

Two new fossil species of *Tillomorphites* Vitali (Coleoptera: Cerambycidae) and remarks on the morphological evolution, mimicry, biogeography and phylogeny of the tribe Tillomorphini

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The genus *Tillomorphites* Vitali, 2011 is revised with the description of two new species from Baltic Amber: *Tillomorphites spinipes* n. sp. and *Tillomorphites otiliae* n. sp. New observations and an improved reconstruction of *Tillomorphites robustus* Vitali, 2011 are provided. The typical characters of this genus are shared by the Ecuadorian extant species *Euderces elachys* Martins & Galileo, 2013 so that *Tillomorphites elachys* (Martins & Galileo, 2013) n. comb. is proposed. Biogeographical and biologic remarks on the genus *Tillomorphites* and on the phylogeny of Tillomorphini concerning distribution and morphologic evolution are hypothesised.

Key-words: Coleoptera, Cerambycidae, Tillomorphini, Baltic amber, taxonomy

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INTRODUCTION

The tribe Tillomorphini Lacordaire, 1869 includes about 30 genera and nearly 240 species including a fossil genus and species from Baltic amber.

A biogeographical analysis of the group is still questionable since the research is in progress and new species are continuously described (Touroult 2014; Miroshnikov 2014; 2015; Miroshnikov & Tichž 2015; Niisato 2015; Vives 2015), while some other ones are moved to other tribes (Slipinski & Escalona 2016). In fact, the typical habitus of this tribe (literally,

“having the aspect of *Tillus*”, Cleridae) is shared by many other cerambycids (Clytini, Anaglyptini, Eumichtini, Ibidionini, Obriini, Aphneopini, even Acanthocinini and Parmenini). However, Tillomorphini seems to be mainly widespread in Intertropical America and Asia with some genera in the Austral Hemisphere and Central Asia. None is known from Europe, except for the fossil genus *Tillomorphites* Vitali, 2011, found in Baltic amber.

The discovery of further fossil species, which are described in this paper, throw more light on the characters, as well as on the origin, evolution and phylogeny of the whole tribe.

MATERIALS AND METHODS

Observations on the fossils were made using a stereomicroscope Antares Geminar 3 with 20 - 40x eyepieces, equipped with a micrometer system. Pictures were furnished by the amber seller Marius Veta (Palanga, Lithuania). Drawings were obtained with a mixed traditional-computer graphic technique.

SYSTEMATIC PART

Cerambycidae Latreille, 1802

Cerambycinae Latreille, 1802

Tillomorphini Lacordaire, 1869

***Tillomorphites* Vitali, 2011**

***Tillomorphites robustus* Vitali, 2011**

(Figs. 1a - b)

Holotype

Tillomorphites robustus Vitali, 2011 Baltic amber, ex coll. M. Veta, author's coll. FS47BS28.

Remarks

The finding of further specimens identifiable as *Tillomorphites* has obliged to re-examine the type-species of the genus. A deeper observation of the left antenna has allowed discovering a very elongated seta on the apex of the antennomeres III and IV. Differently from the other species described here, such setae are recumbent and as long as the antennomeres so that they were initially confused with amber cracks.

Moreover, even if they were correctly described, the body proportions are 7% narrower and the pronotum shows a little different shape with respect to the original drawing (Vitali 2011), making necessary a new reconstruction (Fig. 1b).

The general habitus looks still more similar to *Tillomorpha* Blanchard, 1851 than it was suggested in the original description: the pronotum is less cordiform and inflated, while the elytra are more elongated. Moreover, the

spined antennomeres suggest a close relation to *Euderces* LeConte, 1850, as it will be explained in the remarks.

***Tillomorphites otiliae* n. sp.**

(Figs. 2a - e)

Holotype

Female, Baltic amber, ex coll. M. Veta, author's coll. FS65BS35.

The type is included in a rectangular-trapezoidal, 20 x 15 x 5 mm, oval piece of yellow-orange amber containing the following syninclusions: a Trichoptera, two Diptera Sciaridae (one present as head), an exuvium of a possible neanic stage of Acridoidea (only four legs present), many stellate hairs and wood dust. The beetle is partially covered by turbidity along the right side and lacks the left antennomeres V-XI; the ovipositor is fully exposed.

Paratype

Female, Baltic amber, ex coll. M. Veta, author's coll. FS70BS39.

The type is included in a 25 x 11 x 4 mm parallelogram-shaped piece of yellow-orange amber with many stellate hairs as syninclusions. The beetle is partially covered by turbidity on the pronotum and the mouth pieces; the abdomen looks inflated due to the possible presence of eggs.

Differential diagnosis

This species differs from *T. robustus* and *T. spinipes* n. sp. in the absence of short erect setae on the half of each antennomere and in the more elongated and nearly smooth elytra. Moreover, it differs from *T. robustus* in the different pronotal shape and from *T. spinipes* in the simply recumbent pubescence of the legs.

Description

Female, Body length 4.3 (holotype) to 4.9 mm (paratype). Body throughout black except for the elytra, showing a pre-median transversal



Fig. 1a. *Tillomorphites robustus* Vitali, 2011, Holotype.

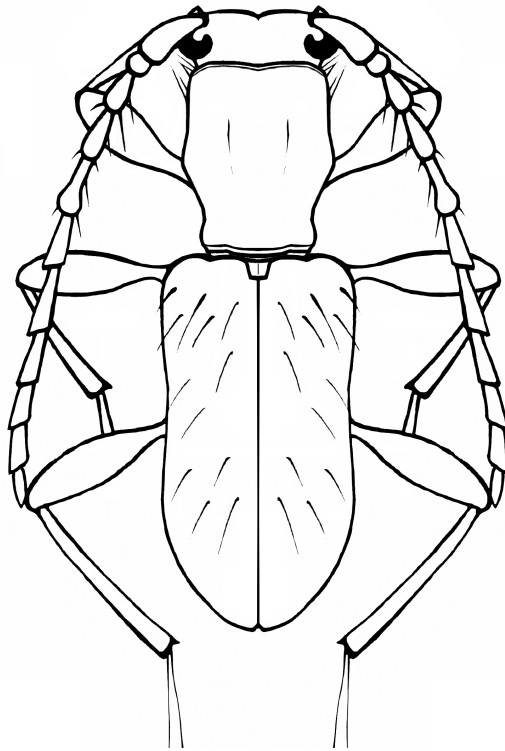


Fig1b. *Tillomorphites robustus* Vitali, 2011, habitus, new reconstruction.

reddish band (holotype) and a similar pre-apical band (paratype).

Head short; forehead oblique, smooth; antennal tubercles widely separated and scarcely elevated; interantennal furrow fine; eyes large, finely faceted, very strongly reniform, scarcely prominent; upper eye-lobes well developed; under eye-lobes nearly occupying all space of genae. Palpomeres sub-equal; last palpomere obovate, longer than the previous one. Antennae 11-segmented, shorter than body, glabrous; antennomeres III - IV with a very fine spine at the apex; antennomeres V - X externally dentate at the apex; scape short, bowed; pedicel transverse one-ninth as long as scape; antennomere III club-shaped, one-half as long as scape; antennomeres IV club-shaped, about one-third longer than III; antennomere V even longer; antennomeres VI and VII equal, hardly longer than V; antennomeres VIII and IX equal, hardly shorter than V, antennomere X even shorter, antennomere XI one-third as long as scape (antennomere proportions according to the formula: 1.8: 0.2: 9.0: 1.3 1.6: 1.7: 1.7: 1.5: 1.5: 1.4: 0.6).

Pronotum longer than wide, ob-ovate, constricted before the base; apex one-fifth wider than base, anteriorly feebly convex, very finely furrowed along its margin; base bilobed, posteriorly convex in the middle, two-fifth narrower than elytral base, finely furrowed along its margin; disc convex, smooth and glabrous. Scutellum small, not guessable since partially covered by turbidity.

Elytra apically inflated, moderately convex, 2.7 times as long as wide at humeri; base feebly convex, concave in correspondence of the basal angles of the pronotum; humeri rounded; lateral margins furrowed; apex largely rounded; disc smooth, covered with some long semi-erect setae at base.

Legs relatively short and robust, pubescent, femora clavate; tibiae linear; tarsi short; metatarsus one-half as long as metatibia; metatarsomere I as long as II and III together or



Fig. 2a. *Tillomorphites otiliae* n. sp., Holotype.



Fig. 2b. *Tillomorphites otiliae* n. sp., Paratype.

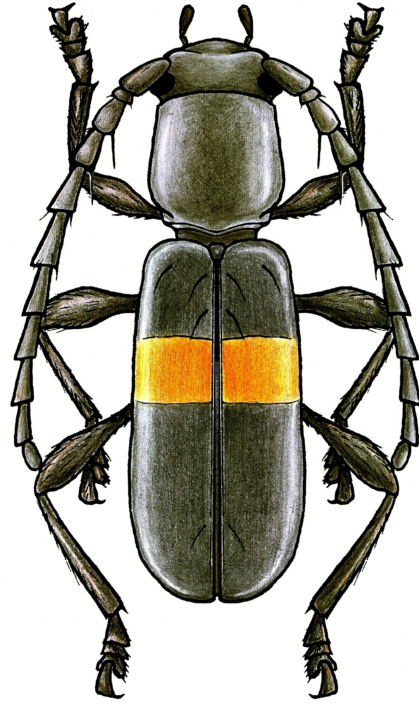


Fig. 2d. *Tillomorphites otiliae* n. sp., Holotype, colour reconstruction.

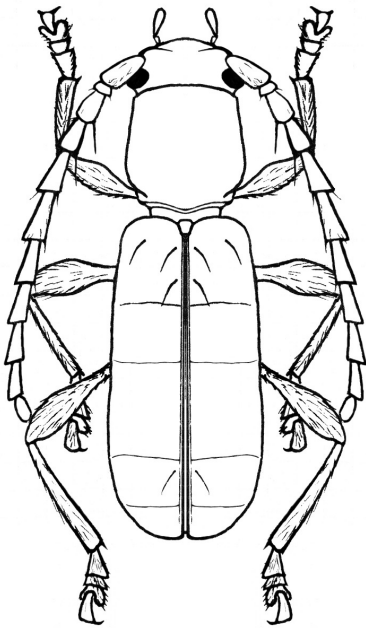


Fig. 2c. *Tillomorphites otiliae* n. sp., habitus, reconstruction.

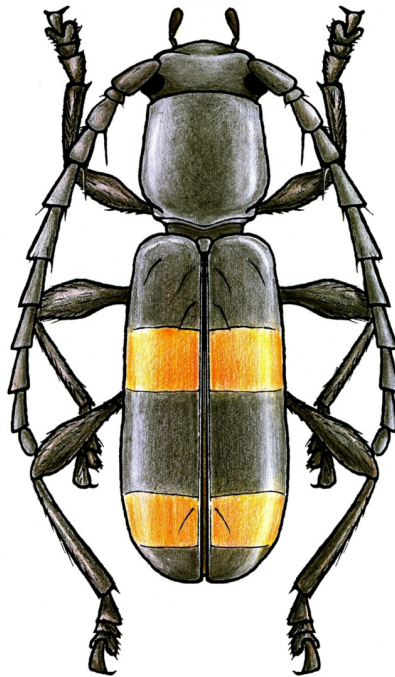


Fig. 2e. *Tillomorphites otiliae* n. sp., Paratype, colour reconstruction.

as onychium; metatarsomeres II and III transverse.

Prosternum with numerous fine transversal ridges; intercoxal process fairly narrow; procoxae globose, procoxal cavities externally rounded, posteriorly open; mesocoxal cavities laterally closed; visible urosternites (I-V) progressively shortened to the apex, very finely and densely punctured, seemingly granulated, covered with some erect setae.

Etymology

I am honoured to dedicate this new species to my wife Otilia, who gave me as a present both typical specimens and selflessly supports my research providing invaluable assistance.

***Tillomorphites spinipes* n. sp.**

(Figs. 3a - b)

Holotype

Baltic amber, ex coll. M. Veta, author's coll. FS56BS30.

The type is included in a 23 x 13 x 6 mm rectangular piece of yellow amber with no observable syninclusions. The beetle is mostly covered by turbidity, especially on the head and along the right side; moreover, it lacks the right antennomeres VII-XI.

Differential diagnosis

Though scarcely visible, this species is well characterised by the presence of an apical spine on the antennomere V and of strong erect setae on the meso- and metatibiae. Moreover, it differs from *T. robustus* in the larger body size and from *T. otiliae* n. sp. in the elytra and the antennae completely covered with erect setae.

Description

Sex unknown, Body length ~6 mm.

Eyes reniform. Antennae 11-segmented, shorter than body, covered by some short sub-erect setae; antennomeres III - V with a long fine spine at the apex; antennomeres V - X externally

dentate at the apex; antennomere proportions according to the formula: ? : ? : ? : ? : ? : 1.2 : 1.1 : 0.9 : 1.0 : 0.8 : 0.5.

Pronotum longer than wide, obtusely angulated before the middle and strongly inflated before the base; regularly convergent anteriorly; disc seemingly uneven, smooth and glabrous. Scutellum transverse.

Elytra parallel-sided, feebly depressed on the middle of the disc, about 2.7 times as long as wide at humeri; base feebly convex, concave in correspondence of the posterior angles of the prothorax; humeri rounded; lateral margins furrowed; apex largely rounded; disc smooth, throughout covered with some semi-erect long setae.

Legs relatively short and robust, apparently smooth, femora clavate; tibiae linear, covered with 3 - 4 conspicuous sub-erect black setae, as long as those of antennae or elytra, on the outer side and some short semi-recumbent setae on the inner side; metatarsus about one-half as long as metatibia; metatarsomere I as long as II and III together or as onychium; metatarsomeres II and III transverse.

Prosternum seemingly smooth; intercoxal process fairly narrow, triangular; procoxae globose, procoxal cavities rounded, externally rounded; visible urosternites (I-V) progressively shortened to the apex, very finely and densely punctured, covered with a fine dense recumbent pubescence and some sparse erect setae.

Etymology

From the Latin "*spini-pes*", i.e. "with spined legs".

***Tillomorphites elachys* (Martins & Galileo, 2013) n. comb.**

(Figs. 4a - b)

The present-day Ecuadorian species *Euderces elachys* Martins & Galileo, 2013 is surprisingly similar to *Tillomorphites otiliae* n. sp. The extant species shows more melanistic elytral pattern: the pre-median reddish band is smaller, reduced on the disc (Fig. 4a) or even absent (Fig. 4b), while the pre-apical band is

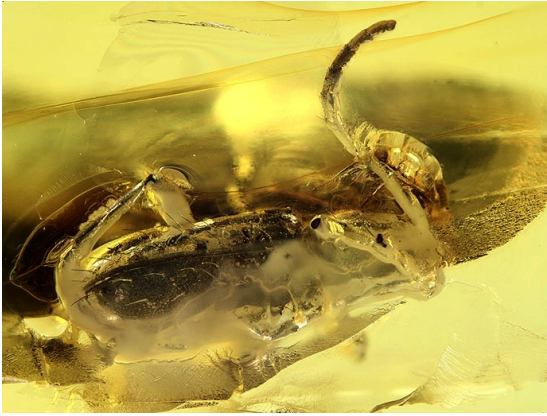


Fig. 3a *Tillomorphites spinipes* n. sp., Holotype, dorsal view.

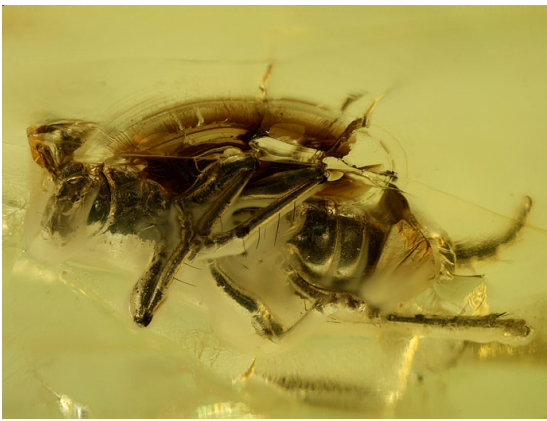


Fig. 3b *Tillomorphites spinipes* n. sp., Holotype, ventral view.



Fig. 3c *Tillomorphites spinipes* n. sp., Holotype, particular.



Fig. 4a. *Tillomorphites elachys* (Martins & Galileo, 2013) n. comb., Holotype.



Fig. 4b. *Tillomorphites elachys* (Martins & Galileo, 2013) n. comb., Paratype.

completely absent. In contrast, antennae of the fossil are more melanistic, being black in *T. otiliae* n. sp. and reddish in *E. elachys*. The length of antennal spines is equal in the fossil and unequal in the extant species and finally, elytra are evenly rounded in *T. otiliae* n. sp. and apically truncated in *E. elachys*.

The complete absence of eburneous strips is another important character, only shared by *E. elachys* and *E. waltli* (Chevrolat 1862). Just for this reason, Giesbert & Chemsak (1997) considered *E. waltli* as a doubtful *Euderces*; however, Chevrolat (1862) had stated: “third antennomere longest of all, armed with a long spine”, well fitting the genus *Euderces*. On the contrary, *E. elachys* shows towards *Euderces* the same differences concerning the antennal structure evidenced in *Tillomorphites*: “antennomere III slightly longer than antennomere IV” and “antennomere V the longest” (Martins & Galileo 2013). Notwithstanding the palpable biogeographical difficulties in accepting this conclusion, *E. elachys* is not related to the extant American genus *Euderces* but to the fossil Baltic genus *Tillomorphites*, to which it is transferred.

Key to the genus *Tillomorphites* Vitali, 2011

- 1. Tibiae with 3 - 4 conspicuous erect setae on the outer side; antennomere V spined; 6 mm (Baltic amber).....*T. spinipes* n. sp.
- . Tibiae with semi-recumbent pubescence; antennomere V unarmed 2.
- 2. Pronotum angulated at the sides; elytra flattened, constricted in the middle; antennomere IV unarmed; 4.2 mm (Baltic Amber).....*T. robustus* Vitali, 2011
- . Pronotum regularly constricted posteriorly; elytra fairly convex, posteriorly inflated; antennomere IV spined 3.
- 3. Elytral apex rounded, antennae black; elytra black with a pre-median and a pre-apical,

sometimes missing, red band; 4.3 - 4.9 mm (Baltic amber) *T. otiliae* n. sp.

- . Elytral apex truncated; antennae reddish; elytra black with a pre-median, sometimes missing, red band; 4.8 - 4.9 mm (Ecuador, Holocene)
T. elachys (Martins & Galileo, 2013) n. comb.

DISCUSSION

Remarks on the genus *Tillomorphites*

Morphology

Tillomorphites is seemingly related to the genus *Euderces*, in particular to that section characterised by long spines on the antennomeres III-IV, for which Chevrolat (1861) created the genus *Eplophorus*.

It differs in the characters already evidenced in the original description, i.e. elytra posteriorly not declivous and without elevations, but the new species allow evidencing more significant features. The antennal proportions are different: the antennomere III is as about as long as IV in *Tillomorphites*, while it is 2 - 3 times as long as IV in *Euderces*. The antennomeres V or VI are subequal and the longest in *Tillomorphites*, while the III is the longest in *Euderces*. The antennomeres V (or VI) to X are short and markedly toothed externally in *Tillomorphites*, while they are long and simply cylindrical in *Euderces*.

Though the descriptor overlooked this fact, *Licracantha formicaria* Lingafelter, 2011 is the only other member of *Tillomorphini* showing spines on the antennomeres 3 - 5. Nonetheless, the peculiar habitus, especially the long scape, strongly differentiates this taxon from *Tillomorphites*.

Apart from the spines, the antennae of *Tillomorphites* are more similar, in the proportions, to those of *Tillomorpha* than to those of *Euderces*. Actually, the relations between these extant genera - nearly

contemporaneously described - were not accurately investigated by previous taxonomists. According to Lacordaire (1869), *Tillomorpha* differs from *Euderces* in the entire eyes (strongly reniform in *Euderces*), but this character is false since the upper eyes lobes of this genus are actually atrophic, as it occurs in several *Euderces* (Giesbert & Chemsak 1997). The main difference concerns the antennal proportions, the antennomere III being barely longer than IV in *Tillomorpha* while it is 2 - 3 times as long as IV in *Euderces*. Analogue character is present in the Palaearctic *Pseudomyrmecion* Bedel, 1885 and *Cleroclytus* Kraatz, 1885. Evidently, the scarce length of the antennomere III is a primitive character common to several taxa.

Biogeography

Tillomorphytes was initially considered similar to *Tillomorpha* (Vitali 2011) but it is actually more related to an extant Ecuadorian species. Together with *Dicentrus* LeConte, 1870, *Tillomorphytes* is the only taxon of the Baltic amber cerambycids showing obvious American affinities (Vitali & Daamgard 2016). According to Alekseev (2017), a very small percentage (13.5%) of the 420 genera of the Baltic amber beetles is currently restricted to one zoogeographical realm, among which Nearctic (5) and Neotropical genera (2) are markedly a minority. This estimation should be reconsidered since *Dorcaschema succineum* Zang, 1905 does not agree with any extant genus of Dorcaschematini (Vitali 2009). Moreover, this rate does not take into account the affinity of extinct genera (191), whose extant relatives - not the same genera - are sometimes widespread in Austral hemisphere, such e.g. *Protachryson* Vitali, 2011. This explains the exiguity of Baltic taxa in American fauna but hides the real affinity among these faunas. Consequently, the presence of American relatives might have been underestimated, as well the ratio of Nearctic versus Neotropical taxa overestimated.

In addition, Alekseev (2016) pointed out the significance of high humidity for Baltic biota, adding that B-type (arid) climates are almost entirely avoided (Alekseev 2017). Now, the only extant *Tillomorphytes* was collected 5 km south from Montecristi (Manabi province) on the Ecuadorian coast. Even if both types were collected in the most rainy months of the year (February-March), this locality belongs to the Mesoamerican subregion, arid Ecuador province (Morrone 2001) and the local climate is classified as BWh (hot desert climate), according to the Köppen - Geiger classification system (Climate-Data.org).

This well corresponds to the fact that *Tillomorphytes* looks similar to *Euderces* but actually, it is morphologically related to *Tillomorpha*, *Pseudomyrmecion* and *Cleroclytus*, which inhabit thermophilic mountain woods (*Pseudomyrmecion* and *Tillomorpha*) or even steppic habitats (*Cleroclytus*). These three extant genera are widespread in mountain dry habitats of the temperate zone, implying that the extant *T. elachys* is not a typical tropical species but an Arcto-Tertiary relict species related to dry climates.

The presence of species related to dry climates has been already evidenced in Baltic amber cerambycids. *Nothorhina granulicollis* Zang, 1905, by far the most abundant longhorn in succinite (Zang 1905; Klebs 1910; Hieke & Pietrzyński 1984; Vitali 2006), shows extant congeners in zones not particularly humid as Sweden and Siberia or even semi-arid as southern Italy (Calabria and Sicily). The same occurs to *Dicentrus mehli* Vitali & Damgaard, 2016, whose extant congeners inhabit the temperate coniferous forests covering the middle-mountain ranges of the Pacific Mountain System. Other extinct Baltic genera - *Mesalocerus* Vitali, 2015; *Eurapatophysis* Vitali, 2016 - show evident affinities with extant genera adapted to variable climatic conditions, including dry summers, supported by the recent

description of the xerophilic darkling beetle *Asida groehni* (Soldati & Nabozhenko 2017). Deductions on Baltic amber climate are scientifically correct on the basis of the analysed taxa, i.e. the only extant genera, whose characteristics are well known. Nonetheless, the analysis is mostly incomplete since a large amount of extinct genera (45.5%) was not taken into consideration.

Moreover, the overwhelming majority of the survived genera (86.5%) - those assumed to show warm-humid preferences - belong to two or more zoogeographical realms today (Alekseev 2017), i.e. they show the widest adaptability to different climatic conditions. In other words, the taxa claiming to show warm-humid preferences are mostly euriecious genera that survived until now. Obviously, this group is more abundant in warm regions but it is not peculiar of them. Actually, it is only a part (47.1%) and not the most typical representative of the Baltic fauna.

In contrast, the analysis on the extinct cerambycid genera suggests climates dryer than those that the mentioned analysis supposed.

Assumed evolution and phylogeny of the tribe Tillomorphyini

Biogeography and phylogeny

The finding of further *Tillomorphytes* in Baltic amber allows hypothesising some points concerning the evolution of this tribe.

Analysing the distribution in the continental Asia, it is possible to observe that Tillomorphyini can be merged in two morphologic-biogeographical groups.

Most of the genera (*Bicon*, *Epipedocera*, *Centroclytus*, *Halme*, *Khampaseuthia*, *Clytellus*) belongs to a tropical south-eastern Asian group, which is characterised by short flat body and antennae shorter than body, sometimes

flattened. This group looks more specialised and it is also widespread in Malaysia, Indonesia and Philippines.

Central Asia is inhabited by the only genus *Cleroclytus*, which is characterised by elongated cylindrical body and long filiform antennae. From a morphological and biogeographical point of view, it is fairly isolated, showing more affinity with the Algerian *Pseudomyrmecion* and some American genera, especially *Euderces* (Heyden 1888; Ganglbauer 1890), *Tillomorpha*, *Epropetes* Bates 1870, and *Epipodocarpus* Bosq, 1951.

The least specialised member of this group (and of the whole tribe) seems to be the Chilean *Epipodocarpus*, which shows cylindrical prothorax, long antennae and uniform elytral colour. The only species is biologically related to the conifers widespread in the temperate zone of the Austral hemisphere: *Araucaria* and *Podocarpus* (Duffy 1960; Barriga Tuñon et al., 1993).

Cleroclytus and *Pseudomyrmecion* are certainly related to the most primitive taxa. Most likely, *Pseudomyrmecion* is a relict genus of European origin, while *Cleroclytus* is the only Asian genus of Eurasian origin. The other Asian genera are probably of Indian origin.

Euderces is widespread from Canada to Bolivia, but the presence of related taxa in Eurasia (central Asia and Baltic amber) implies almost clearly that the common ancestor of these genera evolved in Laurasia before the breakup America - Europe (Late Cretaceous). Thus, even if *Euderces* is today focused in Central America with a large number of species (Giesbert & Chemsak 1997), it is not a Sonoran but an Arcto-Tertiary Alleghenian genus. The colonisation of South America should have occurred only after the collision of the continents (Pliocene). This also explains why *Euderces* is absent in the West Indies: there were no more land-bridges between Caribbean and continental America after the drowning of GAARlandia occurred

during Upper Oligocene - Mid Miocene (Iturralde-Vinent 2006).

This group of more primitive genera seems to show an amphitropical distribution. The presence of primitive taxa in temperate zones of both hemispheres implies that the origin of Tillomorphini antedated the Jurassic breakup of Gondwana. Moreover, this distribution seems to be correlated to the presence of temperate Mesozoic conifers, i.e. Araucariaceae and Podocarpaceae in Austral, Pinaceae and Taxodiaceae in Boreal. This is certainly true for an Austral (i.e. *Epipodocarpus*) and a Boreal genus (i.e. *Pseudomyrmecion*) but it does not seem to correspond to the biology of all extant taxa. According to Darlington (1965), the climate is the most important factor in producing this kind of distributions; thus, it is conceivable that primitive Tillomorphini preferred temperate, though almost thermophilic, environmental conditions. The adaptation to tropical conditions might have occurred during the Eocene or maybe later.

Morphological evolution and mimicry

Tillomorphini is composed by harmless species which mimic the cohabiting harmful species (Batesian mimicry) or other mimicking harmless species (Müllerian mimicry). The imitation of Cleridae should be considered as Batesian mimicry as well, even if few clerids, not mimicked by Tillomorphini, were proved as poisonous (Fietz et al., 2002) or unpalatable (Poulton 1902). Despite this fact, this group of predaceous beetle may be harmful to cerambycids. In this case, the pattern of Tillomorphini might mimic clerids to fool clerids themselves (Boppré et al. 2017).

The evolution of the mimicry complexes of this ancient and sub-cosmopolitan tribe is extremely difficultly traceable. Possibly, models of some taxa became extinct and Tillomorphini remodelled their aspect in order to mimic different models. In some cases, plastic evolution of pattern and body can be observed

still today since many species show variable colours (e.g. red to black) within the same species. However, some points can be fixed.

The aspect of the members of this tribe should have been originally simple, i.e. without elytral pattern, as it occurs to *Epipodocarpus*. This Chilean cerambycid shows the same habitus (black with red prothorax) of the Chilean clerid *Lemidia protea* (Spinola, 1849). This kind of mimic complex might have already been present in Baltic amber as well, since Kolibjč & Gerstmeier (1997) described a fossil belonging to this genus. The complex should be ancient enough since e.g. the West-Palaeartic *Tillus elongatus* (Linnaeus, 1758) and the Australian *Lemidia exilis* (Westwood, 1852), or even many soldier beetles (Cantharidae) share analogue habitus. However, the fact that *Tillus elongatus* is nocturnal while soldier beetles are diurnal implies that this coloration appeared several times in unrelated lineages.

As better supported by fossil findings, species decorated with one-two reddish bands should have evolved before species with eburneous strips. Extant taxa with analogue aposematic pattern (black with two reddish transversal bands or spots) are rather uncommon among Eurasian cerambycids, e.g. only in some Asian *Purpuricenus* and *Semanotus*. Other beetles share same pattern and body size: *Divales* (Melyridae), Coccinellidae and many mycophylic taxa, such as Mycetophagidae, Erotylidae, Tenebrionidae and Scaphidiidae; however, none of them has been recorded from Baltic amber (Alekseev 2017) or seems to be directly related to *Tillomorphites* due to the more rounded habitus. These taxa might be related to a large mimicry-complex involving the toxic Staphylinidae Paederinae (Frank & Kanamitsu 1987), which was also recorded from Baltic amber (Spahr 1981), but the kind of colonised habitat does not seem compatible with *Tillomorphites*. These observations let supposing that models of this mimicry are extinct in Europe today.

One-two eburneous strips should have evolved lately in Tillomorphyini, superposing to or substituting the previous schema, as it occurs to some Central American *Euderces*. Black pattern tended to dominate over reddish one, since many reddish species also have melanistic varieties. As consequence, most of the Holocene taxa show a black body with eburneous pattern.

Models are usually considered black or red ants (Linsley 1959; 1964; Lingafelter 2011), but this relation, certainly correct for some genera (*Clytellus*), seems unconvincing in most cases. Worker ants are seldom poisonous, constituting a weak model; moreover, ants were common in Baltic amber (Spahr 1987), but this kind of mimicry has not been signalised yet.

Another explanation is that most Tillomorphyini mimic members of the family Mutillidae, as it has already been evidenced for a significant group of clerids (Poulton 1902; Mawdsley 1994; Bocakova et al. 2016). Wingless females of velvet ants are strongly poisonous and frequently show analogue pubescence and coloration: black / red, with or without white strips.

In addition, some present-day Chilean and Alleghenian velvet ants, e.g. Myrmosinae, show a simple black / red coloration (Wilson et al. 2012), which might correspond to that hypothetical extinct model of Baltic amber. Interestingly, several species of this subfamily were just described from Baltic amber (Spahr 1987), supporting a close mimicry relation with primitive Tillomorphyini.

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