
48	**Antennomere X with ventral foveae**	**14**	**0.07**	**0.56**	**11**	**0.09**	**0.56**
49	**Antennomere X with ventral pore**	**6**	**0.16**	**0.5**	**4**	**0.25**	**0.62**
50	**Antennomere X ventrally concave**	**6**	**0.16**	**0.5**	**2**	**0.5**	**0.66**
51	**Antennomere XI with basal process (tooth, pore, small fovea)**	**7**	**0.14**	**0.8**	**5**	**0.2**	**0.72**
62	Mesotibial apical elongation	14	0.07	0.67	13	0.5	0.66
63	Mesotrochanter ventral spine	14	0.08	0.56	7	0.14	0.53
64	**Mesofemur mesal spine or tooth on ventral margin**	**6**	**0.16**	**0.54**	**3**	**0.33**	**0.33**
65	**Mesotibial mesal spine**	**7**	**0.14**	**0.75**	**4**	**0.25**	**0.72**
66	**Mesofemur basal spine on ventral margin**	**6**	**0.16**	**0.5**	**2**	**0.5**	**0.8**
67	**Second mesotarsal segment compressed laterally**	**6**	**0.16**	**0.87**	**4**	**0.25**	**0.91**
68	**Second mesotarsal segment ventrally incised pubescent**	**1**	**1**	**1**	**1**	**1**	**1**
69	**Second mesotarsal segment ventrally incised glabrous**	**3**	**0.33**	**0.91**	**2**	**0.5**	**0.95**
70	Protrochanter triangular, with small ventral tooth	4	0.25	0.5	5	0.2	0.33
71	Mesotrochanter ventral blunt projection	1	1	1	1	1	1
77	Posterior corners of last visible abdominal sternite extended apically	5	0.2	0.6	4	0.25	0.7
78	Last visible abdominal sternite with large concavity	2	0.5	0.83	2	0.5	0.83

The characters that showed synapomorphic capacity (*ri* values equal or larger than 0.5 in table 2), were used to compare how their change corresponds across the genus *Batrisodes,* and how these characters relate to those found in the same body structures, but which showed more homoplasy (lower *ci* and *ri* values). In figure 8, the presence of SSC on the antennomeres II to XI are compared to the different forms that antennomeres X and XI take in the different species; the numbers next to different nodes on the bottom tree represent different groups; some of these are recognized lineages (i.e. numbers 1 and 8), and others are species that may be related but do not form clades in this analysis (i.e. 7 and 10). Overall, *Batrisodes* species have antennal modifications throughout the genus, with at least two secondary losses in several Nearctic lineages. The Palearctic species included in this analysis share the presence of a tubercle on the base of antennomere XI (groups 15 and 18), combined in some instances with enlargement of antennomere X (group 15). In the Nearctic species, the tubercle on the base of antennomere XI is a synapomorphy for the subgenus *Empinodes,* and it is present in other species of the genus: *B. (Elytrodes) ionae, B. (Spifemodes) schaumi,* and the *Babnormodes* species *B. (Babnormodes) uncicornis,* and *B. (Babnormodes) profundus,* where antennomere X is not enlarged; in *B. (Babnormodes) riparius* both conditions occur. The subgenus *Excavodes* lacks an obvious tubercle on antennomere XI, but several species can present a small pore. Enlargement of the antennomere X occurs in the *Excavodes* group (2, 3, 5, and 6), and in part of the *(Babnormodes)* group (10).

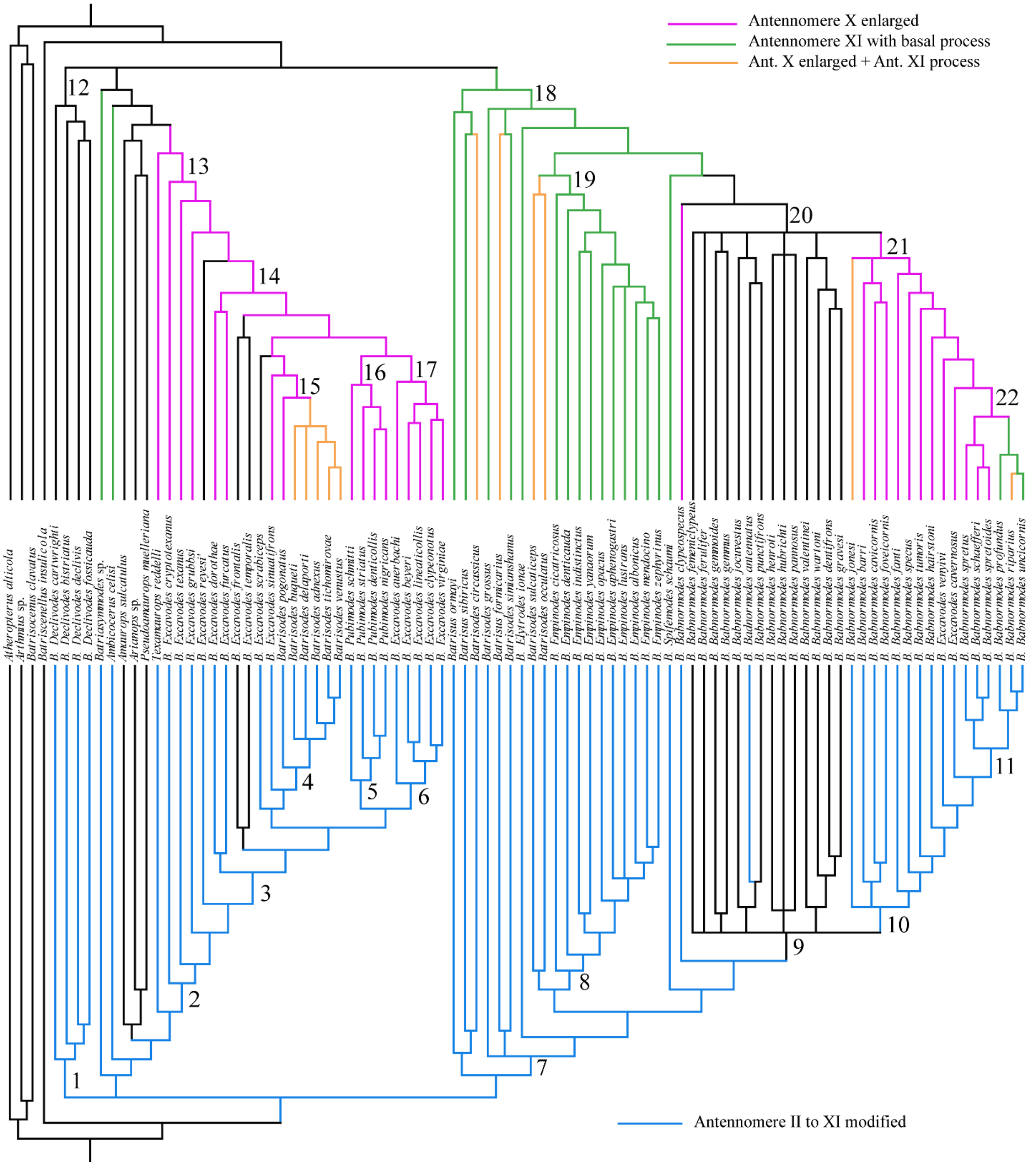


Figure 8. Cladogram of the *Holarctic* analysis comparing secondary sexual characters on antennae (bottom) compared with size of antennomere X and shape of antennomere XI (top).

Another modification that antennomere X exhibits is the presence of a ventral fovea, a small pore, or a concave surface (Figure 9). In the subgenus *Declivodes* (numbers

1 and 12), antennomere X increases in size proportional to all other flagellomeres and carries a ventral fovea. This condition is also present in two species of *Excavodes*: *B. (Excavodes) reyesi* and *B. (Excavodes) scabriceps.* Palearctic species of *Batrisodes* (4 and 15) present the antennomere X concave ventrally; only *Batrisodes sulcaticeps* presents the small pore; *Batrisus* species included in the analysis show the ventral fovea on antennomere X, similarly to species of *(Excavodes)* (13, and 14), all *Pubimodes* (16) and *Babnormodes* (21).

Secondary sexual traits on mesofemora and mesotibiae are present in *Batrisus*, Palearctic *Batrisodes,* and in the Nearctic *B. Empinodes* (8), *B. (Elytrodes) ionae,* and *B. (Spifemodes) schaumi* (Figure 10). The second mesotarsal segment presents three forms: it can be compressed laterally as in the group formed by *B. (Excavodes) auerbachi* - *B. (Excavodes) virginiae* (number 6); it also can be incised and glabrous, a characteristic of the subgenus *Babnormodes* in the Nearctic, but it was also observed in the Palearctic species *Batrisodes delaporti*; and finally it can be incised and pubescent, which is a synapomorphy for the clade *B. (Babnormodes) spretus* - *B. (Babnormodes) uncicornis* (node 11 or 22).

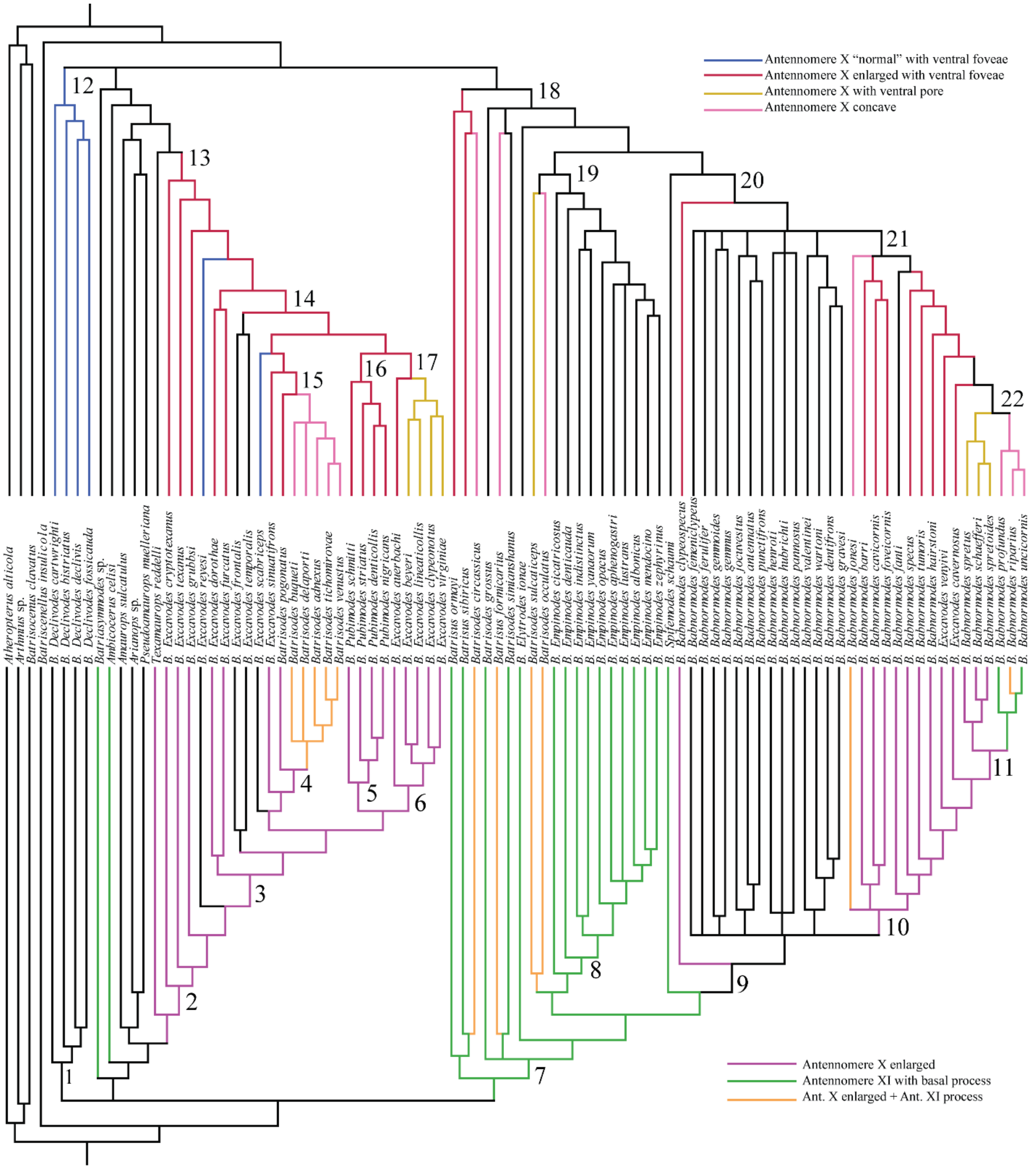


Figure 9. Cladogram of the *Holarctic* analysis comparing secondary sexual characters on antennomeres X and XI (down) to different morphological variations of antennomere X (up).

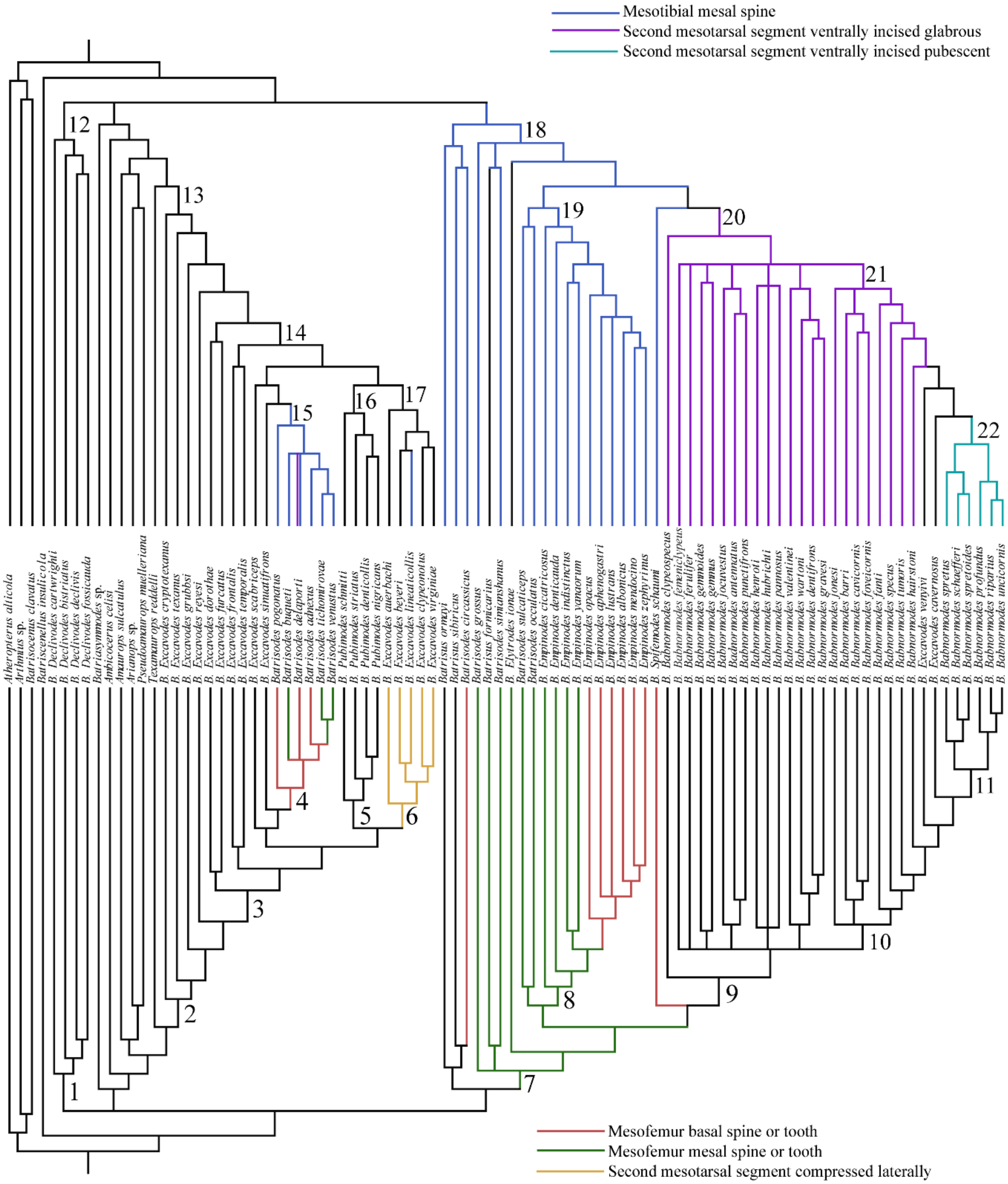


Figure 10. Cladogram of the *Holarctic* analysis comparing secondary sexual characters on mesofemora and mesotarsi.

Figures 11 to 13 present one of the most parsimonious trees found in the analysis of Nearctic species. This topology is used here to compare secondary sexual characters only for *Batrisodes* of the Nearctic region. The modifications on the fronto-clypeal region compared to the characteristic of the antennomeres X and XI, are shown in Figure 11. Nearctic species show a continuous slope between the antennal insertions in the subgenera *Declivodes, Empinodes, Elytrodes, Spifemodes*, and some species of *Babnormodes*. In *Excavodes* (3, 4, and 6) and *Pubimodes* (5)*,* the fronto-clypeal region is interrupted by the transversal excavation between the antennal insertions. Within this clade, the antennomere X can be of normal size with ventral fovea, enlarged with ventral fovea, enlarged with a ventral pore, or without any modifications. In some *Babnormodes* species, the fronto-clypeal region appears only as a constriction between the frons and the clypeus without a true separation. Likewise, in the species where the transverse excavation on the fronto-clypeal region is present, it is covered by short pubescence (Fig. 12). *Excavodes* species show the transverse excavation glabrous or with short pubescence, while in *Pubimodes*, the transversal excavation is densely covered by short hairs.

Comparisons between the habitats of *Batrisodes* species and secondary sexual characters on the two apical antennomeres are presented in Figure 13. Species that have been found within or near to ant colonies are represented in all *Batrisodes* subgenera; in *Declivodes* all the known species seem to be found with ants*;* similarly, *B. (Elytrodes) ionae* and *B. (Spifemodes) schaumi* are as well associated with ants. In *Excavodes*, troglobite species present dimorphism in the antennomere X as do the species found with either ants and/or leaf litter in the same subgenus. On the other hand, *Babnormodes* species with obligate associations with the troglobitic environment, do not show antennal modifications (19 and 20 in Fig. 13), as several other species of facultative troglophiles in this group do.

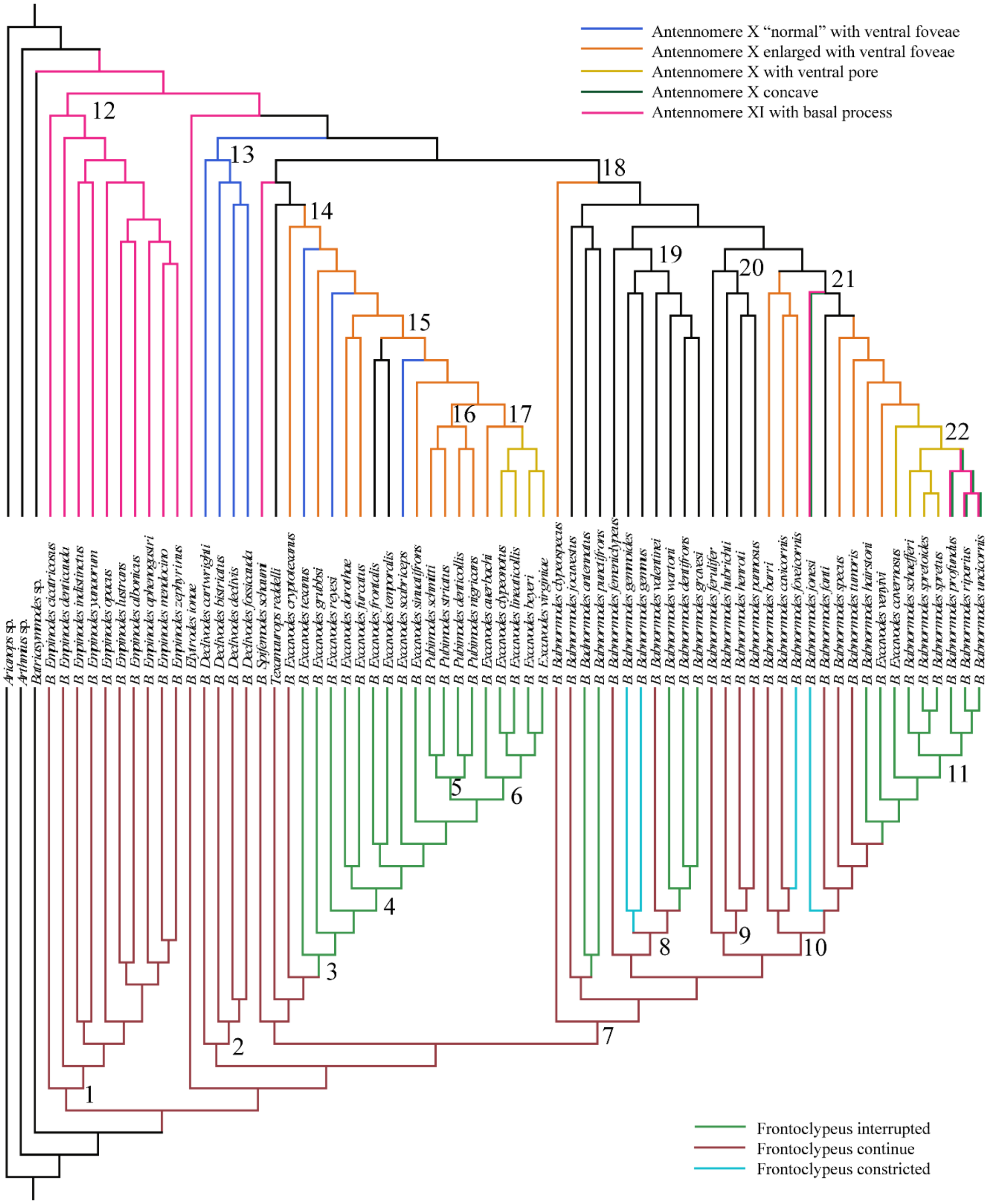


Figure 11. Cladogram of the *Nearctic* analysis comparing secondary sexual characters on the fronto-clypeal region of the head and the variation of antennomere X.

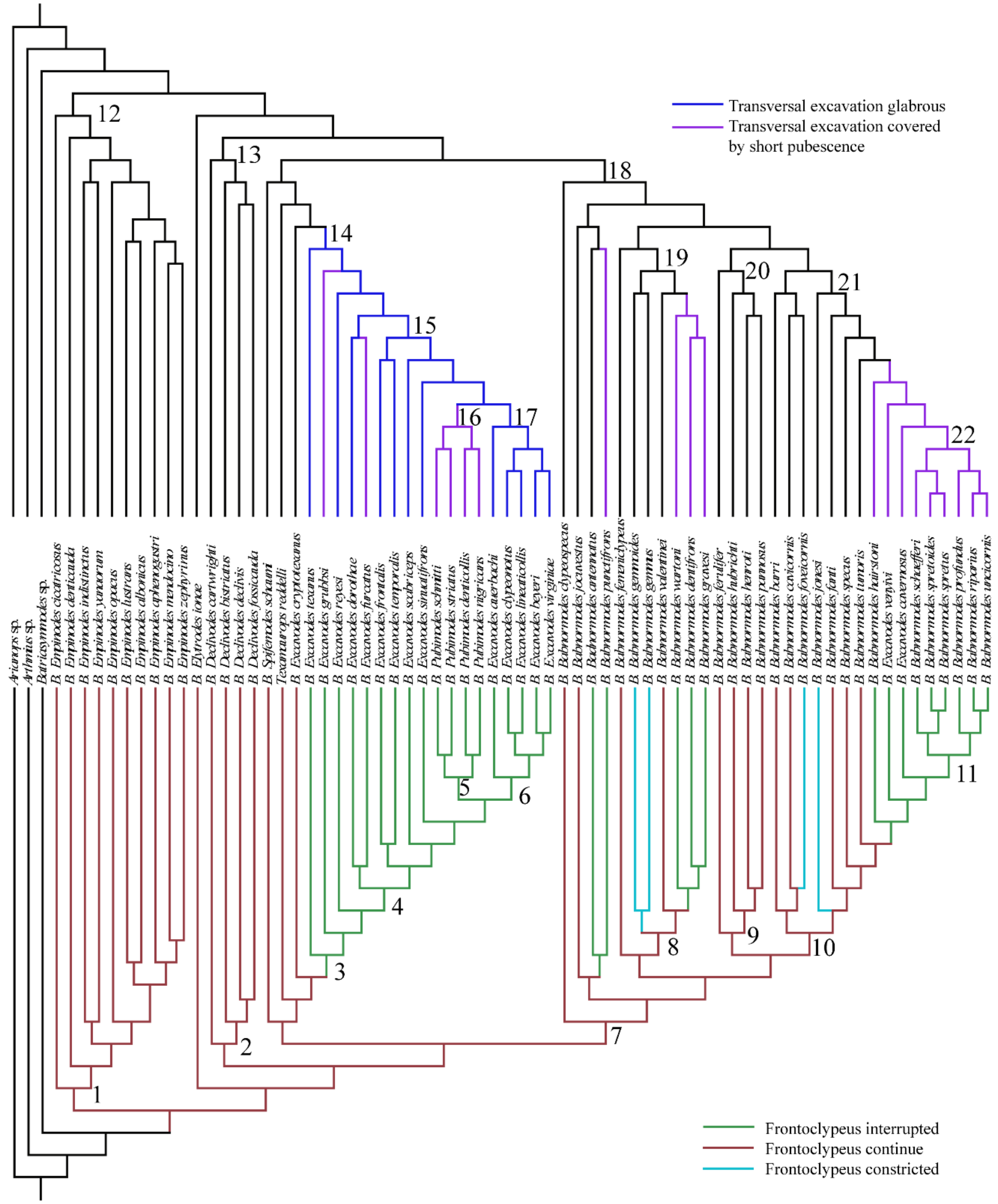


Figure 12. Cladogram of the *Nearctic* analysis comparing secondary sexual characters on fronto-clypeal region and the characteristics of the transversal excavation.

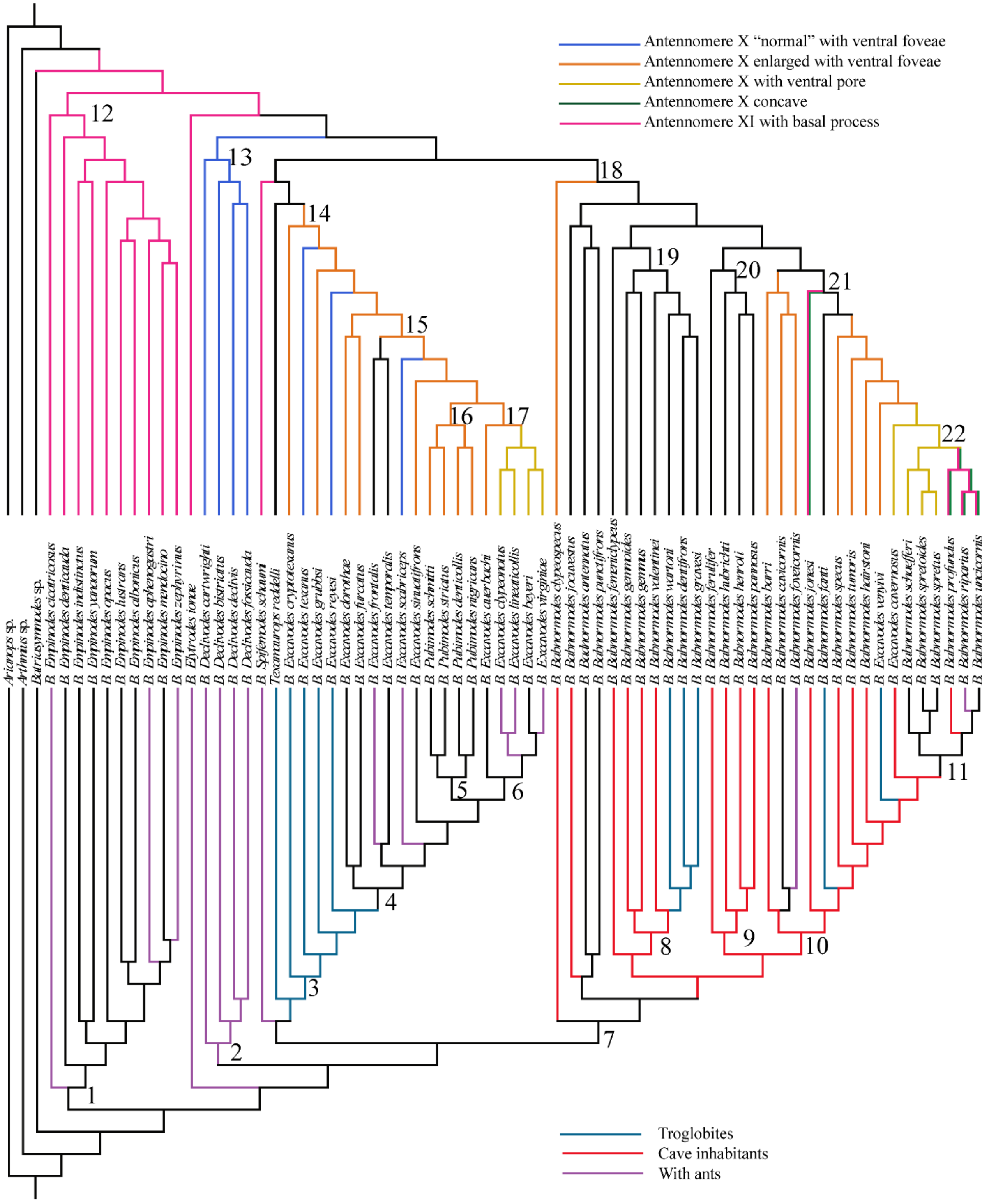


Figure 13. Cladogram of the *Nearctic* analysis comparing *Batrisodes* habitats with secondary sexual characters on antennomeres X and XI.

DISCUSSION

The parsimony analysis of the Holarctic data set (Fig. 1), resulted in the separation of Palearctic species into two different groups, within two clades of Nearctic *Batrisodes:* one group, nested within the subgenus *Excavodes,* and the other among species of *Batrisus* and the subgenus *Empinodes.* Interestingly, these Palearctic species segregated into two of the species groups proposed by Besuchet (1981) in his revision of the *Batrisodes* from the Palearctic, excluding Japan. Besuchet grouped *Batrisodes pogonatus, B. buqueti, B. delaporti, B. adnexus, B. tichomirovae,* and *B. venustus* into the "Group venustus", considering that these species have the discal carina on the first abdominal tergite arising from the outer edge of the mediobasal fovea; they lack the distal tuft of hairs on the metatibiae, and have simple aedeagi. Additionally, the species *B. occulatus,* and *B. sulcaticeps* were in the "Group occulatus", since they present the discal carina on the first abdominal tergite starting on the posterior edge of the mediobasal fovea, they have a distal tuft of hairs on the metatibiae, the frontal region the head is crossed by a transversal sulcus over the clypeus, and their aedeagus is simple (Besuchet 1981: 276). These Palearctic species resemble Nearctic species in the subgenera *Empinodes, Elytrodes,* and *Spifemodes.* Across the distribution of the genus, *Batrisodes* species seem to share three different secondary sexual characters: mesofemora with basal or mesal protuberance, mesotibiae with mesal protuberance, and antennomere XI with basal process. In the Nearctic subgenera *Babnormodes* and *Excavodes*, these three characters are not obvious in many of the species; however, *B. (Excavodes) lineaticollis* presents a small spine on the mesotibiae (Fig. S1 A), and in *B. (Excavodes) auerbachi* antennomere XI presents a small pore, detected only through SEM (Fig. S1 B). Likewise, in *B. (Declivodes) bistriatus* and in *B. (Babnormodes) jonesi* the antennomere XI bears a small pore basally. Thus, it is possible that during the diversification of *Batrisodes* in eastern North America, these three characters were reduced and lost subsequently in multiples species.

Following the resulting cladograms, the most species rich subgenera *Babnormodes* and *Excavodes* showed not only a great diversity in the variation of secondary sexual characters, but also diversification towards cavernicolous environments, that have been reached independently in these two lineages. For instance, in *Babnormodes* 17 of the 29 species included in the analysis have been collected near to or in caves of Kentucky, Indiana, Tennessee, and Alabama, and these show ten independent losses of antennal modifications. Also, there are at least three different modifications on the fronto-clypeal region that these troglophile species have, and only one group of four species (node 9 in Fig. 11) lacks both antennal and head modifications. All this suggests that maybe antennal secondary sexual characters are not under as much selective pressure as secondary sexual characters in the fronto-clypeus. This hypothesis could explain how *Babnormodes* troglobites have an interrupted fronto-clypeal region, but also show unmodified antennae in males. In contrast, two of the four *Excavodes* species that have transitioned into the cave environment show a reduction in size of the antennomere X, while the ventral fovea persists in this flagellomere. Moreover, these four species are all troglobites, possessing the morphological changes associated with life in complete darkness, and they still bear the transversal excavation in the rostrum, common to all *Excavodes* species.

Altogether, *Batrisodes* species in the Nearctic show frequent convergence in the presence of a basal process (either a tooth or a small pore) on antennomere XI (Fig. 6), and less frequently, in the presence of a posterior tooth or spine in mesofemora, and a spine in mesotibiae (Fig. 7A and B). Exceptions, however, include *B. (Elytrodes) ionae, B. (Spifemodes) schaumi,* and *Empinodes*, which retain the plesiomorphic morphology of these characters, similar to Palearctic species. In the case of *Declivodes* species, they seem to have specialized to the point where it is rather difficult to hypothesize, just on the basis of morphology, a clear phylogenetic relationship with any other subgenus. Nonetheless, in *B. (Declivodes) bistriatus,* there is a small pore on antennomere XI (illustrated in Fig. 6C), which is also present on one species of *Excavodes* and one of *Babnormodes*. Literature on *Declivodes* indicates that all its species are found with ants, and the species *B. (Declivodes) bistriatus* and *B. (Declivodes) fossicauda* are found with species of *Formica* (Parker 1947; Chandler 1997), but there is no information about the context of the interaction between these beetles and the ants. In *Excavodes* these three characters states in the antennomere XI, mesofemora and mesotibiae are slightly visible in some species (Appendix C), indicating that maybe in this subgenus those characters have been secondarily lost. Only one lineage within *Babnormodes* shows similarities of antennomere XI with Palearctic *Batrisodes*, *Empinodes, Elytrodes,* and *Spifemodes,* suggesting convergence of this character. Additionally, the facultative troglophile *B. (Babnormodes) jonesi* presents a small pore on the base of antennomere XI. Thus, for the current subgeneric classification of *Batrisodes* in North America, the loss of these characters was the result of convergence in the subgenera *Excavodes* (including *Pubimodes*), *Babnormodes,* and *Declivodes.*

On a smaller scale within the genus, *Babnormodes* and *Excavodes* (including *Pubimodes*) present a series of convergent characters in the species that have the fronto-clypeus excavated; species in both groups present the transverse frontal excavation covered by short hairs, which is common to all *Babnormodes* species with the fronto-clypeus interrupted, to the troglobite *Excavodes*, and to all *Pubimodes.* Furthermore, the enlargement of antennomere X seems to be common to *Babnormodes, Excavodes*, and *Pubimodes* species that are not associated with cave microhabitats. The presence of the ventral fovea on this same antennomere could be the most constant character among the already mentioned subgenera and *Declivodes.* Secondary sexual characters on the antennae appear to be more frequently lost when these beetles transition completely to cave environments, compared to fronto-clypeal modifications.

Looking only at number of species contrasted with the number of secondary sexual traits in *Batrisodes* and all Pselaphinae in general, it could be easy to conclude that there is a direct relationship between species diversity (or speciation) and secondary sexual characters (as consequences of sexual selection). At the same time, when taxa as diverse as *Batrisodes* are observed in more detail, and as more data about their ecology, biology, and natural history has become available, it becomes clear that the success of this group is the result of many factors working in concert. Surely, sexual selection is one of them, as evidenced by the diversity of secondary sexual characters, but also the diversity of morphological adaptations, and the readiness to occupy new habitats.

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CHAPTER FOUR

GENERAL CONCLUSIONS

Secondary sexual characters, as a manifestation of Sexual Selection, are widespread in the diverse group of Pselaphinae beetles. Until now, these characters have primarily been important in the taxonomy of the group; the present research, however, underlines the importance of these characters in an evolutionary context. Having a general overview of these characters' diversity allows for comparisons among different lineages, to identify if certain characters are common to particular groups within Pselaphinae and hypothesize the action of the selective pressure(s) that shaped their evolution.

The information gathered in Chapter two, although limited, sets a baseline to continue looking at the relationship between species richness and presence of secondary sexual characters. To study this relationship, several caveats have to be worked out: the number of taxa on each species group (or tribe) should be comparable, and the sources of information should be assessed for varying amount of detail used to describe the species.

Compact body may have been a selective pressure for the evolution of abdominal sternite modification and subsequent leg segment modifications. Some groups of Pselaphinae may have evolved male chemical attractants suggested by the presence of glandular openings; however, more work on the histology of this glandular tissue is needed, as well as behavioral data to assess the behavioral context in which these putative glands are used.

The Holarctic genus *Batrisodes* shares groups of sexually dimorphic characters in antennomeres X, XI, mesofemora, and mesotibiae. Presence of the head transversal excavation is present throughout the genus's distribution, but it seems to have evolved independently several times.

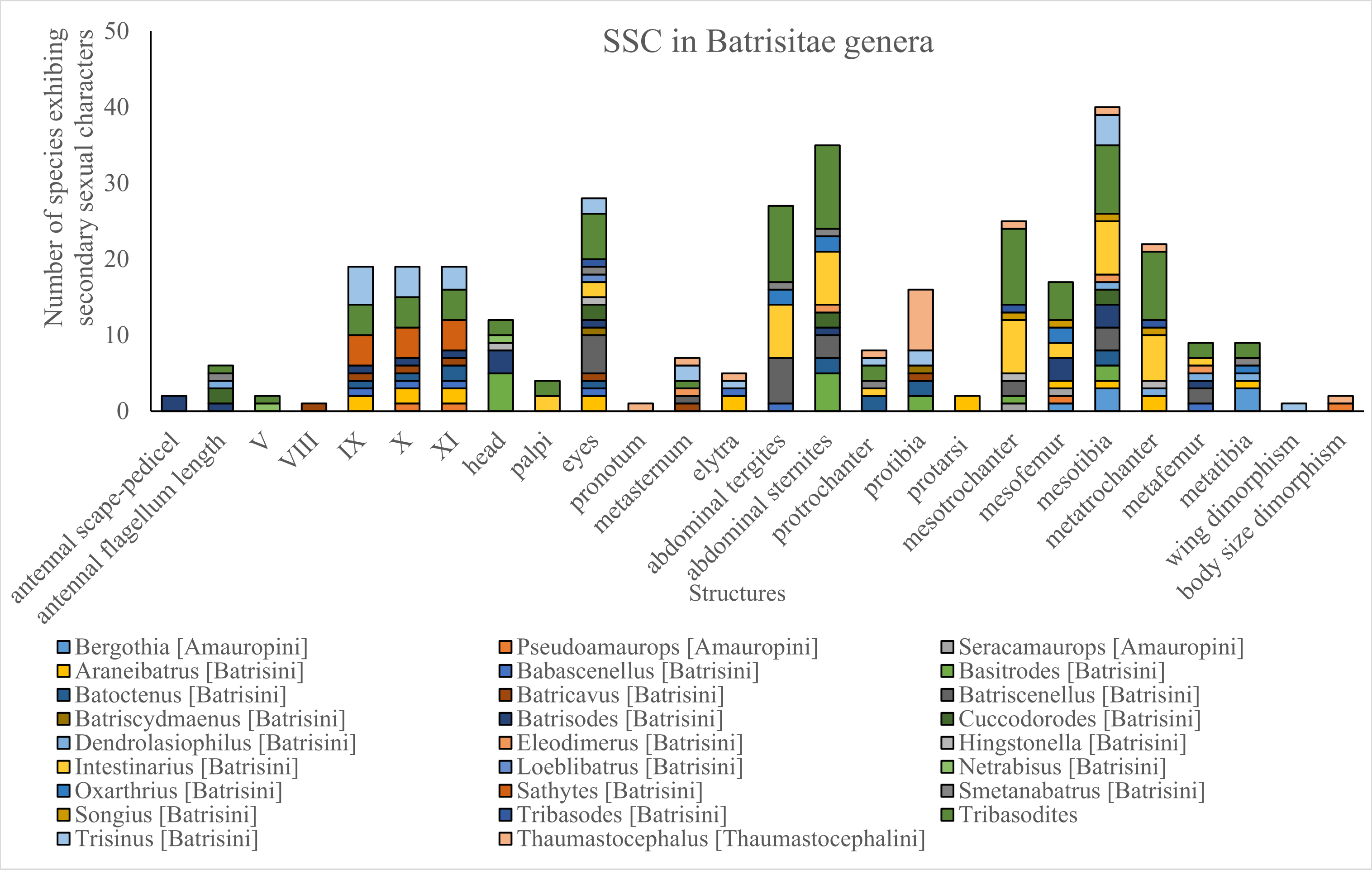
Most species of Nearctic *Batrisodes* are grouped in the subgenera *Babnormodes* and *Excavodes*. In these subgenera, cavernicolous species have evolved multiple times. In *Babnormodes,* cavernicolous species can be facultative (troglophilic) or obligate (troglobitic), while in *Excavodes*, all the species that inhabit caves are troglobitic. The changes from life near the ground surface to the cave habitat differently impacted each group in the losses and permanence of their secondary sexual characters. In *Babnormodes* some troglophilic and all the troglobitic species show loss of the antennal modifications. Troglobites in *Excavodes* present reduction in the size of antennomere X, but some species preserve the ventral foveae, and all of them have the transversal excavation on the head, characteristic of the subgenus.

This research is an initial step towards the documentation of sexually dimorphic characters in Pselaphinae; this information can be used in the future to look at character evolution, character correlation with environment, and with other characters. With the accumulation of this type of information, it is possible to identify patterns in the strength of natural selection, sexual selection, and the mechanisms under which the morphological diversity of groups such as Pselaphinae beetles have evolved to become hyperdiverse.

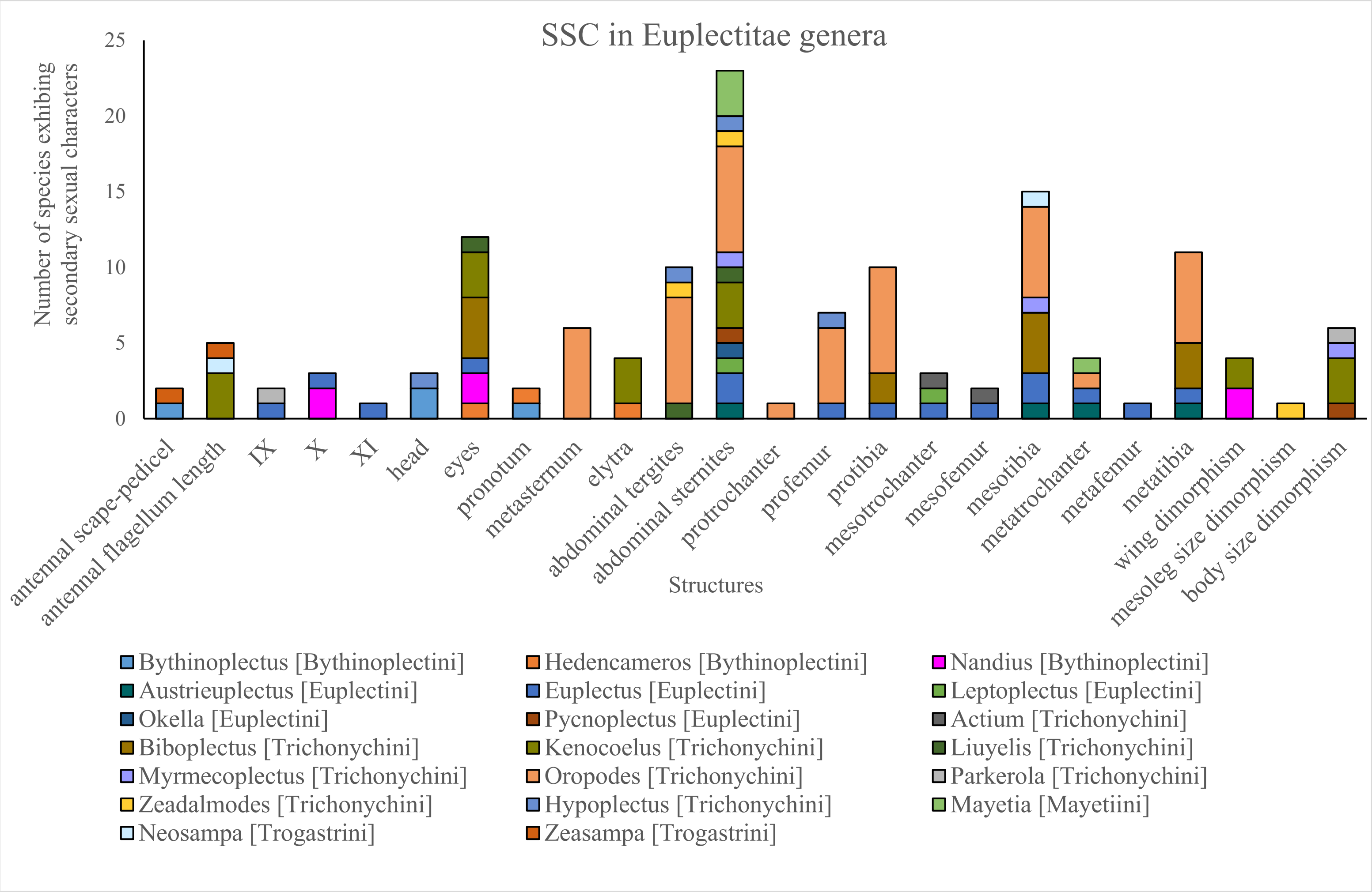
APPENDICES

Appendix A

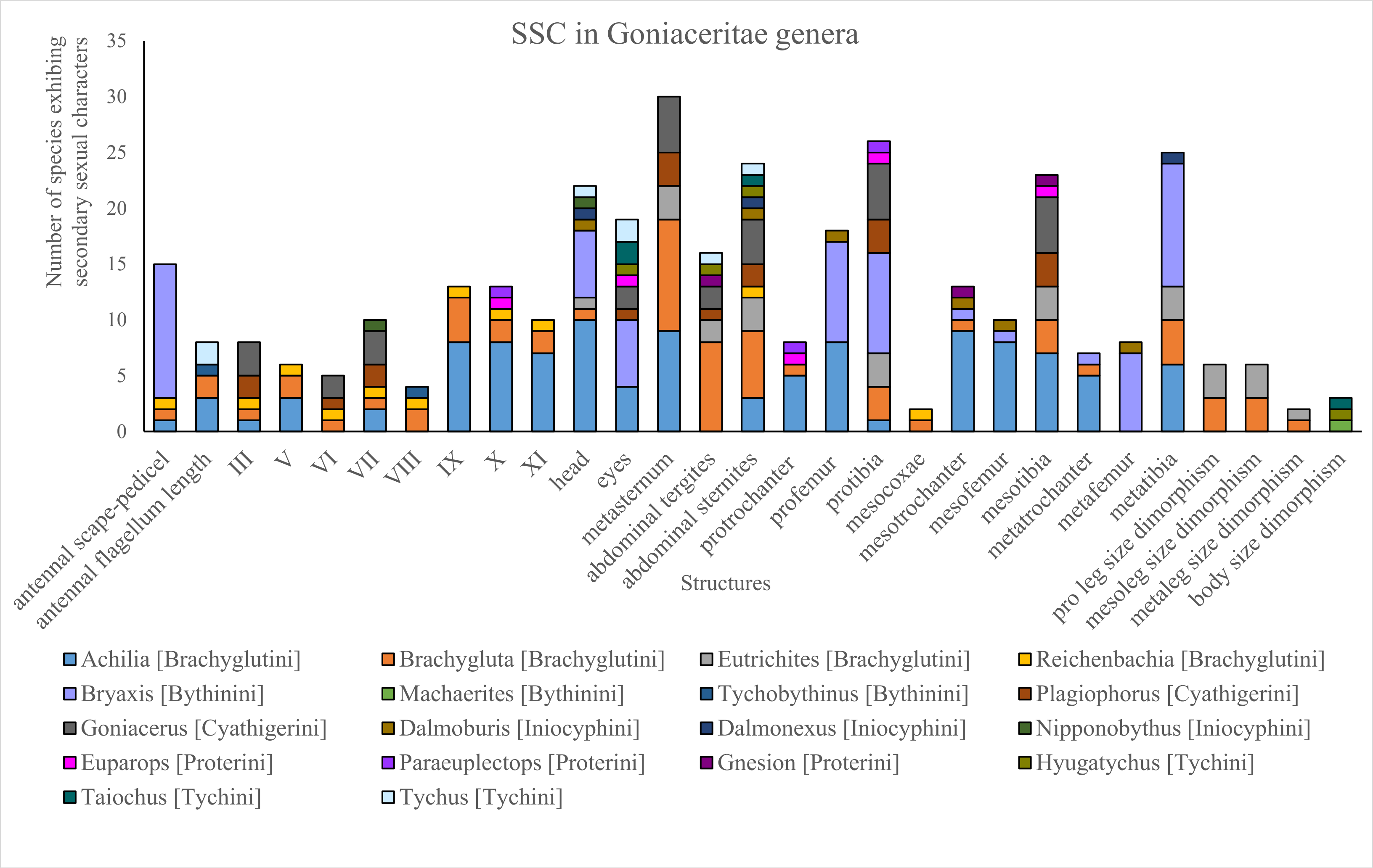
Number of Species within genera of Batrisini showing secondary sexual characters.



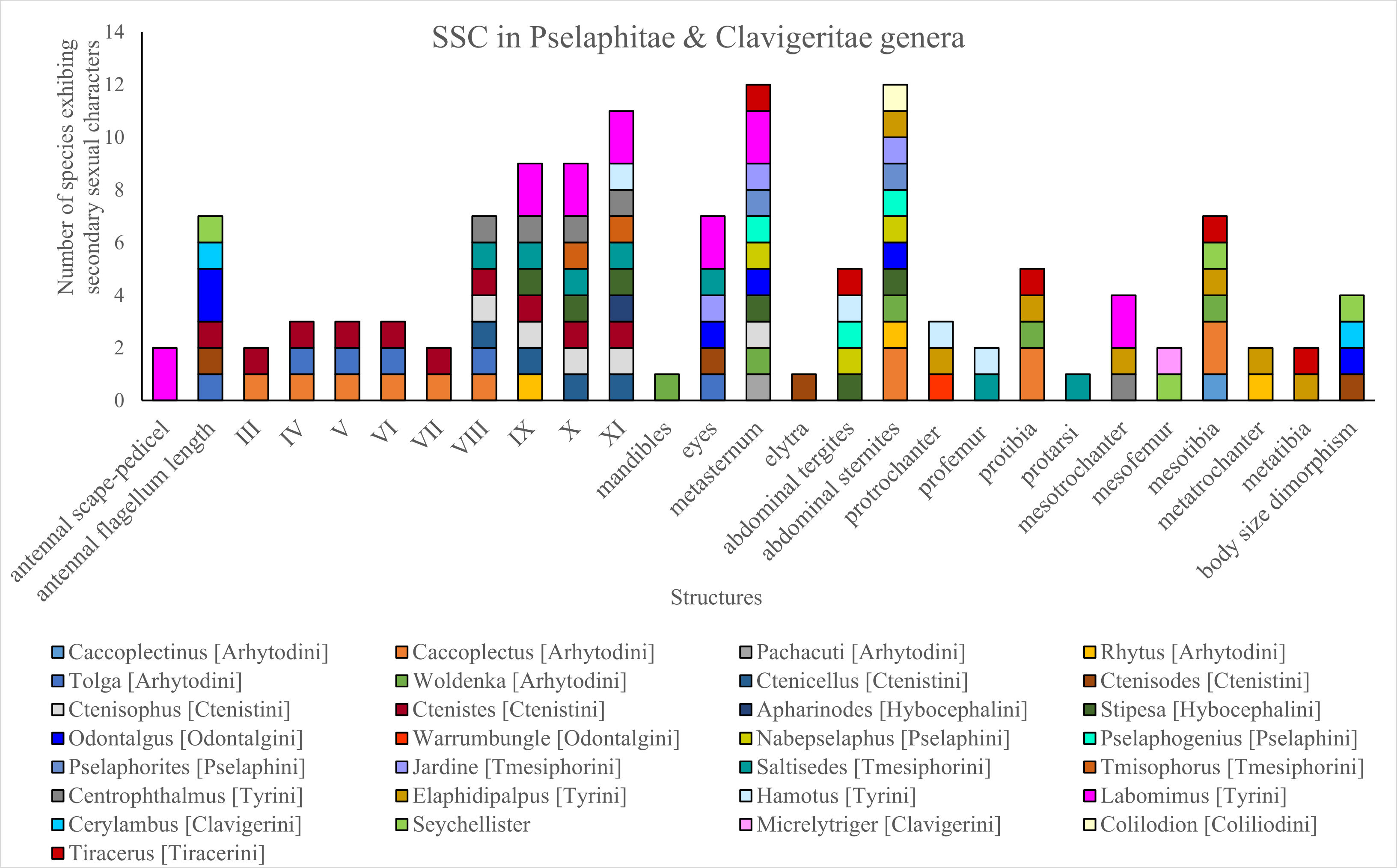
Number of Species within genera of Euplectitae showing secondary sexual characters.



Number of Species within genera of Goniaceritae showing secondary sexual characters.



Number of Species within genera of Pselaphitae and Clavigeritae showing secondary sexual characters.



Appendix B

General information about the taxa selected to sample secondary sexual characters.

Tribe	***Genus***	***species***	**Type locality**	**Region**	**Biology**	**Reference**
Amauropini	*Bergrothia*	*adzharica*	Georgia	Palearctic	on sifted leaflitter in an altitud of 400 m	Hlavac 2004
Amauropini	*Bergrothia*	*solodovnikovi*	Turkey	Palearctic	on sifted leaflitter	Hlavac 2004
Amauropini	*Bergrothia*	*tibialis*	Turkey	Palearctic	on leaflitter of Fagus forest	Hlavac 1999
Amauropini	*Pseudamaurops*	*graecus*	Albania	Palearctic	moist leaflitter and under rocks	Hlavac 2005
Amauropini	*Seracamaurops*	*komarovi*	Russia	Palearctic	cave inhabitant	Hlavac et al 1999
Batrisini	*Araneibatrus*	*curvitibialis*	China	Indo-Malay	cave inhabitant	Yin & Zhou 2018
Batrisini	*Araneibatrus*	*callissimus*	China	Indo-Malay	cave inhabitant	Nomura&Wang 1991
Batrisini	*Atheropterus*	*lunulatus*	Gabon	Afrotropical	N/A	Castellini 1997
Batrisini	*Babascenellus*	*macroscapus*	Japan	Palearctic	sandy soil	Nomura 1995
Batrisini	*Basitrodes*	*godzilla*	Japan	Palearctic	Aphaenogaster japonica	Nomura 2003
Batrisini	*Basitrodes*	*hakusanus*	Japan	Palearctic	Formica lemani	Nomura 2002
Batrisini	*Basitrodes*	*kasahari*	Japan	Palearctic	leaflitter	Nomura 2002
Batrisini	*Basitrodes*	*oscillator*	Japan	Palearctic	ants of the genera Lasius and Formica	Nomura 2002
Batrisini	*Basitrodes*	*vestitus*	Japan	Palearctic	Paratrechina flavipes, Aphaenogaster japonica, Myrmica kotokui, Myrmica jessensis, Aphaenogas famelica	Nomura 2003

Batrisini	*Batoctenus*	*kawmontis*	French Guiana	Neotropic	N/A	Yin 2019
Batrisini	*Batoctenus*	*kociani*	French Guiana	Neotropic	N/A	Yin 2019
Batrisini	*Batricavus*	*tibialis*	China	Indo-Malay	leaflitter	Yin et al 2011f
Batrisini	*Batriscenellus*	*chinensis*	China	Palearctic	N/A	Yin et al 2011d
Batrisini	*Batriscenellus*	*femoralis*	China	Palearctic	N/A	Yin et al 2011d
Batrisini	*Batriscenellus*	*orientalis*	China	Palearctic	N/A	Yin et al 2011d
Batrisini	*Batriscenellus*	*pulcher*	China	Palearctic	N/A	Yin et al 2011d
Batrisini	*Batriscenellus*	*satoi*	China	Palearctic	Formica fusta	Nomura 2003b
Batrisini	*Batriscenellus*	*subalpicolus*	China	Palearctic	leaflitter	Nomura 2003b
Batrisini	*Batriscenellus*	*admonitor*	Russia	Palearctic	N/A	Yin et al 2011d
Batrisini	*Batriscenellus*	*auritus*	North Korea	Palearctic	N/A	Yin et al 2011d
Batrisini	*Batriscydmaenus*	*tishechkini*	Panama	Neotropic	possible myrmecophile	Parker & Owens 2018
Batrisini	*Batrisodes*	*babaianus*	Taiwan	Indo-Malay	N/A	Nomura 2007
Batrisini	*Batrisodes*	*masatakai*	Taiwan	Indo-Malay	N/A	Nomura 2007
Batrisini	*Batrisodes*	*sennin*	Japan	Palearctic	N/A	Nomura 2007
Batrisini	*Cuccodorodes*	*darjeelingensis*	India	Indo-Malay	N/A	Yin 2018
Batrisini	*Cuccodorodes*	*koshiensis*	Nepal	Indo-Malay	N/A	Yin 2018
Batrisini	*Dendrolasiophilus*	*nishikawai*	Japan	Palearctic	Lasius orientalis, L. nipponensis	Nomura 2008
Batrisini	*Eleodimerus*	*comes*	Gabon	Afrotropical	N/A	Castellini 1997
Batrisini	*Hingstoniella*	*lata*	India	Palearctic	with Myrmica sp.	Yin et al 2011a
Batrisini	*Intestinarius*	*crassicornis*	Laos	Indo-Malay	N/A	Kurbatov 2007
Batrisini	*Intestinarius*	*diatretus*	Sarawak	Indo-Malay	N/A	Kurbatov 2007

Batrisini	*Intestinarius*	*distorticeps*	Jawa	Indo-Malay	N/A	Kurbatov 2007
Batrisini	*Intestinarius*	*guangdongensis*	China	Indo-Malay	N/A	Yin et al 2011c
Batrisini	*Intestinarius*	*ingeniosus*	Sarawak	Indo-Malay	N/A	Kurbatov 2007
Batrisini	*Intestinarius*	*kuzmini*	China	Indo-Malay	N/A	Kurbatov 2007
Batrisini	*Intestinarius*	*longiceps*	China	Indo-Malay	N/A	Yin et al 2011c
Batrisini	*Intestinarius*	*orthopygium*	Laos	Indo-Malay	N/A	Kurbatov 2007
Batrisini	*Intestinarius*	*pexatus*	Sarawak	Indo-Malay	N/A	Kurbatov 2007
Batrisini	*Intestinarius*	*quinquesulcatus*	Singapur	Indo-Malay	N/A	Kurbatov 2007
Batrisini	*Loeblibatrus*	*yunnanus*	China	Palearctic	collected with ants *Extomomyrmex*	Yin 2018
Batrisini	*Netrabisus*	*aestuarii*	Gabon	Afrotropical	N/A	Castellini 1997
Batrisini	*Oxarthrius*	*aurora*	Brazil	Neotropic	cave inhabitant	Asenjo et al 2018
Batrisini	*Oxarthrius*	*inexpectatus*	Brazil	Neotropic	cave inhabitant	Asenjo et al 2018
Batrisini	*Sathytes*	*borneoensis*	East Malaysia: Borneo	Indo-Malay	N/A	Shen & Yin 2019
Batrisini	*Sathytes*	*liuyei*	East Malaysia: Borneo	Indo-Malay	N/A	Shen & Yin 2019
Batrisini	*Sathytes*	*larifuga*	East Malaysia: Borneo	Indo-Malay	N/A	Shen & Yin 2019
Batrisini	*Sathytes*	*shihongliangi*	East Malaysia: Borneo	Indo-Malay	N/A	Shen & Yin 2019
Batrisini	*Smetanabatrus*	*loebli*	Peninsular Malaysia	Indo-Malay	wood and bamboo sift	Yin & Cuccodoro 2018
Batrisini	*Songius*	*hlavaci*	China	Indo-Malay	with Lasius niger	Zhao etal. 2010
Batrisini	*Tribasodes*	*chinnensis*	China	Indo-Malay	with Pachycondyla luteipes	Zhao etal. 2010
Batrisini	*Tribasodites*	*abnormalis*	China	Palearctic	cave inhabitant	Yin, Z-W et al 2015

Batrisini	*Tribasodites*	*bama*	China	Palearctic	cave inhabitant	Yin, Z-W et al 2015
Batrisini	*Tribasodites*	*bedosae*	China	Indo-Malay	cave inhabitant	Yin et al 2011e
Batrisini	*Tribasodites*	*biyun*	China	Indo-Malay	cave inhabitant	Yin & Zhou 2018
Batrisini	*Tribasodites*	*cehengensis*	China	Palearctic	cave inhabitant	Yin, Z-W et al 2015
Batrisini	*Tribasodites*	*deharvengi*	China	Indo-Malay	cave inhabitant	Yin et al 2011e
Batrisini	*Tribasodites*	*liboensis*	China	Palearctic	cave inhabitant	Yin, Z-W et al 2015
Batrisini	*Tribasodites*	*thailandicus*	Thailand	Indo-Malay	cave inhabitant	Yin, Z-W et al 2015
Batrisini	*Tribasodites*	*uenoi*	China	Palearctic	cave inhabitant	Yin, Z-W et al 2015
Batrisini	*Tribasodites*	*xingyiensis*	China	Palearctic	cave inhabitant	Yin, Z-W et al 2015
Batrisini	*Trisinus*	*sagamianus*	Japan	Palearctic	N/A	Nomura 1991; Yin et al 2012
Batrisini	*Trisinus*	*tosanus*	Japan	Palearctic	N/A	Nomura 1991; Yin et al 2012
Batrisini	*Trisinus*	*shaolingiger*	China	Indo-Malay	N/A	Yin et al 2012
Batrisini	*Trisinus*	*pharelatus*	China	Indo-Malay	N/A	Yin et al 2012
Batrisini	*Trisinus*	*shuixiuifer*	China	Indo-Malay	N/A	Yin et al 2012
Thaumastocephalini	*Thaumastocephalus*	*bilandzijae*	Croatia	Palearctic	cave inhabitant	Hlavac et al 2019
Thaumastocephalini	*Thaumastocephalus*	*dahnae*	Bosnia & Herzegovina	Palearctic	cave inhabitant	Hlavac et al 2019
Thaumastocephalini	*Thaumastocephalus*	*kirini*	Croatia	Palearctic	cave inhabitant	Hlavac et al 2019
Thaumastocephalini	*Thaumastocephalus*	*marsici*	Croatia	Palearctic	cave inhabitant	Hlavac et al 2019
Thaumastocephalini	*Thaumastocephalus*	*rujnicensis*	Croatia	Palearctic	cave inhabitant	Hlavac et al 2019
Thaumastocephalini	*Thaumastocephalus*	*slavkoi*	Croatia	Palearctic	cave inhabitant	Hlavac et al 2019
Thaumastocephalini	*Thaumastocephalus*	*troglavi*	Croatia	Palearctic	cave inhabitant	Hlavac et al 2019

Thaumastocephalini	*Thaumastocephalus*	*folliculipalpus*	Croatia	Palearctic	cave inhabitant	Poggi et al 2001
EUPLECTITAE						
Tribe	*Genus*	*species*	Type locality	Region	Biology	Reference
Bythinoplectini	*Bythinoplectus*	*bertonii*	Paraguay, Brazil	Neotropic	N/A	Comellini 1985
Bythinoplectini	*Bythinoplectus*	*dechambrieri*	Guatemala	Neotropic	N/A	Comellini 1985
Bythinoplectini	*Bythinoplectus*	*depressus*	Panama	Neotropic	N/A	Comellini 1985
Bythinoplectini	*Hedencameros*	*costaricense*	Costa Rica	Neotropic	N/A	Comellini 1985
Bythinoplectini	*Nandius*	*myriamae*	India	Indo-Malay	N/A	Coulon 1990
Bythinoplectini	*Nandius*	*besucheti*	India	Indo-Malay	N/A	Coulon 1990
Dimerini	*Otomicrus*	*dentifrons*	Iraq	Palearctic	N/A	Besuchet 1999
Euplectini	*Austroeuplectus*	*oz*	Eastern Australia	Australasia	in rotten wood or Eucalyptus bark litter in all forests types	Chandler 2001
Euplectini	*Euplectus*	*caecus*	Tenerife, Spain	Palearctic	N/A	Besuchet 1990
Euplectini	*Euplectus*	*hierrensis*	Canary Is. (El Hierro)	Palearctic	N/A	Besuchet 1990
Euplectini	*Leptoplectus*	*filiformis*	Pennsylvania, Ohio, US	Nearctic	N/A	Casey 1908
Euplectini	*Okella*	*parallelus*	Southeastern Australia	Australasia	in Solenopsis colony	Chandler 2001
Euplectini	*Pycnoplectus*	*impressiceps*	Pennsylvania, US	Nearctic	N/A	Casey 1908
Jubini	*Morphogenia*	*struhli*	Brazil	Neotropic	on leaflitter	Parker 2014
Mayetiini	*Mayetia*	*bowmani*	North Carolina, USA	Nearctic	preference for sandy soil	Schuster et al. 1959
Mayetiini	*Mayetia*	*pearsei*	North Carolina, USA	Nearctic	on clay soil under oaks	Schuster et al. 1959

Mayetiini	*Mayetia*	*mendocinoensis*	California, USA	Nearctic	commonly found in the first few inches of mineral soil of the A2 horizon and are infrequently recovered from the overlying mat of organic debris	Schuster et al. 1960
Metopiasini	*Metopioxys*	*carajas*	Brazil	Neotropic	cave inhabitant	Asenjo et al 2019
Trichonychini	*Actium*	*vestigialis*	California, USA	Nearctic	Lyonothamnus floribundus floribundus and Quercus leaflitter	Caterino&Chandler 2010
Trichonychini	*Bibloplectus*	*ellisi*	North Carolina, USA	Nearctic	on Sphagnum moss	Owens&Carlton 2018
Trichonychini	*Bibloplectus*	*parki*	Florida, USA	Nearctic	on palmetto and scrub debris	Owens&Carlton 2018
Trichonychini	*Bibloplectus*	*quadratum*	Connecticut, USA	Nearctic	on Sphagnum	Owens&Carlton 2018
Trichonychini	*Bibloplectus*	*tishechkini*	Florida and South Carolina, USA	Nearctic	on Sphagnum	Owens&Carlton 2018
Trichonychini	*Kenocoelus*	*dimorphus*	New Zeland	Australasia	in litter`	Nomura&Leschen 2015
Trichonychini	*Kenocoelus*	*mikonuiensis*	New Zeland	Australasia	with ants in wood	Nomura&Leschen 2015
Trichonychini	*Kenocoelus*	*johni*	New Zeland	Australasia	with Huberia striata ants (Myrmicinae)	Nomura&Leschen 2015
Trichonychini	*Liuyelis*	*camponotophila*	China	Palearctic	with Camponotus sp	Yin et al 2011
Trichonychini	*Myrmecoplectus*	*wellingtonicus*	New Zeland	Australasia	with Austroponera castanea (Ponerinae)	Nomura&Leschen 2015
Trichonychini	*Oropodes*	*arcaps*	California, USA	Nearctic	taken from redwood and fearn leaflitters near or at the coast	Chandler&Caterino 2011

Trichonychini	*Oropodes*	*dybasi*	Oregon, USA	Nearctic	on old growth and 30 year-old clearcut regrowth	Chandler&Caterino 2011
Trichonychini	*Oropodes*	*orbiceps*	California, USA	Nearctic	oak (Quercus lobata) wooland	Chandler&Caterino 2011
Trichonychini	*Oropodes*	*tataviam*	California, USA	Nearctic	in scrub oaks, gray or Digger pine, and mid-elevation chaparral	Chandler&Caterino 2011
Trichonychini	*Oropodes*	*chumash*	California, USA	Nearctic	semiriparian woodland	Chandler&Caterino 2011
Trichonychini	*Oropodes*	*hardyi*	California, USA	Nearctic	at black light without any nearby patches of native vegetation	Chandler&Caterino 2011
Trichonychini	*Oropodes*	*tongva*	California, USA	Nearctic	FIT in small pocketof live oak woodland surrounded by mid-elevation chaparral	Chandler&Caterino 2011
Trichonychini	*Parkerola*	*gigantea*	New Zeland	Australasia	with Huberia striata ants (Myrmicinae)	Nomura&Leschen 2015
Trichonychini	*Zeadalmodes*	*myrmecophilus*	New Zeland	Australasia	with Austroponera castanea and A. castaneicolor	Nomura&Leschen 2015
Trichonychini	*Hypoplectus*	*palmi*	Kenya	Afrotropical	N/A	Castellini 1997
Trogastrini	*Neosampa*	*granulata*	New Zeland	Australasia	with Prolasius advenus (Formicinae)	Nomura&Leschen 2015
Trogastrini	*Zeasampa*	*nunni*	New Zeland	Australasia	with Prolasius advenus (Formicinae)	Nomura&Leschen 2015
GONIACERITAE						
Tribe	*Genus*	*species*	Type locality	Region	Biology	Reference
Arnylliini	*Awas*	*gigas*	China	Indo-Malay	with Pachyccondyla	Yin et al 2015

Brachyglutini	*Achilia*	*adorabilis*	Chile	Neotropic	FIT in Valdivian rainforest	Sabella et al 2019
Brachyglutini	*Achilia*	*baburra*	Chile	Neotropic	Valvidian rainforest	Sabella et al 2019
Brachyglutini	*Achilia*	*caracolana*	Chile	Neotropic	In Nothofagus, Cupressus, and Eucalyptus forests	Kurbatov et al 2018
Brachyglutini	*Achilia*	*crassicornis*	Chile	Neotropic	on Nothofagus and Araucaria leaflitter	Sabella et al 2017
Brachyglutini	*Achilia*	*lobifera*	Southern Chile	Neotropic	on Nothofagus and Araucaria leaflitter	Sabella et al 2017
Brachyglutini	*Achilia*	*longispina*	Chile	Neotropic	N/A	Kurbatov et al 2018
Brachyglutini	*Achilia*	*pachycera*	Chile	Neotropic	on Nothofagus and Araucaria leaflitter	Kurbatov et al 2018
Brachyglutini	*Achilia*	*puncticeps*	Chile	Neotropic	Valdivian rainforest and Saxogathaea	Sabella et al 2019
Brachyglutini	*Achilia*	*reitteri*	Chile	Neotropic	Valdivian rainforest and Saxogathaea	Sabella et al 2019
Brachyglutini	*Achilia*	*testacea*	Chile	Neotropic	Valdivia rainforest; remnets and disturbed forest	Kurbatov et al 2018
Brachyglutini	*Brachygluta*	*cavicornis*	Virginia, USA	Nearctic	with Myrmica sabuleti in salt march	Chandler et al 2018
Brachyglutini	*Brachygluta*	*floridiana*	Eastern USA	Nearctic	beneath washed logs and boards on beaches	Chandler et al 2018
Brachyglutini	*Brachygluta*	*corniventris*	Midwestern USA	Nearctic	under driftwood on river banks	Chandler et al 2018
Brachyglutini	*Brachygluta*	*dentata*	Eastern and Midwestern USA	Nearctic	Under washed up log, UV light	Chandler et al 2018

Brachyglutini	*Brachygluta*	*eldredgei*	California, USA	Nearctic	with Pogonomyrmex under rock	Chandler et al 2018
Brachyglutini	*Brachygluta*	*arguta*	Midwestern to Northwestern part of Eastern NA	Nearctic	leaflitter around freshwater swamps and marings of streams	Chandler et al 2018
Brachyglutini	*Brachygluta*	*infinita*	Southern Texas	Nearctic	ultraviolet light	Chandler et al 2018
Brachyglutini	*Brachygluta*	*mormon*	Eastern California to Northern Utah	Neractic	beneath rocks by a pond in high deserts	Chandler et al 2018
Brachyglutini	*Eutrichites*	*simulatrix*	El Salvador, Costa Rica	Neotropic, Mesoamerican	N/A	Carlton&Leschen 1996
Brachyglutini	*Eutrichites*	*sotoi*	Mexico	Neotropic, Mesoamerican	N/A	Carlton&Leschen 1996
Brachyglutini	*Eutrichites*	*confusum*	Bolivia, Costa Rica, Mexico	Neotropic	N/A	Carlton&Leschen 1996
Brachyglutini	*Reichenbachia*	*fovearthra*	Panama	Neotropic	N/A	Park 1942
Bythinini	*Bryaxis*	*hypocritus*	Georgia	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*ipsimus*	Russia	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*kovali*	Russia	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*lederi*	Russia	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*mekischesiamus*	Georgia	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*polemon*	Turkey	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*pygmaeus*	Russia	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*rivularis*	Georgia	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*rousi*	Russia	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*temporalis*	Turkey	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Bryaxis*	*tenuicornis*	Turkey	Palearctic	N/A	Besuchet&Kurbatov 2007

Bythinini	*Bryaxis*	*viti*	Turkey	Palearctic	N/A	Besuchet&Kurbatov 2007
Bythinini	*Machaerites*	*marjanaci*	Croatia	Palearctic	cave inhabitant	Hlavac&Jalzic 2010
Bythinini	*Tychobythinus*	*lukici*	Croatia	Palearctic	cave inhabitant	Hlavac&Jalzic 2009
Cyathigerini	*Plagiophorus*	*hispidus*	Japan	Palearctic	in leaflitter	Sugaya et al 2004
Cyathigerini	*Plagiophorus*	*hlavaci*	China	Palearctic	N/A	Sugaya et al 2004
Cyathigerini	*Plagiophorus*	*amygdalinus*	Taiwan	Indo-Malay	in wet leaflitter in secondary forest or along roadsides. By sifting	Sugaya 2005
Goniacerini	*Goniacerus*	*schuteri*	Brazil	Neotropic	N/A	Comellini 1990
Goniacerini	*Goniacerus*	*lamellatus*	Venezuela	Neotropic	N/A	Comellini 1990
Goniacerini	*Goniacerus*	*microphthalmus*	Brazil	Neotropic	N/A	Comellini 1990
Imirni	*Imirus*	*outereloi*	Spain	Palearctic	N/A	Besuquet 1980
Iniocyphini	*Dalmoburis*	*petrunkevitchii*	Central America	Neotropic	in soft, moist, decayed log mold	Park 1942
Iniocyphini	*Dalmonexus*	*seeversi*	Panama	Neotropic	in rotten log mold, sifting floor mold	Park 1942
Iniocyphini	*Nipponobythus*	*dolharubang*	South Korea	Palearctic	N/A	Nomura&Lee 1992
Proterini	*Euparops*	*styx*	New South Wales, Australia	Australasia	from rotten logs in wet sclerophyll forest and rainforest	Chandler 2001; Kurvatov&Cuccodoro 2009
Proterini	*Pareuplectops*	*factor*	Vietnam	Indo-Malay	in rainforest leaflitter samples	Kurvatov & Cuccodoro 2009
Proterini	*Gnesion*	*rufulum*	New South Wales, Australia	Australasia	in rainforest leaflitter samples	Chandler 2001
Speleopbamini	*Prespelea*	*quirsfeldi*	North Carolina, USA	Nearctic	On leaflitter	Caterino&Vasquez-Velez 2017

Speleopbamini	*Prespelea*	*myersae*	North& South Carolina, USA	Nearctic	on leaflitter	Caterino&Vasquez-Velez 2017
Tychini	*Hyugatychus*	*teizonagatomoi*	Japan	Palearctic	N/A	Nomura 1996
Tychini	*Tainochus*	*iwaoi*	Japan	Palearctic	N/A	Nomura 1996
Tychini	*Tainochus*	*puncticeps*	Japan	Palearctic	N/A	Nomura 1996
Tychini	*Tychus*	*latebrosus*	Turkey	Palearctic	N/A	Sabella et al 2011
Tychini	*Tychus*	*algericus*	North of Africa	Palearctic	N/A	Sabella et al 2011b
Tychini	*Tychus*	*depexus*	North of Africa	Palearctic	N/A	Sabella et al 2011b
Tychini	*Tychus*	*yezoensis*	Japan	Palearctic	collected from decayed leaves of the common reed on wetland	Nomura 1996
Tychini	*Tychus*	*altivagus*	Turkey	Palearctic	N/A	Sabella et al 2011
Valdini	*Valda*	*frontalis*	California, USA	Nearctic	N/A	Casey 1893 (1894)
PSELAPHITAE						
Tribe	*Genus*	*species*	Type locality	Region	Biology	Reference
Arhytodini	*Caccoplectinus*	*afoveatus*	French Guiana	Neotropic	N/A	Chandler & Wolda 1986
Arhytodini	*Caccoplectus*	*incitus*	Panama	Neotropic	on UV light, canal zone	Chandler & Wolda 1986
Arhytodini	*Caccoplectus*	*orbis*	Panama	Neotropic	on UV light, canal zone	Chandler &Wolda 1989
Arhytodini	*Pachacuti*	*hugger*	Ecuador	Neotropic	N/A	Besuchet 1987
Arhytodini	*Rhytus*	*panamensis*	Panama	Neotropic	collected only at UV light	Chandler 1992
Arhytodini	*Tolga*	*curticornis*	Queensland, Australia	Australasia	collected at UV light or FIT	Chandler 2001
Arhytodini	*Woldenka*	*barroensis*	Panama	Neotropic	collected only at UV light	Chandler 1992

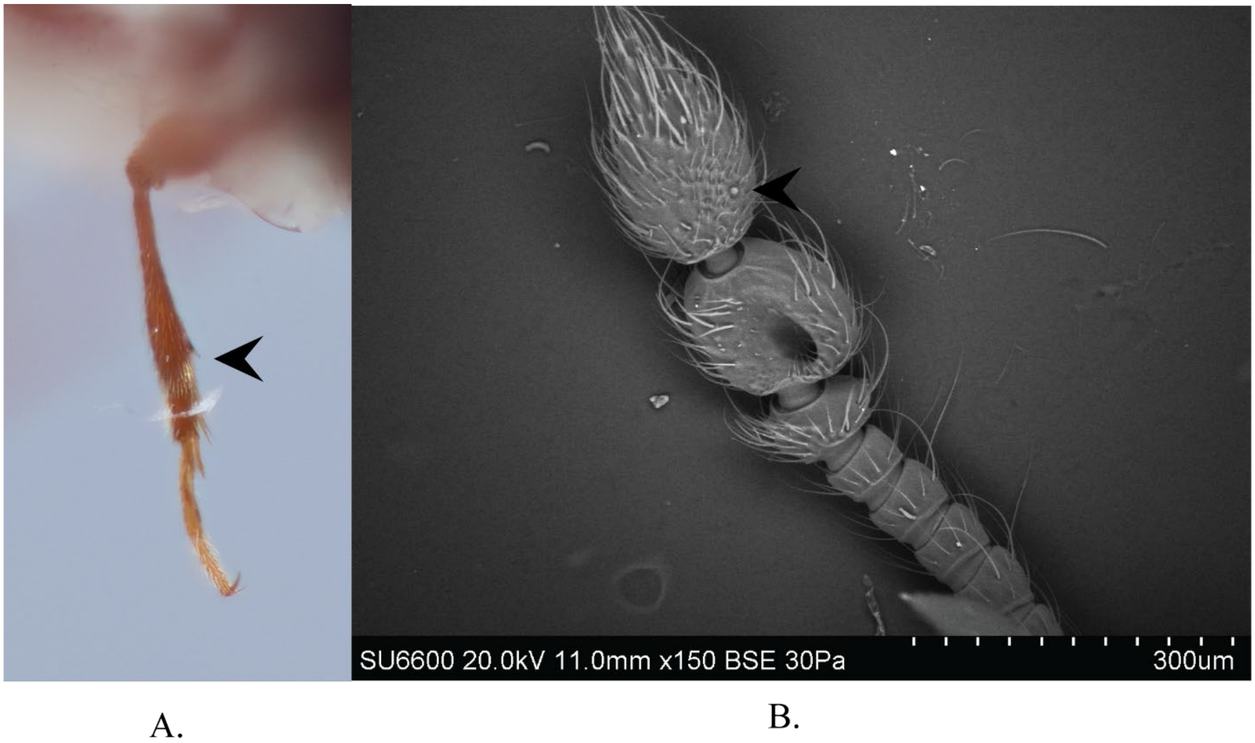
Ctenistini	*Ctenicellus*	*major*	Southeastern Australia	Australasia	collected with ant Rhytodoponera sp	Chandler 2001
Ctenistini	*Ctenisodes*	*granicollis*	New York, USA	Nearctic	N/A	Casey 1897
Ctenistini	*Ctenisophus*	*morosus*	Australia	Australasia	probably associated with ants and termites	Chandler 2001
Ctenistini	*Ctenistes*	*vaulogeri*	Morocco, Argelia, and Tunisia	Palearctic	N/A	Jeannel 1956
Hybocephalini	*Apharinodes*	*papageno*	Japan	Palearctic	N/A	Nomura 1989
Hybocephalini	*Stipesa*	*australiae*	Northen Territory, Australia	Australasia	only known from FIT	Chandler 2001
Hybocephalini	*Stipesa*	*utimia*	Sierra Leone	Afrotropical	N/A	Castellini 1986
Odontalgini	*Odontalgus*	*dongbaiensis*	China	Palearctic	sifted beneath a pile of straw	Yin et al 2016
Odontalgini	*Odontalgus*	*masaoi*	Japan	Palearctic	most type specimens were collected form litter of grassland on the banks of the Tokigawa River dominated by Miscanthus sinensis	Arai & Nomura 2003
Odontalgini	*Warrumbungle*	*orientalis*	Western Australia	Australasia	collected from Eucalyptus or Oxylobium leaf litter in dry sclerophyll forest	Chandler 2001
Phalepsini	*Phalepsus*	*neotropicus*	Mexico	Neotropic	collected from light at nigth	Park 1945
Pselaphini	*Nabepselaphus*	*yinae*	China, Yunan	Indo-Malay	N/A	Nomura 2004
Pselaphini	*Pselaphogenius*	*emeishanus*	Southwest China	Palearctic	N/A	Nomura 2003
Pselaphini	*Pselaphorites*	*zoiai*	Zaire	Afrotropical	N/A	Castellini 1997
Schistodactylini	*Leanymus*	*mirus*	Australia	Australasia	collected from Araucaria, Archontophoenix,	Lea 1919; Chandler 2001

					Dendrocnide, Eucalyptud and other leaf litters from wet sclerophyll forest and rainforest	
Schistodactylini	*Schitodactylus*	*brevipennis*	Australia	Australasia	from leaf litter in Eucalyptus and Nothofagus forests, and in grass tussocks	Chandler 2001
Tmesiphorini	*Jardine*	*kistnerorum*	Queensland, Australia	Australasia	found in colonies of the termite Nasutitermes graveolus	Chandler 2001
Tmesiphorini	*Saltisedes*	*hainanensis*	China: Hainan Prov.	Indo-Malay	N/A	Yin et al 2013
Tmesiphorini	*Tmesiphorus*	*amoenus*	Ghana	Afrotropical	N/A	Castellini 1997
Tyrini	*Centrophthalmus*	*bartolozzi*	Somalia	Afrotropical	N/A	Castellini 1997
Tyrini	*Elaphidipalpus*	*bonsarte*	South Africa	Afrotropical	N/A	Coulon 1994
Tyrini	*Hamotus*	*populus*	Arizona, USA	Nearctic	male in UV light, female under bark of dead cottonwood	Chandler 1974
Tyrini	*Hamotus*	*aztekus*	Veracruz, Mexico	Neotropic	N/A	Park 1942
Tyrini	*Labomimus*	*dadongmontis*	China: Taiwan	Indo-Malay	in leaf litter	Zhang & Yin 2019
Tyrini	*Labomimus*	*dilaticeps*	China: Taiwan	Indo-Malay	in leaf litter	Zhang & Yin 2019
CLAVIGERITAE						
Tribe	*Genus*	*species*	Type locality	Region	Biology	Reference
Clavigerini	*Cerylambus*	*maruyami*	Malaysia	Indo-Malay	N/A	Nomura et al. 2008
	Seychellister	*mornicus*	Seychelles	Afrotropical	Pandanus sifted litter	Hlavac & Nakladal 2018
Clavigerini	*Micrelytriger*	*mirabilis*	Japan	Palearctic	N/A	Nomura 1997
Colilodionini	*Colilodion*	*mirus*	Malaysia	Indo-Malay	on sifted vegetation	Besuchet 1991
Tiracerini	*Tiracerus*	*curvicornis*	Australia	Australasia	presumed to be obligate assiciates of ants, though	Chandler 2001

					few records from termites' nests. Most species in the genus collected on nests of Dolichoderinae ants near to the genus Iridomyrmex	

Appendix C

Secondary sexual characters in *Excavodes* species: Left: Spine in mesotibia in male of *B. (Excavodes) lineaticollis*. Right: Scanning electron microscopy (SEM) of antenna in male of *B. (Excavodes) auerbachi,* antennomere XI with microscopic basal pore.



A.

B.