

Kladistička analiza determinacijskih svojstava širokonosnih trnovratki (Orthoptera: Tetrigidae: Cladonotinae)

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Sveučilište u Zagrebu
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Biološki odsjek

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Zagreb, 2021.

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**Cladistic analysis of diagnostic characters of
wide-nosed pygmy grasshoppers
(Orthoptera: Tetrigidae: Cladonotinae)**

Master thesis

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Ovaj rad je izrađen u Laboratoriju za evoluciju na Zoologijskom zavodu Prirodoslovno-matematičkog fakulteta u Zagrebu, pod voditeljstvom izv. prof. dr. sc. Damjana Franjevića, neposrednim voditeljstvom asistenta mag. biol. exp. Josipa Skeje. Rad je predan na ocjenu Biološkom odsjeku Prirodoslovno-matematičkog fakulteta Sveučilišta u Zagrebu radi zvanja magistar eksperimentalne biologije.

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I dedicate this thesis to every present and future tetrigidologist.

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Diplomski rad

Kladistička analiza determinacijskih svojstva trnovratki (Orthoptera: Tetrigidae: Cladonotinae)

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Ignacio Bolívar Urrutia je Cladonotinae zamislio kao potporodicu koju čine vrste koje posjeduju široki scutellum koje se od drugih potporodica mogu razlikovati i po brojim drugim manje uočljivim morfološkim karakteristikama. Iako se danas koriste brojna svojstva kako bi se pokazalo da nova vrsta ne pripada drugim potporodicama, svojstvo širokog scutelluma je gotovo jedino svojstvo koje se koristi ne bi li se opravdalo smještanje novoopisane vrste baš u potporodicu Cladonotinae. Zbog toga danas potporodica Cladonotinae sadrži vrste izuzetno različitih morfologija kojima je jedina sličnost relativno širok nosni štitić, iako čak ni to nije uvijek tako. Ovaj diplomski rad je kladistički analizirao gotovo sve ikada korištene morfološke karakteristike jedinki potporodice Cladonotinae ne bi li pokazao koja svojstva su potencijalno dobri pokazatelji holofiletskih taksona unutar potporodice. Rezultati pokazuju da su svojstva pronotuma, ponajviše projekcije, slabi pokazatelji holofiletskih taksona. Svojstva koja su se pokazala kao najbolji kandidati za daljnja istraživanja povezanosti morfologije i stvarnog stanja evolucijskih odnosa su svojstva nogu. Pokazalo se da korištenje isključivo morfologije za opisivanje i determinaciju vrsta potporodice Cladonotinae daje rezultate upitne ispravnosti. Mnoge vrste danas smještene u Cladonotinae morfologijom ne pokazuju pripadnost potporodici te su nužno potrebna daljnja molekularna istraživanja kako bi se moglo odrediti koja su svojstva praktični pokazatelji pripadnosti vrsta potporodici Cladonotinae.

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Cladistic analysis of diagnostic characters of wide-nosed pygmy grasshoppers (Orthoptera: Tetrigidae: Cladonotinae)

Maks Deranja

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Ignacio Bolívar Urrutia envisioned Cladonotinae as a subfamily composed of species bearing broad scutellum, distinguished from other subfamilies by other less noticeable morphological characteristics. Although many traits are used today to show that new species do not belong to other subfamilies, the broad scutellum is almost the only trait used to justify the placement of the newly described species in the Cladonotinae subfamily. Therefore, subfamily Cladonotinae contains species of extremely different morphologies, the only similarity being relatively wide scutellum, although even that is not always the case. This thesis cladistically analyzed almost every historically used morphological characteristic of individuals of the subfamily Cladonotinae in order to show which characters are potentially good indicators of holophyletic taxa within the subfamily. Results show that characters of pronotum, mostly projections, are weak indicators of holophyletic taxa. The properties that have proven to be the best candidates for further research into the relationship between morphology and the actual state of evolutionary relationships are the properties of legs. The exclusive use of morphology to describe and determine the species of the subfamily Cladonotinae has been shown to give results of questionable correctness. Many species placed in Cladonotinae do not show morphological similarities to other Cladonotinae species, hence further molecular research is necessary to determine which characters are good practical indicators of species belonging to the Cladonotinae subfamily.

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Abbreviations

AMS—Australian Museum, Sydney, New South Wales

ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania

BMNH—The Natural History Museum, London

BPBM—Bernice P. Bishop Museum, Honolulu, Hawaii

CI—Consistency index

CMNH—USA, Pennsylvania, Pittsburgh, Carnegie Museum of Natural History

CNMS—Sri Lanka, Colombo, National Museum

Coll. Tumbrinck—Collection Josef Tumbrinck, Germany, Wassenberg

DNA—Deoxyribonucleic acid

FL1—1st frontolateral projection

FL2—2nd frontolateral projection

FL3—3rd frontolateral projection

FL—frontolateral projection

FM—frontomedial projection

HuaiBei—HuaiBei Normal University, HuaiBei, Anhui, China

IES—Instituto de Ecología y Sistemática, La Habana, Cuba

ISNB—Belgium, Brussels, Institut Royal des Sciences Naturelles de Belgique

IUCN—International Union for Conservation of Nature

Kasetsart—Department of Entomology, Kasetsart University, Bangkok, Thailand

MCSN—Italy, Genova, Museo Civico di Storia Naturale "Giacomo Doria"

MCZ—USA, Massachusetts, Cambridge, Harvard University, Museum of Comparative Zoology

MfN—Museum für Naturkunde (Naturkundemuseum or Humboldt-Museum), Berlin

MHNG—Muséum d'histoire naturelle de Genève; MNCN—Museo Nacional de Ciencias Naturales, Madrid

MM1—1st metamedial projection

MM2—2nd metamedial projection

MM3—3rd metamedial projection

MM4—4th metamedial projection

MML1—1st metamediolateral projection

MML2—2nd metamediolateral projection

MML3—3rd metamediolateral projection

MML4—4th metamediolateral projection

MML5—5th metamediolateral projection

MNHN—Muséum National d'Histoire Naturelle, Paris

NBC—Naturalis Biodiversity Center (National Museum of Natural History), Leiden

NHRS—Naturhistoriska Riksmuseet, Stockholm

NMW—Naturhistorisches Museum Wien

OSF—The Orthoptera Species File

PML1 —1st promedial projection

PML2—2nd promedial projection

PML—promedial projection

PM—promedial projection

PM—romedial projection

RI—Retention index

SDEI—Senckenberg Deutsches Entomologisches Institut, Münchenberg

Shaanxi Normal—China, Shaanxi Normal University, Department of Biology

SMTD—Staatliche Naturhistorische Sammlung Dresden, Museum für Tierkunde, Dresden

UMO—United Kingdom, Oxford, University Museum, Hope Entomological Collections

UPGMA—unweighted pair group method with arithmetic mean

UPLBMNH—Museum of Natural History, University of the Philippines Los Baños

VL—ventrolateral projection

Yong—Collection of Sheyla Yong, La Habana, Cuba

ZFMK—Zoologisches Forschungsmuseum Alexander Koenig, Bonn

ZIN—Russia, St. Petersburg, Russian Academy of Sciences, Zoological Institute

ZMUM—Russia, Moscow, Moscow State University

ZSM—Zoologische Staatssammlung, Munich

1. Introduction

1.1. About evolution, phylogeny and cladistics

Biological evolution is a process of change in the properties of groups of organisms over the course of generations (Futuyma 2009, Stearns & Hoekstra 2000). The changes in populations are considered evolutionary if the changes are passed via the genetic material to the next generation (Futuyma 2009). Over the course of many generations, many changes may accumulate. Over the generations changes ranged from slight to substantial; evolution embraces everything from tiny changes in morphology within a population, to the alterations that led from the earliest organisms to sponges, grasshoppers, bananas, and humans (Futuyma 2009, Stearns & Hoekstra 2000). Such complex evolutionary relations are hard to grasp unless categorically analyzed. This is where phylogeny kicks in, helping us understand what actually happened in the evolutionary history of the living world. Phylogeny is a branch of biology that deals with reconstructing or assembling the tree of life by estimating relationships among organisms (Futuyma 2009). Research in phylogeny of a group of organisms results in phylogenetic trees portraying the relationships between taxa, but most importantly, phylogeny can show us how any given character in that group of organisms has evolved (Futuyma 2009). Based on those characters and by using Mayr's biological species concept (Mayr 1999) we can deduce what characters can be used to distinguish one species from another. Thus, scientists can create a key to species identification—a detailed and easy to follow way of distinguishing species. When the critical mass of knowledge about phylogeny of a group of species belonging to a certain taxon is accumulated, it is always needed to group them in some evolutionary meaningful way. Problems of that nature are solved by using knowledge in cladistics. Cladistics is a way of thinking about phylogenetic trees in the sense of finding a purposeful way to subdivide them (Futuyma 2009, Stearns & Hoekstra 2000). Cladistics thus combines knowledge about relation of taxons and gathers so far acquired knowledge about what “good characters” for distinguishing taxa are, and it results in a natural way of dividing groups of organisms that accords with evolution of those groups. Results in cladistics are usually phylogenetic trees consisting of monophyletic groups of organisms (Futuyma 2009, Skejo & Franjević 2020). Monophyletic means that a group of organisms all share a singular common ancestor (Futuyma 2009, Skejo & Franjević 2020). Monophyletic groups, also known as clades, can be divided into two groups - holophyletic and paraphyletic. Holophyletic groups consist of all descendants of one common ancestor, while

paraphyletic groups consist of one common ancestor, and only some of its descendants (Skejo & Franjević 2020). On the contrary polyphyletic groups consist of multiple common ancestors and their descendants (Futuyma 2009, Skejo & Franjević 2020). Those groups are artificially made based on wrong interpretations of characters of analyzed organisms, and thus bear no scientific significance (Futuyma 2009). On the other hand, monophyletic groups, especially holophyletic groups are considered scientifically justified and are only ones accepted when presenting new findings in the field of biological evolution. Monophyletic groups are formed based on apomorphies. Apomorphies are characters that are present in members of a clade, but were not present in their ancestors (Futuyma 2009, Stearns & Hoekstra 2000). If the same apomorphy is shared between two clades, it is called synapomorphy (Futuyma 2009, Stearns & Hoekstra 2000). Synapomorphy is an apomorphy, meaning the common ancestor of clades bearing that character never had that character, but at the same time meaning that that character evolved before those two clades diverged, thus both inherited that apomorphy. Such closely related clades bearing the same synapomorphy can be described as having homologous character. Homologous meaning apomorphies sharing the same evolutionary history (Futuyma 2009, Stearns & Hoekstra 2000). The opposite phenomenon of apomorphy is plesiomorphy. Plesiomorphy is a character inherited from distant ancestors, in other words, not a newly evolved character specific to one particular clade (Futuyma 2009, Stearns & Hoekstra 2000). Plesiomorphies are useful in detecting paraphyletic groups, and vice versa. Scientists can deduce the plesiomorphy if genetic analysis shows that a group is paraphyletic, or can infer the far points of the paraphyletic group if evidence of character being plesiomorphic comes up. Characters can also be functionally or morphologically similar, but without sharing evolutionary history. Such an occurrence is called homoplasy. Homoplasy is a phenomenon of characters appearing independently more than once and can not be used to infer phylogenetic relations between organisms sharing those analogies (Futuyma 2009, Stearns & Hoekstra 2000).

Scientists can choose among many different types of characters they will use to determine evolutionary relations between organisms they analyse. Genetic information in the form of sequenced DNA (e.g. Zhang et al. 2020) is considered to give the most precise and comprehensive results about the phylogeny of studied organisms. Morphological characters can be used in a similar fashion (e.g. Cadena-Castañeda et al. 2019). Using characters clearly visible on an organism has

its advantages and disadvantages in comparison to genetic data. Advantages are easier, less expensive analysis and less time needed to obtain the necessary information about organisms. Another big advantage is that other specimens can be used to obtain the same data as the analyzed individual. Disadvantages are the possibility of a biased look on what characters are present on the specimen, and the need for well-preserved specimens. This bias can influence our interpretation, but beyond that, it may even be a systematic error based on false assumptions. We can be mistaken about what characters are reflection of evolution, and inadvertently use non-informative characters to carry out the phylogenetic analysis.

1.2. Systematics, ecology, general morphology and ethology of Tetrigidae

Tetrigidae Rambur, 1838 (Orthoptera: Caelifera), commonly known as pygmy grasshoppers, are a family of Orthoptera which can be found on all continents, except Antarctica and New Zealand. As of May of 2021, there have been 2009 described subspecies and species without species in this family, 11 of which are described from fossils found in amber and are now extinct. Family Tetrigidae consists of seven subfamilies—Batrachideinae Bolívar, 1887, Cladonotinae Bolívar, 1887, Lophotettiginae Hancock, 1909, Metrodorinae Bolívar, 1887, Scelimeninae Bolívar, 1887, Tetriginae Rambur, 1838, and Tripetalocerinae Bolívar, 1887, while 18 genera are yet to be placed in any of those subfamilies (Cigliano et al. 2021).

As is the case with most living taxa on Earth (Saupe et al. 2019), species density of Tetrigidae members is highest in tropical areas and decreases as latitude increases towards the poles (Cigliano et al. 2021). Most species of Tetrigidae prefer moist habitats such as lowland and mountainous tropical rainforests, bamboo forests, moist grasslands, primary and secondary moist mountain forests, swamps, wetlands, cloud forests, ect., all of which are rich in various water habitats (IUCN 2021). Thus, they are easily found near any sizable body of water in geographical areas that they inhabit. On the other hand, some species (e.g. *Cyphotettix camelus* Rehn, 1952, *Charagotettix nannus* Günther, 1974, and *Procytettix thalassanax* Günther, 1939) prefer less moist habitats such as patches of bare, sandy ground, woodland and low shrubland, wooded valleys of seasonally dry lowland forest and coastal scrub (IUCN 2021).

All Tetrigidae species can be recognised by following apomorphies: (1) elongated pronotum covering the hind wings, (2) greatly reduced fore wings, (3) having 2-2-3 segments on

their front, mid and hind tarsi respectively, (4) lack of arolium between tarsal claws, (5) lack of tympana, and (6) first thoracic sternite being modified into collar-like sternomentum. Their small size of less than 30 millimeters, although not unique among Orthoptera, is another trait that is shared among all Tetrigidae (Cigliano et al. 2021, Grant 1962, Hancock 1907, Muhammad et al. 2018, Shishodia 1991, Tumbrinck 2014).

Tetrigidae are herbivores, more precisely, they have a detrito-bryophagous diet consisting mostly of algae, diatoms, lichens, liverworts and detritus, all of which are abundant in the environments they inhabit (Hancock 1907, IUCN 2021, Kuřavová, Šipoš & Kočárek 2020). They get most of the energy needed from the detritus, while moss and other cellulose-rich food they consume have a function of slowing the passing of food through their digestive system, thus improving nutrient absorption (Kuřavová, Šipoš & Kočárek 2020).

Tetrigidae can be artificially divided into three groups according to their flight capabilities. Firstly, non-flyers that have reduced and non-functional hind wings (Cigliano et al. 2021, Skejo et al. 2020a). The second group are Tetrigidae fully capable of controlled flight over longer periods of time (e. g. more than 10 seconds) (Skejo et al. 2020b, Muhammad et al. 2018, Zha et al. 2017a, personal observation). Their wings are long and have clear and defined venation (Cigliano et al. 2021). The third group are semi-flyers that have functional wings, but are not capable of prolonged flight. They use their wings to extend the length of their jumps by weakly flapping their wings so they glide in the chosen direction (personal observations).

Pygmy grasshoppers are mostly terrestrial, although semiaquatic species are known from the subfamily Scelimeninae. A few species in the Scelimeninae subfamily (e.g. *Scelimenia gombakensis* Muhammad, Tan & Skejo, 2018 and *Criotettix bispinosus* (Dalman, 1818)) are known for jumping into the water to avoid danger, but they have also been observed swimming, diving, and resting underwater (Hancock 1904, Muhammad et al. 2018). Their tarsi are noticeably flattened and wide when compared to other Tetrigidae (Cigliano et al. 2021, Hancock 1904, Hancock 1907, Muhammad et al. 2018, personal observations). Such specialised tarsi are then used as a pair of oars, giving these semi-aquatic grasshoppers directional and depth control when swimming (Cigliano et al. 2021, Hancock 1904 personal observations). Occasionally, other non-Scelimeninae members of Tetrigidae are known for jumping in water and are somewhat capable of navigating to dry land afterwards (personal observation).

Tetrigidae are a monophyletic group that branched off from other Orthoptera around 224 million years ago in the Upper Triassic period, being the second oldest Caelifera, younger being

only Tridactyloidea Brullé, 1835 (Song et al. 2015). Such a long period of diversification gave rise to species bearing many (syn)apomorphies characteristic to their subfamily, tribus, genus, species or even subspecies (Cigliano et al. 2021).

1.3. About Cladonotinae

Cladonotinae, commonly known as wide-nosed pygmy grasshoppers (Caelifera: Tetrigidae) are one of seven existing subfamilies of the family Tetrigidae. Cladonotinae can be found across Africa, Madagascar, in South, East, and Southeast Asia, islands of Oceania, eastern parts of Australia, Caribbean islands and South America (Cigliano et al., 2021). Those are mostly tropical environments which did not change much even during the ice ages (Barron, E. J. et al. 1995, Pearson 2007). As of May 2021, 259 species of Cladonotinae are known to science, 3 of which are described from fossils found in amber and are now extinct (Cigliano et al., 2021). So far there hasn't been any comprehensive field research on their ecology, but considering they share similar habitats where food they consume is not a limiting factor in their growth and reproduction, it is widely considered in the scientific community that Cladonotinae share many basic ecological characteristics with other Tetrigidae. When a new species of Cladonotinae is described, authors occasionally include some notes on ecology of the described species which shows that Cladonotinae are ecologically very similar to other tropical Tetrigidae (Cigliano et al. 2021, IUCN 2021, Tan et al. 2019, Tumbrinck 2014, Zha et al. 2016, Zha et al. 2017b).

It is known that Cladonotinae is a polyphyletic group of Tetrigidae, but the extent of polyphyly is not yet fully researched (Skejo et Bertner 2017, Zhang et al. 2020).

1.4. History of Cladonotinae research

1.4.1. Ignacio Bolívar y Urrutia

Cladonotinae were described as a subfamily in 1887 when Ignacio Bolívar y Urrutia published the very first monumental work on revision of Tetrigidae systematics—*Essay on locusts of the Tettigidae tribes* (original title *Essai sur les Acridiens de la tribus des Tettigidae*) (Bolívar 1887).

Bolívar did a complete and comprehensive review of all genera and species which resulted

in a new system of classification. In his work Bolívar also described 26 new genera and 118 new species, which put the total number of genera to about 45, and the total number of species to around 300. This fact alone was enough for Bolívar to form a supergeneric classification of the Tetrigidae family into subfamilies.

Among other taxa, Bolívar in 1887 formed seven sections—Batrachideae, Cladonotae, Cleostratae, Metrodoraе, Scelimenae, Tettigiae, and Tripetalocerae. Those sections later became the basis for today's subfamilies Batrachideinae Bolívar, 1887, Cladonotinae Bolívar, 1887, Metrodorinae Bolívar, 1887, Scelimeninae Bolívar, 1887, and Tripetalocerinae Bolívar, 1887, and tribe Cleostratini Bolívar, 1887 which is today a tribe belonging to aforementioned subfamily of Metrodorinae. Bolívar taught that sufficient justification for forming those sections were differences in their morphology. He noticed regularities in the position of antennal grooves and its relation to vertex, number and morphology of antennal segments, width of frontal costa, morphology of paranota, and sulcation of mid femora. Bolívar thought that Cladonote (today's Cladonotinae) were distinguished by a combination of a few distinct characteristics. Firstly Bolívar defined the overall morphology of Cladonote as having hairs on their body, loaded with irregular tubercles, often having a strongly compressed and even leafy [pronotum] body. Secondly, Bolívar noticed that all Cladonote have a broad head with a slightly oblique and wide vertex, and wide scutellum. Bolívar also observed that Cladonote are usually apterous, lacking both elytra and hind wings, the only exception in his times being the genus *Trachytettix* Stål, 1876.

Scientists today understand that Bolívar's (1887) taxonomic system was not based on apomorphies, but was organized according to the characters most useful in identification (Skejo et Bertner 2017, Zhang et al. 2020).

1.4.2. Joseph Lane Hancock

Taxonomic history of the subfamily Cladonotinae is full of surprising changes. Joseph Lane Hancock proposed some changes to Bolívar's sections system, accepting most of it and adding, among others, section Bufonidae (Hancock 1907). Bufonidinae were then regarded as synonymous with Cladonotinae by Tumbrinck in 2014 when he allocated Bufonidinae to Cladonotinae due to their broadened scutellum. Then finally in 2017 Tumbrinck & Skejo made Bufonidinae synonymous with Batrachideinae rather than Cladonotinae. Tumbrinck and Skejo in 2017 argued their position by claiming that “Strong synapomorphies of the (sub)family are (1) female

spermatheca with two diverticula (shared by all the members after Grant (1962)), (2) rectangular paranota (shared by all the members except *Ascetotettix* Grant, 1956), (3) sulcate dorsal margin of the fore and mid femora, (4) antennae with more than 20 segments (except for certain brachypronotal genera, such as *Vingselina* Sjöstedt, 1921, *Ascetotettix* Grant, 1956), (5) projected frontal margin of the pronotum (except in certain genera, e.g. *Paurotarsus* Hancock, 1900, certain Tettigidea Scudder, 1862 species) and (6) fastigium of the vertex convex and slightly projected above the compound eyes. Despite of [the] recent placement of *Bufonides* Bolívar, 1898 within Cladonotinae, we assign the genus here to Batrachideinae, based on all the above presented statements (the only anatomical feature we did not examine is if *Bufonides* spp. possess two diverticula in female spermatheca).”

1.4.3. Klaus Günther

Klaus Günther, even though considered as one of the most influential tetrigidologist by producing the most comprehensive revision of Tetrigidae in history, didn't change the views on section Cladonote (subfamily Cladonotinae) (Günther 1938a, Günther 1938b, Günther 1942, Günther 1968, Günther 1972). Günther did a lot of valuable revisions of the section, but also brought some confusion by not having access to all specimens (Günther 1938a). By pointing to other researches, including new genera in the section, and making comments about what were then considered good deterministic characters for determining Cladonotine, Günther paved a long and bumpy road for the future tetrigidologist. Günther did little to none research on South American and North American taxa, and his revisions were made in a hurry, and in a lot of descriptions he was too brief, not giving a detailed description of the head, especially the frontal view, which is significant part of species descriptions (Blackith 1992).

1.4.4. Moder Cladonotinae taxonomists

Many more important taxonomists enriched our knowledge about Cladonotinae. After Günter's period in Tetrigidology (1934-1975), the Modern period begins (1980 - rec.) (Adžić et al. 2021). Just to name a few who were describing new species and enriching knowledge of Cladonotinae taxonomy in other ways (with the number of described Cladonotinae species in parentheses): S. Yu. Storozhenko (8), Z.-M. Zheng (13), M. S. Shishodia, R. E. Blackith, H. Devriese (8), W.-A. Deng (12), S. W. Heads (3), J. Skejo (3), M. K. Tan (2) and J. Tumbrinck (39) (Adžić et al. 2021).

1.5. About apomorphies hitherto used in Cladonotinae

In Bolívar 1887 key to subfamilies states good characteristics for Cladonotinae determination—filiform or moniliform antennae, rarely are the last two antennal segments flattened [similar to genus *Phaesticus* or *Discotettix*], other antennal segments not wide. Head perpendicular to the ground, rarely oblique to the ground, median ocellus much below the median ocelli. Frontal costa located between compound eyes, scutellum diverges widely.

Characteristics Bolívar regularly took into account when describing Cladonotinae species: (1) overall morphology (e.g. loaded with irregular tubercles, smooth), (2) general pronotum morphology (e.g. strongly compressed or leafy), (3) head width, (4) head [vertex] angle relative to the ground, (5) vertex width relative to compound eye width, (6) scutellum width, (7) existence of hind wings or elitra, (8) hair coverage of the body, (9) antennal form, (10) descriptive shape of scutellum (e.g. heart shaped), (11) reach of pronotum over the head, (12) ratio of width and length of femurs, (13) general morphology of top and bottom parts of femurs (e.g. leaf-like, wavy), (14) ratio of first and third tarsal segment of hind legs, (15) general (descriptive) ovipositor shape, (16) distance between antennae [antennal grooves], (17) position of lateral carinae in relation on to another (e.g. parallel, converging), (18) general shape of posterior end of pronotum (e.g. truncated, bilobated), and (19) general shape of genicular tooth.

In Hancock 1907 key to subfamilies states good characteristics for Cladonotinae determination—antenna filiform, or moniliform and rarely little compressed, or having two or three articles near the apices strongly compresso-dilated or foliaceous. Posterior angles of the lateral lobes straight, sinuses wanting. Frontal casta forked between the ocelli, the rami strongly divergent

forming a frontal scutellum Median ocellus and antenna placed below the eyes; face more or less oblique. Hancock gives no importance to the length of the third and first tarsal segment of hind legs.

Hancock 1907 in key to Cladonotinae genera and description of genera uses this characteristics: (1) general pronotum morphology (e.g. strongly compressed, leafy), (2) descriptive shape of scutellum (e.g. piriform [pear shaped]), (3) shape of scutellum in dorsal view, (4) descriptive shape of pronotum from lateral view (e.g. triangular), (5) highest point of pronotum in relation to other parts of the body, (6) relation of widest part of scutellum to other parts of head, (7) position of lateral carinae in relation on to another (e.g. parallel, converging), (8) ratio of width and length of femurs, (9) general morphology of top and bottom parts of femurs (e.g. margins entire, distinct lobes), (10) ratio of first and third tarsal segment of hind legs, (11) reach of pronotum over the head, (12) level of anterior overhang of median carina of vertex, (13) general shape of posterior end of pronotum (e.g. truncated, bilobated), (14) existence of hind wings or elitra, (15) existence of spiniform tubercles on body, pronotum or legs, (16) existence of fastigial horn [*“vertex armed with small tooth on each side”*], (17) descriptive shape of carine of head, (18) width of vertex, (19) convexity of vertex, (20) general (descriptive) ovipositor shape, (21) descriptive eye shape (e.g. triangular conico-rotundate), (21) ratio of distance between antennae [antennal grooves] and eye width, (22) advancement of frontal costa after eyes in lateral view, (23) ratio of distance between ocelli to distance from ocelli to compound eye, (24) vertex width relative to compound eye width in frontal view, (25) descriptive shape of lateral lobes of pronotum, (26) existence of tarsal teeth on first segment of tarsus on any leg, and (27) position of antenatal grooves in relation to compound eye.

Günther in 1938 stated good characteristics for Cladonotinae determination - frontal costa wider than the basal part of the antennae [antennal groove] and elevated, frontal costa located under the compound eyes (Günther 1938a).

Günther regularly used this characteristics when describing and determining Cladonotine: (1) general pronotum morphology (e.g. strongly compressed, leafy), (2) descriptive morphology of frontomedial projection, (3) descriptive shape of scutellum (e.g. pear-shaped), (4) relation to spot on scutellum of its greatest width to other parts of the head (e.g. in the level of antennal grooves, below the compound eyes), (5) location of highest part of pronotum in lateral view in relation to

other body parts, (6) general morphology of top and bottom parts of femurs, (7) geographical distribution, (8) existence of hind wings or elitra, (9) reach of pronotum anteriorly in relation to other body parts, (10) general shape of posterior end of pronotum, (11) scutellum width in relation to antennal grooves width, (12) position of antennal grooves in relation to compound eyes, (13) length of the antenna in relation to other body parts (e.g. outstretched front legs), (14) ratio of distance between ocelli to distance from ocelli to compound eye, (15) descriptive morphology of shoulders [metalateral projection], (16) shape of vertex in dorsal view, (17) protruding of vertex in front of eyes, (18) existence of fastigial horns, (19) ratio of width and length of antennal segments, and (20) level of protrusion of frontal costa anteriorly.

In the modern era of Tetrigidology aforementioned morphological characters are still used by describers of a new Cladonotinae species. Devriese (1991, 1999) gave new insights into what “good characters” in the morphology of Tetrigidae really means. He gave a detailed representation of all visible formations on the exoskeleton of Tetrigidae. Another attempt to modernise and uniform nomenclature of the morphology of Tetrigidae is demonstrated in Tumbrinck’s (2014) work on Cladonotinae. In the paper Tumbrinck gave a detailed figure showing important morphological characteristics in Tetrigidae. Mention-worthy updates to the terminology of morphology of Tetrigide were given by Storozhenko & Paik (2007) and Kuřavová (2017).

1.6. Invention of terminology for pronotal projections of Tetrigidae

Frontolateral projections (FL1, FL2, FL3), frontomedial projection (FM), promediolateral projections (PML1, PML2), and prolateral projections (PL1, PL2) have been proposed as valid characters of pronotum by Skejo in his Master thesis (2017) which was later officially published in Skejo & Bertner (2017). Skejo (2017) continued on the aforementioned Tumbrinck’s (2014) work and expanded on the work on Storozhenko & Pushkar (2017). Skejo's (2017) terminology of morphology is used since in descriptions of species by some tetrigidologists (e.g. Deng & Lei 2019, Li et al. 2020, Patano et al. 2021, Tumbrinck et al. 2020, Xin & Deng 2019). The ease of use of those characters made it an appealing choice when describing fine details of an organism. Such a way of describing morphology rendered descriptive and personalized descriptions (e.g. Bolívar 1887, Günther 1935a, Günther 1935b, Defaut 1987) obsolete. That is because it gave tetrigidologists a way to communicate about morphology more accurately and precisely, thus

lowering the possibility of misunderstanding between scientists about what morphological characters the specimen bears.

1.6. About the process of making cladograms

1.6.1. General information about the process of making cladograms

When trying to reconstruct the evolutionary past of a group of organisms, there are a few ways of doing that. The first and most important thing needed for reconstructing phylogenetic trees is information about some of the organisms' characteristics. Information may be about their DNA or genes from any source, proteins or morphological characters. Morphological characters can come in three different types of states. Binary, meaning the character can exist in one of two discrete states, for example, presence of wings on an organism, either the organism has them or does not. The second type of character is meristic. Those are characters that can exist in more than two discrete states, for example, the number of segments of antennae of some group of insects that can vary from 10 to 20. The third type are continuous characters. Those are characters that can have any value in some range, for example, length of an organism that can be represented with any rational number above zero. When enough data about researched taxa is gathered, the next step in making a cladogram is making a character matrix from those characters. That is done by listing all taxa in the first column of the matrix, and arranging states of characters in subsequent columns, thus joining one state of every character to each taxon. Such a matrix is then ready to be analyzed by one of many computer programs specialized for doing just that. Analysis of matrix gives us cladogram(s) and all other data we care about, such as reconstruction of character history, analysis of speciation and extinction or any other data about the cladogram.

1.6.2. Retention index and consistency index

Important information to extract from the cladistic analysis are retention and consistency indexes. The relative amount of homoplasy can be measured using the consistency index (often abbreviated CI). It is calculated as the number of steps expected given the number of character states in the data, divided by the actual number of steps multiplied by 100. The formula for the CI is: $CI = \frac{\text{total character state changes expected given the data set}}{\text{actual number of steps on the tree}} * 100$ (Kluge & Farris 1969, Farris 1989). In other words, the consistency index tells the relative abundance of characters that changed its state back to the state it previously had through the cladogram. That is a sign of homoplasy in

most cases because characters that change back and forth their states behave just like a homoplastic character would, emerging multiple times on the cladogram. On the other hand, retention index (RI) measures the amount of synapomorphy expected from a data set that is retained as synapomorphy on a cladogram. The formula for the RI is:

$$RI = \frac{\text{maximum number of steps on a hypothetical tree} - \text{number of state changes on the tree analysis gave us}}{\text{maximum number of steps on the hypothetical tree} - \text{number of state changes in the used data}} * 100.$$

The formula may not be as intuitive as one of CI, but it is as useful as CI for determining the quality of characters used in the analysis (Kluge & Farris 1969, Farris 1989).

1.7. Today's knowledge on the systematics and phylogeny of Cladonotinae

The only way scientists in the past assigned new species to Cladonotinae was on the basis of morphology, and never it was confirmed using molecular data that any species truly belongs to the Cladonotinae. Some research has been done on phylogeny of Cladonotinae as a whole using molecular data (Zhang et al. 2020) and on one genus *Cladonotella* Hancock, 1909 using morphometrics (Tan et al. 2019). Molecular data (Zhang et al. 2020) indicates that Cladonotinae subfamily has members scattered among other subfamilies and as such are „controversial group“. Few other papers have been published on the phylogeny of other subfamilies, but which include Cladonotinae species (Deng et al. 2021, Li et al. 2021, Lin et al. 2017). Those papers do not indicate any new facts about Cladonotinae phylogeny, although in Li et al. 2021 they commented how Cladonotinae members used in the analysis did not form a single clade, thus not forming a monophyletic clade. The same was shown in two other papers (Lin et al. 2015, Yao 2008). Cladonotinae are again and again shown not to be monophyletic group, confirming what we already know, yet, nothing was done to correct the systematic of Cladonotinae and other subfamilies belonging to Tetrigidae. That is a hard task that first needs a good understanding of apomorphies in morphology of Cladonotinae in order to be resolved. Because systematics and questions of apomorphies are not yet resolved, the work of Zhang et al. 2020, however important, is only partly informative. We do not know which of Cladonotinae species truly belong to Cladonotinae subfamily, and subsequently, the results they published do not really tell us anything about Cladonotinae phylogeny.

As Josip Skejo said in his Master thesis (2017) : “Subfamily Cladonotinae Bolívar, 1887 is one of the subfamilies without any evolutionary values. It is group made for genera and species

that are brachypronotal, most of them apterous, with widened frontal costa forming wide scutellum.”

2. Goals and hypothesis

Goals of this research are:

1. Investigate the validity of characters used to determine whether a new species belongs to a subfamily Cladonotinae
2. Analyze the relative amount of homoplasy among species of Cladonotinae
3. Find characters that would serve as good criteria for declaring a new species a member of Cladonotinae (note: not necessarily homologies, but good guiding characters)
4. Find characters that give little to no insight in evolutionary relations between species of Cladonotinae.

Hypothesis of this research are:

1. Not all characters used in distinguishing Cladonotinae from other subfamilies actually distinguish specimens between subfamilies
2. There are at least some homoplasies among Cladonotinae species
3. Characters that would serve as signs for species belonging to Cladonotinae exist and can be found
4. Some characters (e.g. broad scutellum) used for inferring evolutionary relations between species of Cladonotinae give little to no insight in given problem

3. Materials and methods

3.1. Characters used

Terminology of morphological characters follows Rehn (1904), Grant (1962), and Tumbrinck (2014). Characters chosen for the analysis are, firstly, the ones that Cladonotinae possesses, for example that means that VL projections, character specific for Scelimeninae, were not included. Second criteria was that characters were binary, meaning only two valid states (1=present, 0=absent) of character exist. Characters chosen are either previously used in description of some Cladonotine species, or new characters of Cladonotinae that I took into account for the first time. New character is one that has not been used in any way before, meaning that there has not been any mention of using any state of that character in any way, and they are 24, 27, 29, 32, 46, 47, 48, 70, 71, and 93 (see Table 1.), while other characters used in this thesis have been used before in various scientific papers on Cladonotinae members.

Table 1. **List of characters and their states used to make character matrix.** Characters colored red are head characters, blue are pronotum characters, green are leg characters, and yellow are wing characters.

#	CHARACTER	DESCRIPTION
1	Frontal costa bifurcation in the level of top margin of a compound eye	0=no, 1=yes
2	Frontal costa bifurcation above the midlevel of a compound eye	0=no, 1=yes
3	Frontal costa bifurcation above bottom margin of a compound eye	0=no, 1=yes
4	Scutellum width in its widest part more than width of scapus	0=no, 1=yes
5	Scutellum width in the level of antennal groove more than width of scapus	0=no, 1=yes
6	The top margin of antennal groove above the level of the lower margin of a compound eye	0=no, 1=yes
7	The top margin of antennal groove on the level of lower margin of a compound eye	0=no, 1=yes
8	Distance between the antennal grooves wider than width a compound eye	0=no, 1=yes
9	Position of the paired (lateral) ocellus above the middle of a compound eye	0=no, 1=yes
10	Position of the paired (lateral) ocellus above the lower margin of a compound eye	0=no, 1=yes
11	In frontal view, top margin of a compound eye below vertex	0=no, 1=yes

Table 1. (continued) **List of characters and their states used to make character matrix.**

12	In frontal view, top margin of a compound eye on the same level vertex	0=no, 1=yes
13	In frontal view, top margin of a compound eye above vertex	0=no, 1=yes
14	In dorsal view, fastigium of the vertex between the eyes (frontmost part) wider than a compound eye	0=no, 1=yes
15	Lateral carinae of the vertex visible from dorsal or frontal view	0=no, 1=yes
16	Fastigial horns visible in lateral or frontal view	0=no, 1=yes
17	Facial carinae straight after bifurcation	0=no, 1=yes
18	Median carina of the vertex visible in dorsal or frontal view	0=no, 1=yes
19	In dorsal view, anterior margin of the vertex protruded before the compound eye	0=no, 1=yes
20	In dorsal view, vertex truncated	0=no, 1=yes
21	In frontal view, vertex flat, truncated	0=no, 1=yes
22	In frontal view, vertex convex, bulging	0=no, 1=yes
23	In frontal view, vertex concave, "U" shaped	0=no, 1=yes
24	In dorsal or lateral view, anterior margin of frontal costa more protruded than vertex	0=no, 1=yes
25	Vertex lower than anterior margin of pronotum	0=no, 1=yes
26	Lateral carinae of vertex forming false hornlike tubercle	0=no, 1=yes
27	In frontal view, the widest part of scutellum wider than a compound eye	0=no, 1=yes
28	Width of the fastigium of the vertex between the eyes (in the middle of length of compound eye) from above wider than compound eye	0=no, 1=yes
29	In dorsal view, vertex triangular or rhomboid	0=no, 1=yes
30	In lateral view, fastigium of vertex parallel with ground	0=no, 1=yes
31	In frontal view, height of scutellum greater than (not equal or less) height of a compound eye	0=no, 1=yes
32	In lateral or dorsal view, compound eye distanced from pronotum by less than 1/3 of its length (occipital area absent)	0=no, 1=yes
33	In dorsal view, anterior margin of the pronotum truncated	0=no, 1=yes
34	In dorsal or lateral view, prozonal carinae visible	0=no, 1=yes
35	In dorsal view, prozonal carinae parallel or divergent towards anterior part of pronotum	0=no, 1=yes
36	In lateral view, extralateral carinae visible	0=no, 1=yes
37	Sulci visible	0=no, 1=yes
38	Humero-apical carinae visible	0=no, 1=yes
39	Interhumeral carinae visible	0=no, 1=yes
40	Ventral sinus visible	0=no, 1=yes
41	Tegminal sinus distinct (not covered by infrascapular area)	0=no, 1=yes
42	In lateral view, median carina smoothly curved	0=no, 1=yes

Table 1. (continued) **List of characters and their states used to make character matrix.**

43	Median carina of the pronotum undulated from anterior margin to shoulders	0=no, 1=yes
44	Median carina of the pronotum undulated from shoulders to posterior margin	0=no, 1=yes
45	Median carina of the pronotum strongly compressed, leaf-like	0=no, 1=yes
46	Apex of lateral lobe of paranota U shaped	0=no, 1=yes
47	Apex of lateral lobe of paranota V shaped	0=no, 1=yes
48	Apex of lateral lobe of paranota \sqsupset shaped	0=no, 1=yes
49	Posterior apex of pronotum obliquely bilobated	0=no, 1=yes
50	Posterior apex of pronotum overall curved	0=no, 1=yes
51	Posterior apex of pronotum acutely bilobated (M shaped, bispiked)	0=no, 1=yes
52	Posterior apex of pronotum trilobate or trident-shaped	0=no, 1=yes
53	In dorsal view, posterior end of pronotum very narrow or pointy	0=no, 1=yes
54	In dorsolateral view, PM visible	0=no, 1=yes
55	In dorsolateral view, MM1 visible	0=no, 1=yes
56	In dorsolateral view, MM2 visible	0=no, 1=yes
57	In dorsolateral view, MM3 visible	0=no, 1=yes
58	In dorsolateral view, MM4 visible	0=no, 1=yes
59	In dorsal view, humeral angles more protruded than lateral lobes of pronotum	0=no, 1=yes
60	In dorsal view, humeral angles situated above lateral lobe	0=no, 1=yes
61	In dorsal view, humeral angles situated above mid leg coxa	0=no, 1=yes
62	In dorsal view, humeral angles situated between mid and hind leg coxa	0=no, 1=yes
63	In dorsolateral view, MML1 visible	0=no, 1=yes
64	In dorsolateral view, MML2 visible	0=no, 1=yes
65	In dorsolateral view, MML3 visible	0=no, 1=yes
66	In dorsolateral view, MML4 visible	0=no, 1=yes
67	In dorsolateral view, MML5 visible	0=no, 1=yes
68	Pronotal and leg exoskeleton covered in spikes	0=no, 1=yes
69	In frontal view, pronotum tectate (roof shaped)	0=no, 1=yes
70	In lateral view, ventral sinus V-shaped with sharp corner, not oblique	0=no, 1=yes
71	First segment of front tarsus bearing pulvilli	0=no, 1=yes
72	Dorsal carina of frontal femur continuous	0=no, 1=yes
73	Dorsal carina of frontal femur undulated	0=no, 1=yes
74	Dorsal carina of frontal femur bearing tubercles	0=no, 1=yes
75	Ventral carina of frontal femur continuous	0=no, 1=yes
76	Ventral carina of frontal femur undulated	0=no, 1=yes
77	Ventral carina of frontal femur bearing tubercles	0=no, 1=yes

Table 1. (continued) **List of characters and their states used to make character matrix.**

78	Fore femur carinae leaf-like	0=no, 1=yes
79	Dorsal carina of middle femur continuous	0=no, 1=yes
80	Dorsal carina of middle femur undulated	0=no, 1=yes
81	Dorsal carina of middle femur bearing tubercles	0=no, 1=yes
82	Ventral carina of middle femur continuous	0=no, 1=yes
83	Ventral carina of middle femur undulated	0=no, 1=yes
84	Ventral carina of middle femur bearing tubercles	0=no, 1=yes
85	Middle femur carinae leaf-like	0=no, 1=yes
86	Dorsal carina of front femur bearing dentiform spines	0=no, 1=yes
87	Ventral carina of front femur bearing dentiform spines	0=no, 1=yes
88	Dorsal carina of middle femur bearing dentiform spines	0=no, 1=yes
89	Ventral carina of middle femur bearing dentiform spines	0=no, 1=yes
90	Dorsal margin of hind femur without lappets, spines, tubercles, and not undulated	0=no, 1=yes
91	Ventral margin of hind femur without lappets, spines, tubercles, and not undulated	0=no, 1=yes
92	External surface of hind femur with recognizable, not-projected external carinae and transversal ridges	0=no, 1=yes
93	Hind tibia with finely serrated outer and/or inner margins	0=no, 1=yes
94	Outer margin of hind tibia with 4 or more strong spines	0=no, 1=yes
95	Inter margin of hind tibia with 4 or more strong spines	0=no, 1=yes
96	Third segment of hind tarsus shorter than first or equal	0=no, 1=yes
97	Third tarsal segment of hind leg half or less length as first segment	0=no, 1=yes
98	Tegmenula (fore wings) visible	0=no, 1=yes
99	Alae (hind wings) visible	0=no, 1=yes

Below are photographic explanations of characters which are not self explanatory as, for example, is character 37 or 99. Numbers in brackets before the name of character indicate position of character in that figure. Numbers in brackets after the name of character indicate their number in Table 1. (Fig. 1 to Fig. 12).

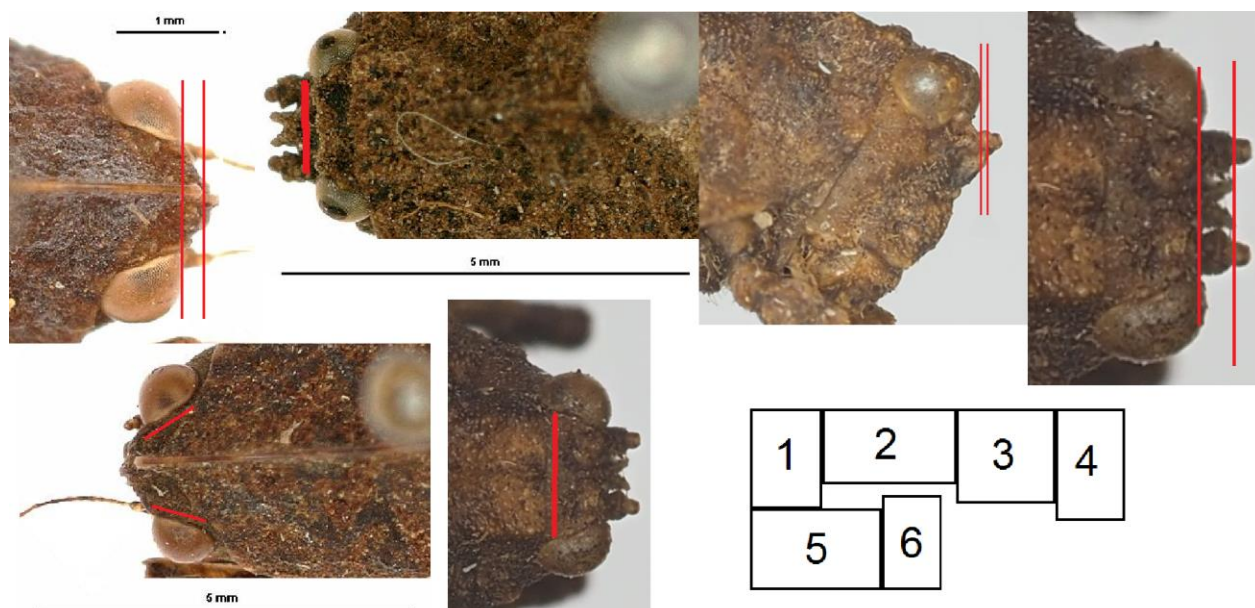


Figure 1. **Explanation of characters 19, 20, 24, 29, and 33.** (1) Anterior margin of the vertex protruded before the compound eye (19), left vertical line shows the frontmost level of compound eyes, right vertical line shows anterior margin of vertex, *Boczkittettix manokwariensis* Tumbrinck, 2014, Source: © Bernice P. Bishop Museum, Honolulu, photo Josef Tumbrinck; (2) vertex truncated (20), vertical line shows and emphasizes the truncatedness of the vertex, *Cladonotella interrupta* (Bolívar, 1898), Source: © Museo Civico di Storia Naturale "Giacomo Doria" (MCSN), Genova, photo Josef Tumbrinck; (3, 4) anterior margin of frontal costa more protruded than vertex (24), both left vertical lines show the anterior margin of vertex, both right lines show the anterior margin of frontal costa, *Tondanotettix brevis* (Haan, 1843), Source: © Nederlands Centrum voor Biodiversiteit, Leiden, photo Josef Tumbrinck; (5) vertex triangular or rhomboid (29), lines show and emphasizes the rhomboidal shape of vertex, *Boczkittettix manokwariensis* Tumbrinck, 2014, Source: © Bernice P. Bishop Museum, Honolulu, photo Josef Tumbrinck; (6) anterior margin of the pronotum truncated (33), vertical line shows and emphasises the anterior margin of pronotum being truncated, *Tondanotettix brevis* (Haan, 1843), Source: © Nederlands Centrum voor Biodiversiteit, Leiden, photo Josef Tumbrinck.



Figure 2. **Explanation of characters 21, 22, and 23 (vertex shape in frontal view).** From left to right: vertex concave, "U" shaped (23) red curve showing and emphasising the concave vertex, *Ichikawatettix exsertus* (Günther, 1938), Source: © Museum für Naturkunde, Berlin (MFN), photo Josef Tumbrinck; vertex convex, bulging (22), red curve showing and emphasising the convex vertex, *Hymenotes westwoodi* Bolívar, 1887, Source: © Naturhistoriska Riksmuseet Stockholm (NHRS), photo Josef Tumbrinck; vertex flat, truncated (21), red line showing and emphasising the flat vertex, *Potua coronata sumatrensis* Bolívar, 1898, Source: © Staatliches Museum für Tierkunde (SMTD), Dresden, photo Josef Tumbrinck.



Figure 3. **Explanation of characters 93, 94, and 95.** Top left: hind tibia with finely serrated margins (93), red line showing and emphasising the finely serrated margins of tibia, *Cladoramus crenulatus* Hancock, 1907, Source: © University Museum, Hope Entomological Collections (UMO), Oxford, photo Josef Tumbrinck; top right and bottom: hind tibia without finely serrated margins, but bearing 4 or more strong spines on outer and inner margins (94, 95), red line showing and emphasising hind tibia without finely serrated margins, *Coptottigia cristata* Bolívar, 1912, Source: © Axel Hochkirch, 2013 Natural History Museum, London; © The Natural History Museum, London (BMNH), photo Josef Tumbrinck.



Figure 4. **Explanation of characters 68 and 70.** On top: ventral sinus V-shaped (70), red line showing and emphasising the V-shaped ventral sinus, *Seyidotettix swahili* Rehn, 1939, Source: Rehn, J.A.G. 1938. Proc. Acad. Nat. Sci. Philad. 90:361-387, Fig. 1; on bottom: exoskeleton covered in spikes (68), *Misythus echinatus* (Stål, 1877), Source: © Naturhistoriska Riksmuseet Stockholm (NHRS), photo Josef Tumbrinck. Scale on the bottom photo shows a length of 1 millimeter.



Figure 5. **Explanation of characters 49, 50, 51, 52, and 53 (morphology of the end of pronotum).** (1) posterior end of pronotum very narrow (53), *Morphopoides tessmanni* Günther, 1939, Source: © Museo Civico di Storia Naturale "Giacomo Doria" (MCSN), Genova, photo Josef Tumbrinck; (2) posterior apex of pronotum obliquely bilobated (49), *Misythus securifer* (Walker, 1871), Source: © Naturhistoriska Riksmuseet Stockholm (NHRS), photo Josef Tumbrinck; (3) posterior apex of pronotum acutely bilobated (51), *Gestroana discoidea* (Bolívar, 1898), Source: © Museo Nacional de Ciencias Naturales (MNCN), Madrid, photo Josef Tumbrinck; (4) posterior apex of pronotum overall curved (50), *Ingrischitettix mountabilalaensis* Tumbrinck, 2014, Source: © Bernice P. Bishop Museum, Honolulu, photo Josef Tumbrinck; (5) posterior apex of pronotum trilobate (52) *Piezotettix sulcatus* (Stål, 1877), Source: © Naturhistoriska Riksmuseet Stockholm (NHRS), photo Josef Tumbrinck.

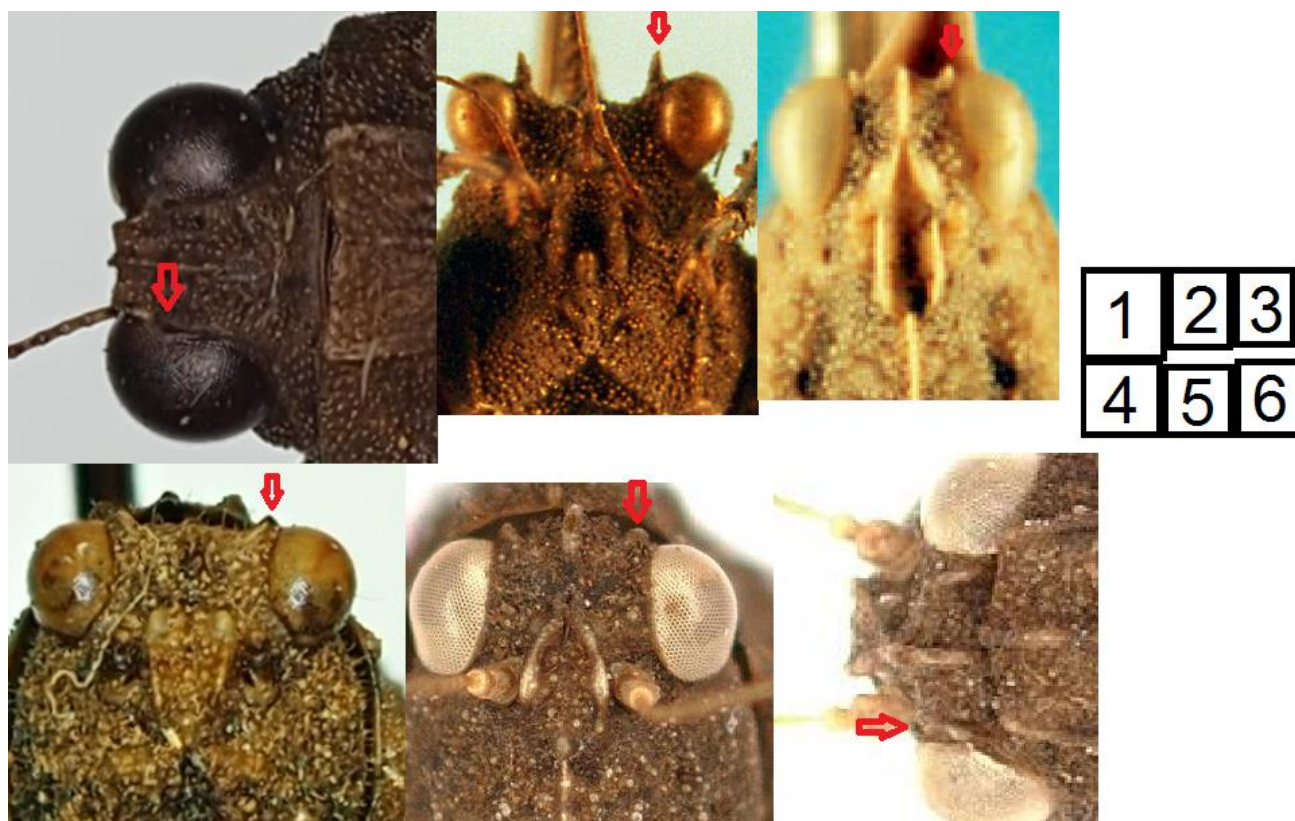


Figure 6. **Explanation of characters 15, 16, and 26.** (1) lateral carina visible (15), red arrow pointing to the lateral carina, *Morphopoides coriaceum* Rehn, 1930, Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck; (2, 3) fastigial horns visible (16), red arrows pointing to the fastigial horns, (2) *Pantelia horrenda* (Walker, 1871), Source: © Sigfrid Ingrisch, DORSA, (3) *Trypophyllum glabrifrons* Karsch, 1890, Source: © Sigfrid Ingrisch, DORSA; (4, 5, 6) lateral carinae of vertex forming false hornlike tubercule (26), red arrows pointing to the lateral carinae bulging slightly thus somewhat resembling the fastigial horn, (4) *Potua coronata coronata* Bolívar, 1887, Source: © Naturhistorisches Museum Wien (NMW), Vienna, Austria, photo Josef Tumbrinck, (5, 6) *Willemsetettix missai* Tumbrinck, 2014, Source: © Muséum des sciences naturelles de Belgique (IRSNB), Bruxelles, photo Josef Tumbrinck.

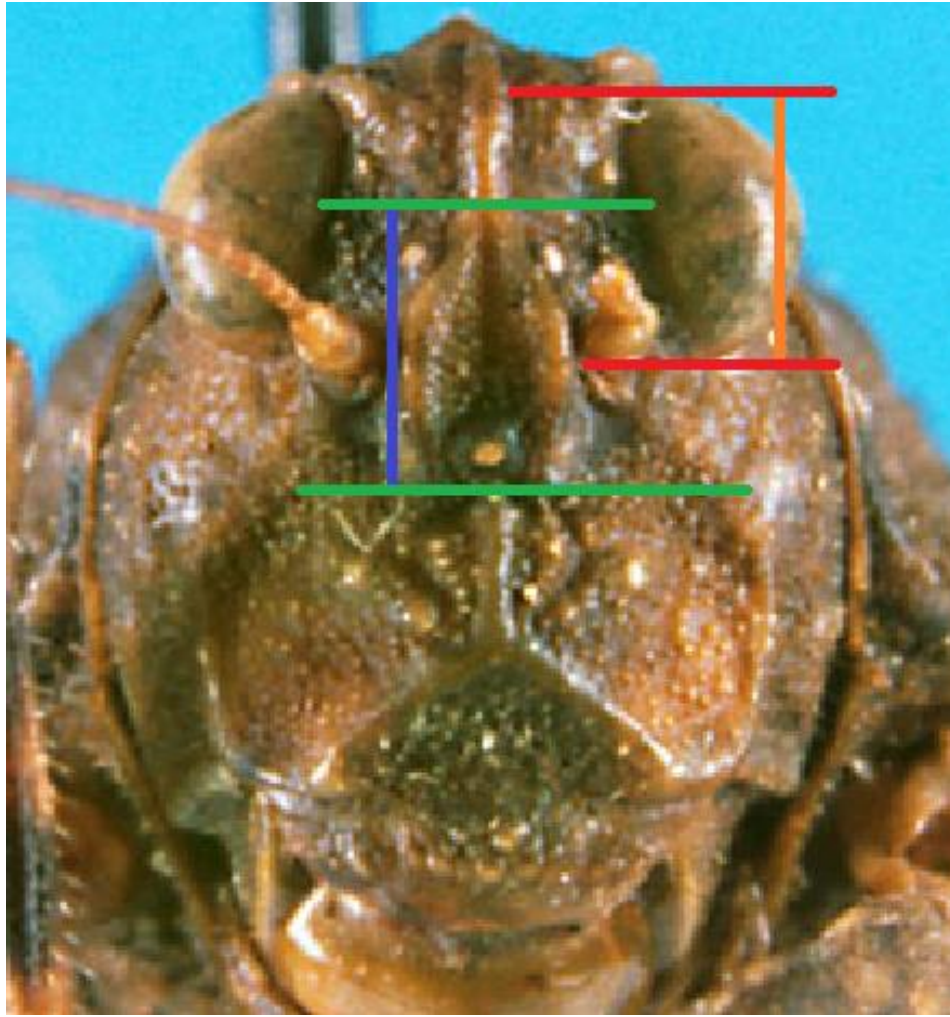


Figure 7. **Explanation of character 31.** How to determine the height of scutellum and the height of a compound eye (31), red lines show top and bottom margin of the compound eye, orange line shows the height of the compound eye, green lines show the top and bottom margin of scutellum, blue line shows the height of scutellum, *Pseudohyboella weylandiana* Günther, 1938, Source: © Sigfrid Ingrisch, DORSA.

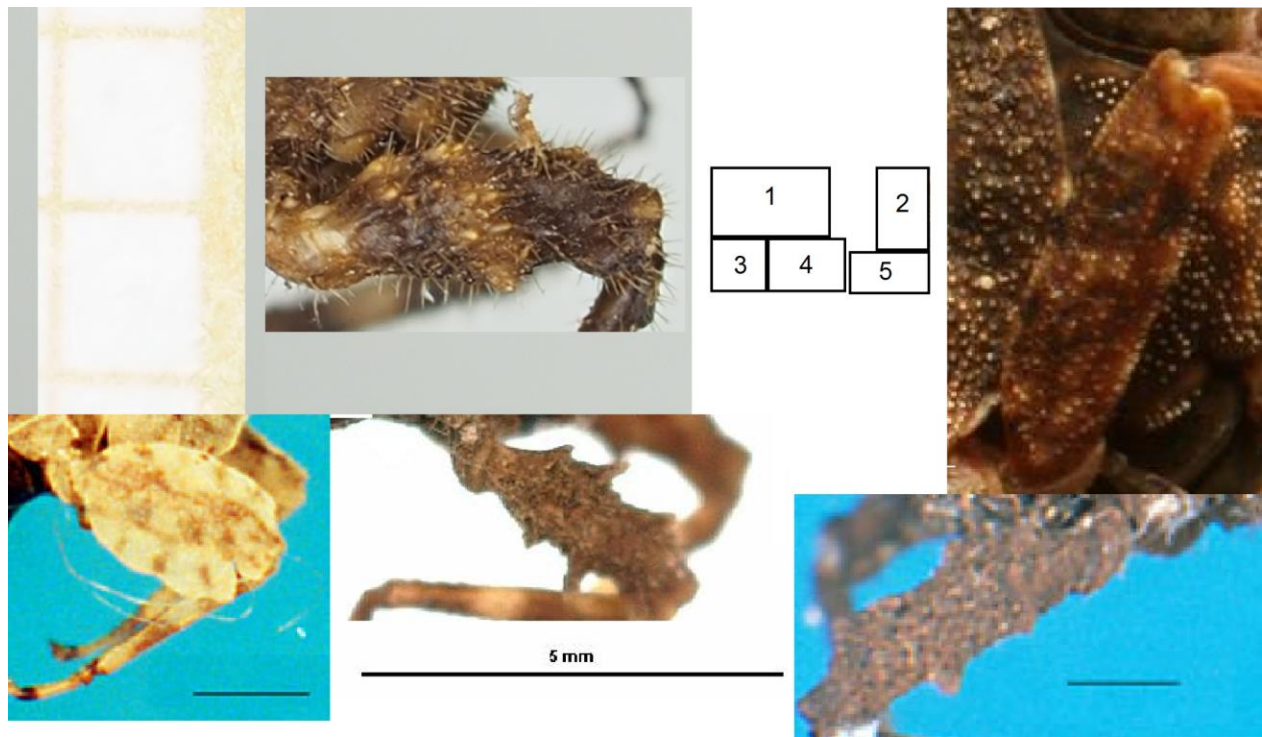


Figure 8. **Explanation of characters 72, 73, 74, 78, and 86 (the morphology of front femur).** (1) front femur undulated (73), *Potua morbillosa* (Walker, 1871), Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck; (2) carina of frontal femur continuous (72), *Epitettix obtusus* Storozhenko & Dawwrueng, 2014, Source: Copyright © Pattarawich Dawwrueng; (3) fore femur carinae leaf-like (78), *Trypophyllum glabrifrons* Karsch, 1890, Source: © Sigfrid Ingrisch, DORSA; (4) front femur bearing dentiform spines (86), *Cladonotella gibbosa* (Haan, 1843), Source: © Staatliches Museum für Tierkunde (SMTD), Dresden, photo Josef Tumbrinck; (5) frontal femur bearing tubercles (74), *Austrohancockia kwangtungensis* (Tinkham, 1936), Source: © Sigfrid Ingrisch, DORSA. Scales show a length of 1 millimeter if not stated otherwise.

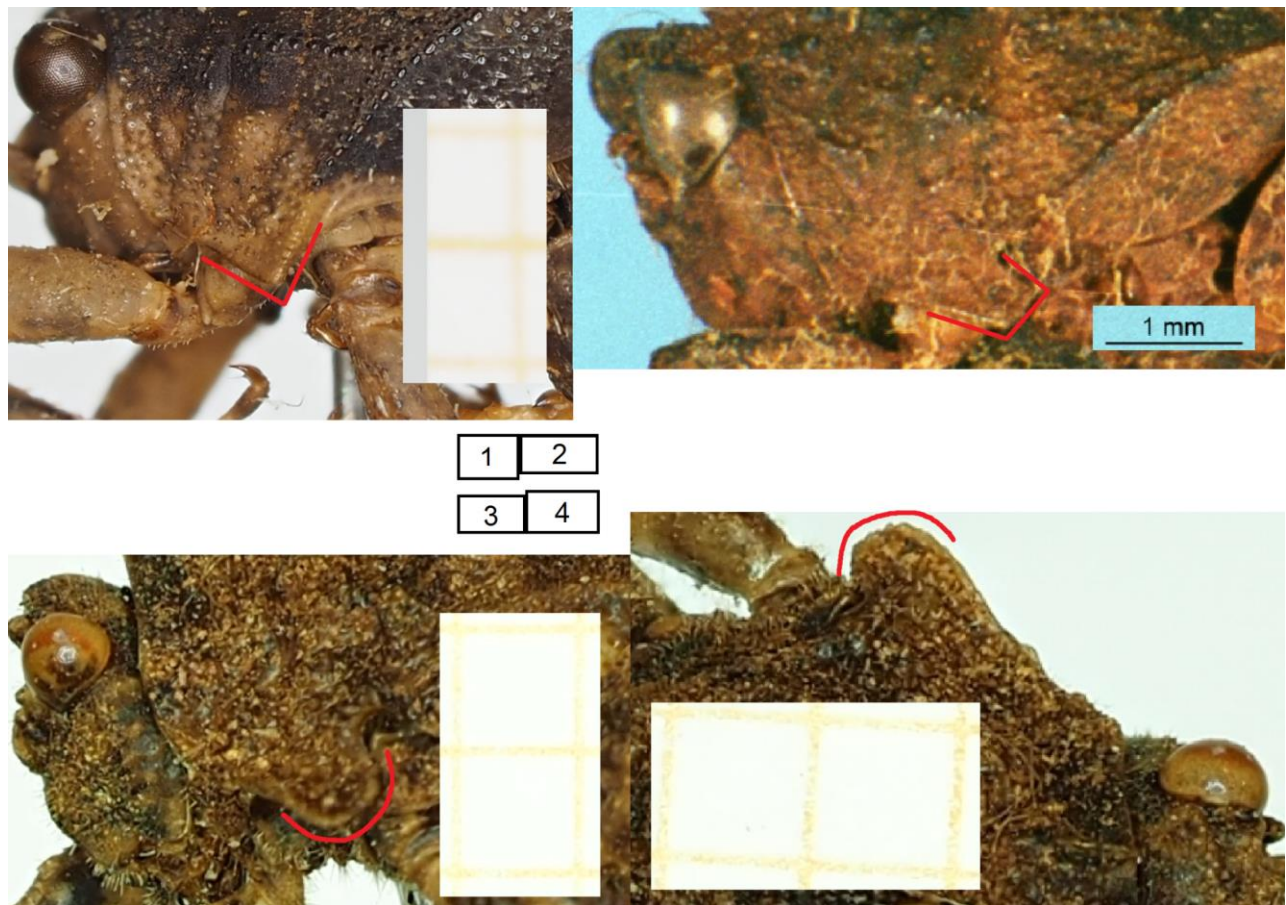


Figure 9. **Explanation of characters 46, 47, and 48 (the morphology of lateral lobes of paranota).** (1) Lateral lobe of paranota V-shaped (47), red line showing and emphasising the V-shaped lateral lobe of paranota, *Bufonides uvarovi* Hinton, 1940, Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck; (2) lateral lobe of paranota U shaped (48), red line showing and emphasising the U shaped lateral lobe of paranota, *Deltonotus gibbiceps* (Bolívar, 1902), Source: Copyright © 1994 Sigfrid Ingrisch and MNHN Paris, France; (3, 4) lateral lobe of paranota U shaped (46), red line showing and emphasising the U-shaped lateral lobe of paranota, *Potua coronata coronata* (Bolívar, 1887), Source: © Naturhistorisches Museum Wien (NMW), Vienna, Austria, photo Josef Tumbrinck. All scales show a length of 1 millimeter.



Figure 10. **Explanation of character 71 (pulvili of the first tarsal segment).** The first segment of front tarsus bearing pulvilli (71), *Thymochares galeatus* Rehn, 1929, Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck. Scale shows a length of 1 millimeter.

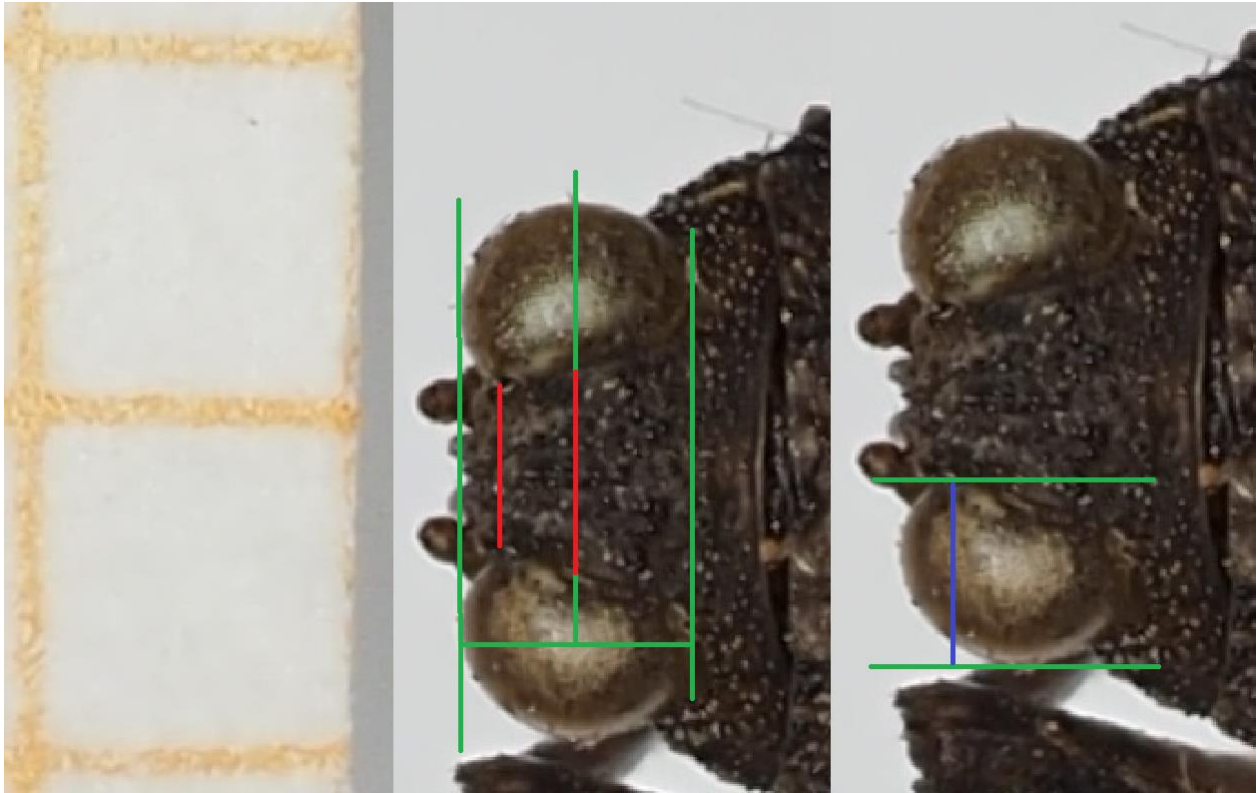


Figure 11. **Explanation of characters 14 and 28.** Ratio of vertex widths and compound eye width (14, 28), on the left side green lines show anterior and posterior margins of compound eye, and the midline of compound eyes, on the left side red lines show anterior margin of vertex and the width of vertex on that part of vertex, and width of vertex in the level of midline of the compound eye, on the right side green lines show outer and inner margin of the compound eye, and blue line shows the width of the compound eye, *Morphopoides folipes* (Hancock, 1909), Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck. Scale shows a length of 1 millimeter.

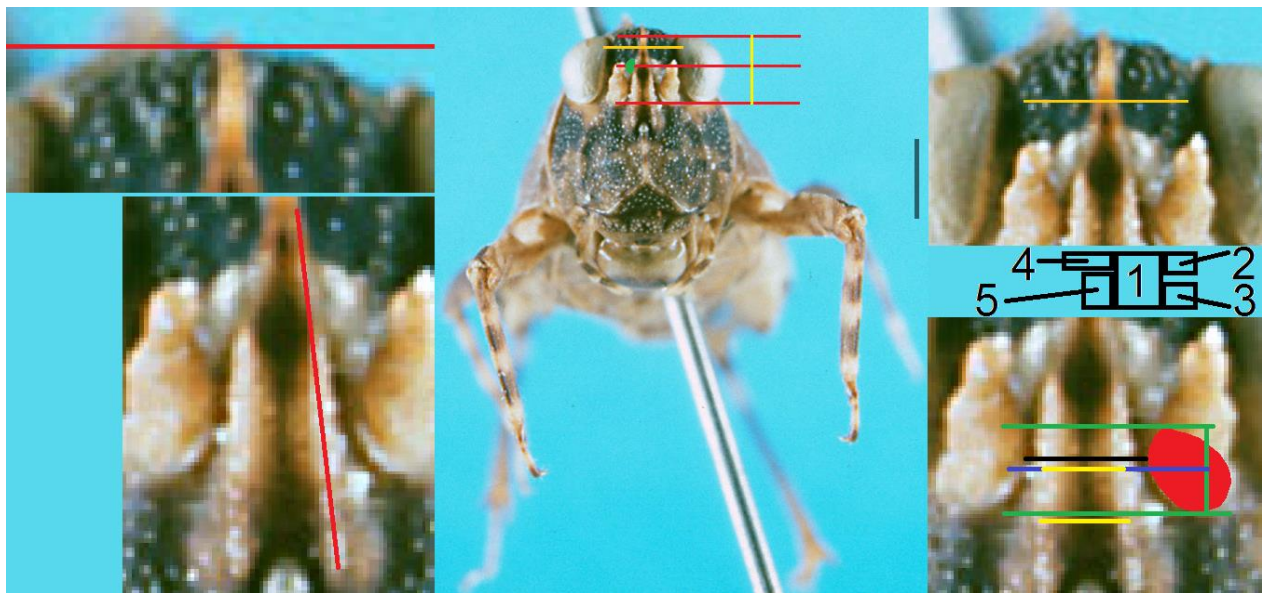


Figure 12. **Important characters of the head.** (1) Top, mid and bottom margins of compound eye (red lines), the position paired ocellus (green dot), height of the compound eye (yellow line), width between the compound eyes (orange line); (2) location of frontal costa bifurcation; (3) location of antennal groove (red dot), its top and bottom margin (green lines) and its mid-level (blue line), location of widest part of scutellum and part in the level of antennal groove (yellow lines), width between antennal grooves (black line); (4) location of top margin of vertex; (5) example of facial carinae straight after bifurcation (character 17), *Hippodes vicarius* Karsch, 1890, Source: © Sigfrid Ingrisch, DORSA.

3.2. Reason for omitting of geographical distribution from the analysis

Exact location of some specimens' collection place was not known and in many cases, the only information about locality of collecting was the name of country where it was collected. I omitted the geographical distribution from the analysis because the geographical distribution has, on average, more weight and informativity than any other morphological character. Also, not every two distributions have the same difference of probability of occurring in the same clade. For example, the distribution of Sri Lanka and India has a greater probability of occurrence in the same clade than Cuba and Madagascar (personal observation). Ergo, I did not include distribution, also because I did not know how to properly weigh all the possible locations on Earth to use them in this analysis.

3.3. Specimens examined

Photos of species were downloaded from OSF. Photos of species *Armasius iberianus* Perez-Gelabert & Yong, 2014, *Cubanotettix turquinensis* Perez-Gelabert, Hierro & Otte, 1998, *Cubonotus altinotatus* Perez-Gelabert, Hierro & Otte, 1998, *Eleleus curtus* Bolívar, 1887, *Haitianotettix tuberculatus* Perez-Gelabert, Hierro & Otte, 1998, *Hottettix haitianus* Perez-Gelabert, Hierro & Otte, 1998, *Mucrotettix gibbosus* Perez-Gelabert, Hierro & Otte, 1998, *Mucrotettix spinifer* Perez-Gelabert, Hierro & Otte, 1998, *Sierratettix carinatus* Perez-Gelabert, Hierro & Otte, 1998, *Tiburonotus peninsularis* Perez-Gelabert, Hierro & Otte, 1998, *Truncotettix fronterizus* Perez-Gelabert, Hierro & Otte, 1998, and *Truncotettix interruptus* Perez-Gelabert, Hierro & Otte 1998 were accessed from Silva et al. 2019, *Austrohancockia orlovi* Storozhenko, 2016 from Storozhenko 2016, *Cladonotus bhaskari* Tumbrinck, Deranja, Adžić, Pavlović & Skejo, 2020 from Tumbrinck et al. 2020. *Thymochares exiguus* Günther, 1974 *Epitettix spheniscus* Günther, 1974, and *Lepocranus fuscus* Devriese, 1991 was examined from Skejo's private photo collection from MNHN, *Notredamia dora* Skejo, Deranja & Adžić, 2020 from Skejo et al. 2020a, *Pseudepitettix pimkarnae* Storozhenko & Dawwrueng, 2014 from Storozhenko & Dawwrueng 2014, *Pseudepitettix torulosinota* (Zheng & Lin, 2016) from Zheng & Liu 2016, *Tetradinodula bambusae* Zha, 2017 from Zha et al. 2017b, and *Tettilobus trishula* Skejo, Bhaskar & Stermšek 2020 was examined from Bhaskar et al. 2020.

Two species of each genus in Cladonotinae subfamily for which photographs were available, have been chosen randomly, eliminating any potential bias. If photographs of only single species of a genus were available, they were chosen for the analysis as the sole representative of the genus. Genera *Austrohancockia*, *Cladonotella*, *Epitettix*, *Gestroana*, *Holoarcus*, *Misythus*, *Morphopoides*, *Piezotettix*, *Potua*, and *Tettilobus* have 3 or more species represented in matrix. Reason for that is their peculiar morphology that greatly distincts them from other genera of Cladonotinae (personal communication with Josip Skejo). In this way it was expected that groupings of certain genera would be more noticeable and thus more easily discussed if specific groupings occur in the results.

Only clear photos were considered while examining species morphology; any drawings were ignored in the process. Any low-quality photos were also ignored in the process of identifying

all morphological structures on the exoskeleton of the specimens. Also, any descriptions of the species were not considered in determining morphology.

Below is given a complete list of species and specimens used in the analysis.

Materials examined are written in the form of: (1) species name, (2) number of individuals, their sex, and kind of type, (3) abbreviation of depository, (4) city where it is deposited, (5) location from where the individual was collected, (6) date of collecting, (7) name of the collector. Individual specimens are separated by semicolons. Only information that is not known is missing in the list below.

3.3.1. Tribe Cladonotini Bolívar, 1887

***Boczkittix* Tumbrinck, 2014**

Boczkittix borneensis (Günther, 1935), 1 ♂ holotype, NBC, Leiden, Malesia, Borneo, Kalimantan, October 19, 1925, H.C. Siebers; 1 ♀ allotype, SMTD, Dresden, Malesia, Borneo, October 17, 1925, H.C. Siebers, 1 ♀ not a type, NBC, Leiden, Malesia, Borneo: Bettotan, near Sandakan; 1 ♀ paratype, NBC, Leiden, Malesia, Borneo, Kalimantan, October 18, 1925, H.C. Siebers

Boczkittix manokwariensis Tumbrinck, 2014, 1 ♂ holotype, BPBM, Honolulu Museum, Papuasias, New Guinea: environs of Manokwari; S 0.855500, E 134.090900, July 19, 1957, D. Elmo Hardy

***Cladonotus* Saussure, 1862**

Cladonotus bhaskari Tumbrinck, Deranja, Adžić, Pavlović & Skejo, 2020, 1 ♀ holotype, CNMS, Colombo, Indian Subcontinent, Sri Lanka: Sabaragamawa, Sinharaja Rainforest; N 6.345800, E 80.488100, November 19, 2016, T. Kirschey

Cladonotus humbertianus Saussure, 1862, 1 ♂ holotype, MHNG, Geneva Museum, Indian Subcontinent, Sri Lanka: Peradeniya; N 7.272000, E 80.594400

***Deltonotus* Hancock, 1904**

Deltonotus gibbiceps (Bolívar, 1902), 1 ♀ holotype of synonym *Deltonotus humilis* Hebard, 1930, MHNG, Geneva Museum, Indian Subcontinent, India, Tamil Nadu: Nilgiri Hills, Elkhill; N 11.393553, E 76.709403; 2400 meters, January 01, 1927 to January 31, 1927, Carl & Escher; 1 ♀ syntype of synonym *Poecilotettix gibbiceps* Bolívar, 1902, MNHN, Paris, Indian Subcontinent, India, Tamil Nadu: Madurai; N 9.928906, E 78.151689; 1 ♂ allotype of synonym *Deltonotus humilis* Hebard, 1930, MHNG, Geneva Museum, Indian Subcontinent, India, Tamil Nadu, March 05, 1927, Carl & Escher

Deltonotus subcucullatus (Walker, 1871), 1 ♀ unspecified primary type of synonym *Tettix subcucullata* Walker, 1871, BMNH, London NH Mus, Indian Subcontinent, Sri Lanka; 1 ♀ not a type of synonym *Tettix subcucullata*, C. Willemse Netherlands, Indian Subcontinent, Sri Lanka: Western Province, Labugama; N 6.860175, E 80.171013, March 17, 1932; 1 ♀ unspecified primary type of synonym *Tettix subcucullata*, BMNH, London NH Mus, Indian Subcontinent, Sri Lanka; 1 ♀ paratype of synonym *Deltonotus tectiformis* Hancock, 1904, BMNH, London NH Mus, Indian Subcontinent, Sri Lanka: Pundaluoya; N 7.011202, E 80.660420; 1 ♀ not a type, MHNG, Geneva Museum, Indian Subcontinent, India, Tamil Nadu: mountain creek near Gudalu

***Diotarus* Stål, 1877**

Diotarus ikonnikovi Bey-Bienko, 1935, 1 ♀ paratype, NBC, Leiden, Malesia, Philippines: Luzon, Laguna, Los Baños; N 14.168500, E 121.231400, May 15, 1917; N. Ikonnikov; 1 ♂ paratype, NBC, Leiden, Malesia, Philippines: Luzon, Laguna, Los Baños; N 14.168500, E 121.231400, May 15, 1917; N. Ikonnikov; 1 ♀ not a type, ZMUM, Moscow Univ, Malesia, Philippines: Luzon, Laguna, Los Baños; N 14.168500, E 121.231400, May 15, 1917, N. Ikonnikov

Diotarus verrucifer Stål, 1877, 1 ♂ holotype, NHRS, Stockholm, Malesia, Philippines

***Dolatettix* Hancock, 1907**

Dolatettix hochkirchi Tumbrinck, 2014, 1 ♀ holotype, BPBM, Honolulu Museum, Papuasias, New Guinea, Papua New Guinea: East Sepik Province, Wewak; S 3.583800, E 143.656900; 2 to 30 meters, October 13, 1957; J.L. Gressitt; 1 ♂ paratype, ZFMK, Bonn, Papuasias,

New Guinea, Papua New Guinea: East Sepik Prov., Amok; S 3.583333, E 142.950000; 165 meters, January 06, 1960; T. C. Maa

Dolatettix spinifrons Hancock, 1907, 1 ♀ holotype, ANSP, Philadelphia, ocality Papuasias, New Guinea, Papua New Guinea: Moroka; 610 meters, January 01, 1891 to December 31, 1891; Anthony

***Gignotettix* Hancock, 1909**

Gignotettix burri Hancock, 1909, 1 ♂ holotype, UMO, Oxford, Indian Subcontinent, Sri Lanka: Pundaluoya; N 7.011202, E 80.660420, E.E. Green

***Hancockella* Uvarov, 1940**

Hancockella portentosa (Kirby, 1914), 1 ♀ syntype, BMNH, London NH Mus, Indian Subcontinent, India, Kerala: Western Ghats (W. side), Thenmalai, Travancore; N 8.962190, E 77.057325, November 22, 1908; 1 ♂, syntype, BMNH, London NH Mus, Indian Subcontinent, India, Kerala: Western Ghats (W. side), Thenmalai, Travancore, November 18, 1908

***Holoarcus* Hancock, 1909**

Holoarcus altinotus Hancock, 1909, 1 ♀ female holotype, UMO, Oxford, Malesia, Maluka: Aru Islands

Holoarcus arcuatus (Haan, 1843), 1 ♀ syntype of synonym *Acrydium* (*Hymenotes*) *arcuatum* Haan. 1843, UMO, Oxford, Papuasias, New Guinea: West Papua; 1 ♂ syntype of synonym *Acrydium* (*Hymenotes*) *arcuatum*, NBC, Leiden, Papuasias, New Guinea: West Papua; 1 ♀ not a type of synonym *Acrydium* (*Hymenotes*) *arcuatum*, NBC, Leiden, Papuasias, New Guinea: West Papua

Holoarcus ferwillemsi Tumbrinck, 2014, 1 ♂ holotype of synonym *Piezotettix truncatus* Willemse, 1932, ISNB, Brussels, Papuasias, New Guinea, Irian Jaya: Siwi; S 1.500000, E 134.033333, March 08, 1929; 1 ♀ paratype of synonym *Piezotettix truncatus*, ISNB, Brussels,

Papuasias, New Guinea, Irian Jaya: Siwi; S 1.500000, E 134.033333, March 08, 1929; 1 ♀ paratype of synonym *Piezotettix truncatus*, NHME, Maastricht, Papuasias, New Guinea, Irian Jaya: Sakoemi; S 2.200000, E 133.350000, March 12, 1929

***Hymenotes* Westwood, 1837**

Hymenotes triangularis Westwood, 1837, 1 ♀ syntype of synonym *Hymenotes 3-angularis* Westwood, 1837, BMNH, London NH Mus., Malesia, Philippines; 1 ♂ syntype of synonym *Hymenotes 3-angularis* Westwood, 1837, BMNH, London NH Mus., Malesia, Philippines

Hymenotes westwoodi (Bolívar, 1887), 1 ♂ holotype of synonym *Hymenotes westwoodi* (Bolívar, 1887), NHRS, Stockholm, Malesia, Philippines: Luzon; N 16.533655, E 121.343256; 1 ♀ not a type, NHRS, Stockholm, Malesia, Philippines: Luzon, Mt. Banahao; N 14.066700, E 121.483300; 1 ♂ not a type, NHRS, Stockholm, Malesia, Philippines: South Luzon, Albay; N 13.000000, E 123.666700

***Lepocranus* Devriese, 1991**

Lepocranus fuscus Devriese, 1991, 1 ♂ holotype, MNCN, Madrid Mus., Western Indian Ocean, Madagascar: Forêt de Tampolo; S 15.733642, E 49.966860

***Misythus* Stål, 1877**

Misythus cristicornis (Walker, 1871), 1 ♀ holotype, BMNH, London NH Mus., Malesia, Philippines; 1 ♂ holotype of synonym *Misythus appendiculatus* Stål, 1877, NHRS, Stockholm, Malesia, Philippines

Misythus echinatus (Stål, 1877), 1 ♂ holotype of synonym *Cladonotus echinatus* Stål. 1877, NHRS, Stockholm, Malesia, Philippines

Misythus securifer (Walker, 1871), 1 ♀ holotype of synonym *Cladonotus securifer* Walker, F. 1871., BMNH, London NH Mus., Malesia, Philippines; 1 ♂ holotype of synonym *Misythus*

histrionicus Stål, 1877, NHRS, Stockholm, Malesia, Philippines; 1 ♀ allotype of synonym *Misythus histrionicus*, NHRS, Stockholm, Malesia, Philippines

***Piezotettix* Bolívar, 1887**

Piezotettix cultratus (Stål, 1877), 1 ♀ holotype of synonym *Hymenotes cultratus* Stål, 1877, NHRS, Stockholm, Malesia, Philippines

Piezotettix sulcatus (Stål, 1877), 1 ♀ holotype of synonym *Hymenotes sulcatus* Stål, 1877, NHRS, Stockholm, Malesia, Philippines; 1 ♀ paratype of synonym *Hymenotes sulcatus* Stål, 1877, NHRS, Stockholm, Malesia, Philippines

3.3.2. tribe Mucrotettigini Cadena-Castañeda & Silva, 2019

***Antillotettix* Perez-Gelabert, 2003**

Antillotettix nanus Perez-Gelabert, 2003, 1 ♂ holotype, CMNH, Pittsburgh, Caribbean, Dominican Republic: Pedernales, 30 km N Cabo Rojo; N 18.116700, W 71.650000; 1070 meters, September 27, 1991

***Armasius* Perez-Gelabert & Yong, 2014**

Armasius iberianus Perez-Gelabert & Yong, 2014, 1 ♀ holotype, IES, Havana, Caribbean, Cuba: Monte Iberia, Nibujón; N 20.477778, W 74.730556; 610 meters, March 01, 1972 to March 31, 1972; L. de Armas; 1 ♂ not a type, Yong, Caribbean, Cuba: Holguín Province, Moa, El Toldo High Plateau, source of Río Piloto; N 20.477500, W 74.899444; 850 meters, July 14, 1997; R. Teruel

Notes: from Yong (2017) about the specimen: "Monte Iberia. Nibujón. Bcoa. Ote. III-1972 L. Armas" [actually: CUBA: Guantánamo Province: Baracoa Municipality: Monte Iberia High Plateau (20°28'40"N - 74°43'50"W, 610 m a.s.l.); on tree trunk 0.50 m above ground, montane rainforest; 5/March/1972; L. F. de Armas]; adult female holotype (IES, dry pinned). Note: this

specimen was officially loaned to Daniel E. Perez-Gelabert in September 2013, but it has not been returned yet to IES collection.

***Cubanotettix* Perez-Gelabert, Hierro & Otte, 1998**

Cubanotettix turquinensis Perez-Gelabert, Hierro & Otte, 1998, 1 ♂ holotype, ANSP, Philadelphia, Caribbean, Cuba: Macizo del Turquino; N 19.982867, W 76.834130, June 16, 1936 to June 21, 1936; P.J. Darlington, Jr.

***Cubonotus* Perez-Gelabert, Hierro & Otte, 1998**

Cubonotus altinotatus Perez-Gelabert, Hierro & Otte, 1998, 1 ♂ holotype, ANSP, Philadelphia, Caribbean, Cuba: S side of Pico Turquino; N 19.989240, W 76.833818; 914 to 1524 meters, June 01, 1936 to June 30, 1936; P.J. Darlington, Jr.

***Eleleus* Bolívar, 1887**

Eleleus curtus Bolívar, 1887, 1 ♀ holotype, NMW, Vienna Museum, Brazil

***Haitianotettix* Perez-Gelabert, Hierro & Otte, 1998**

Haitianotettix tuberculatus Perez-Gelabert, Hierro & Otte, 1998, 1 ♀ holotype of synonym *Haitianotettix monstrosus* Perez-Gelabert, Hierro & Otte, 1998, ANSP, Philadelphia, Caribbean, Haiti: Département de l'Ouest, Kenscoff near Port-au-Prince; 1219 to 1829 meters, September 02, 1934; 1 ♂ holotype, CMNH, Pittsburgh, Caribbean, Dominican Republic: Pedernales Prov., 5 Km NE of Los Arroyos, Western Sierra de Bahoruco; N 18.250000, W 71.750000; 1680 meters, July 28, 1990; C.W. Young, J.E. Rawlins, S. Thompson

***Hottettix* Perez-Gelabert, Hierro & Otte, 1998**

Hottettix haitianus Perez-Gelabert, Hierro & Otte, 1998, 1 ♀ holotype, ANSP, Philadelphia, Caribbean, Haiti: Dept. du Sud, northeastern foothills of Massif de La Hotte; 610 to 1219 meters, October 10, 1934 to October 24, 1934; P.J. Darlington, Jr.

***Mucrotettix* Perez-Gelabert, Hierro & Otte, 1998**

Mucrotettix gibbosus Perez-Gelabert, Hierro & Otte, 1998, 1 ♂ holotype, ANSP, Philadelphia, Caribbean, Dominican Republic: Santiago, Monte Diego de Ocampo; N 19.581242, W 70.748861; 1300 meters, August 26, 1995; D.E. Perez, B. Hierro, S. Navarro

Mucrotettix spinifer Perez-Gelabert, Hierro & Otte, 1998, 1 ♂ holotype, ANSP, Philadelphia, Caribbean, Dominican Republic: La Vega, Los Tablones, Parque Nacional J. A. Bermudez, Cordillera Central; N 19.050000, W 70.883300; 1245 meters, July 07, 1992 to August 25, 1992; M.A. Ivie & D.S. Sikes

***Sierratettix* Perez-Gelabert, Hierro & Otte, 1998**

Sierratettix carinatus Perez-Gelabert, Hierro & Otte, 1998, 1 ♂ holotype, ANSP, Philadelphia, Caribbean, Dominican Republic: Barahona, Sierra De Bahoruco, on way to Cortico; 1350 meters, September 07, 1997; D. Perez, B. Hierro & S. Navarro

***Tiburonotus* Perez-Gelabert, Hierro & Otte, 1998**

Tiburonotus peninsularis Perez-Gelabert, Hierro & Otte, 1998, 1 ♂ holotype, ANSP, Philadelphia, Caribbean, Haiti: La Hotte; 914 to 1219 meters, October 12, 1934; Darlington

***Truncotettix* Perez-Gelabert, Hierro & Otte, 1998**

Truncotettix fronterizus Perez-Gelabert, Hierro & Otte, 1998, 1 ♂ holotype, ANSP, Philadelphia, Caribbean, Dominican Republic: Independencia, Los Pinos del Eden, Sierra de Neiba; N 18.578056, W 71.764444; 454 meters, December 03, 1994, D.E. Perez, B. Hierro, R. Bastardo, J. Mateo & J. Almonte,

Truncotettix interruptus Perez-Gelabert, Hierro & Otte, 1998, 1 ♂ holotype, ANSP, Philadelphia, Caribbean, Dominican Republic: Monsenor Nouel Prov., Arroyo Toro Arriba, near Bonao, Cordillera Central; 76 meters, June 02, 1993, D.E. Perez

3.3.3. tribe Xerophyllini Günther, 1979

***Cladonotella* Hancock, 1909**

Cladonotella beccarii (Bolívar, 1898), 1 ♂ holotype of synonym *Cladonotella insulana* Willemse, 1961, NBC, Leiden, ocality Papuasias, New Guinea, Irian Jaya: Waigeo Island; S 0.185488, E 131.083562, August 03, 1948; M.A. Lieftinck; 1 ♀ holotype, MCSN, Genoa, Papuasias, New Guinea, Irian Jaya: Ramoi; S 1.116667, E 131.250000, February 01, 1875 to February 28, 1875; O. Beccari

Cladonotella gibbosa (Haan, 1843), 1 ♂ syntype of synonym *Acridium (Tetrix) gibbosum* Haan, 1843, NBC, Leiden, Malesia, Jawa: Label: "Japan"; 1 ♀ syntype of synonym *Acridium (Tetrix) gibbosum* Haan, 1843, NBC, Leiden, Malesia, Jawa: Label: "Japan"

Cladonotella interrupta (Bolívar, 1898), 1 ♀ holotype of synonym *Cladonotus interruptus* Bolívar, 1898, MCSN, Genoa, Malesia, Jawa: West Java, Cibodas [Tjibodas]; S 6.716700, E 107.000000; 1300 to 1500 meters, October 01, 1874 to October 31, 1874; O. Beccari

Cladonotella riedeli Tumbrinck, 2014, 1 ♀ holotype, ZSM, Munich, Papuasias, New Guinea, Irian Jaya: Jayawijaya Province, Samboka, upper Kolff River; 200 meters, October 10, 1996 to October 14, 1996; A. Riedel

Cladonotella spinulosa Tan, Tumbrinck, Baroga-Barbecho & Yap, 2019, 1 ♀ holotype, The holotype was deposited in the University of the Philippines Los Baños, Museum of Natural History (UPLBMNH), Philippines, Malesia, Philippines: Surigao del Norte, Siargao Island, Del Carmen, Mahayahay; N 9.864940, E 126.033580; 83 meters, October 17, 2018; M.K. Tan & J.B. Baroga-Barbecho

***Gestroana* Berg, 1898**

Gestroana discoidea (Bolívar, 1898), 1 ♂ holotype, MCSN, Genoa, Papuasia, New Guinea, Papua New Guinea: Fly River, January 01, 1876 to December 31, 1877; L. M. D'Albertis; 1 ♀ paratype, MNCN, Madrid Mus., Papuasia, New Guinea, Papua New Guinea: Fly River, January 01, 1876 to December 31, 1877; L. M. D'Albertis; 1 ♂ paratype, MCSN, Genoa, Papuasia, New Guinea, Papua New Guinea: Fly River, January 01, 1876 to December 31, 1877; L. M. D'Albertis

Gestroana kleukersi Tumbrinck, 2014, 1 ♀ holotype, NBC, Leiden, Papuasia, New Guinea, Irian Jaya: Araucaria Camp; S 3.500000, E 139.183333; 800 meters, March 02, 1939; L. J. Toxopeus

Gestroana willemsei Tumbrinck, 2014, 1 ♂ holotype, NBC, Leiden, Papuasia, New Guinea, Irian Jaya: Rattan Camp; S 3.500000, E 139.150000; 1000 to 1500 meters, February 18, 1939; L.J. Toxopeus; 1 ♀ paratype, NBC, Leiden, Papuasia, New Guinea, Irian Jaya: Rattan Camp; S 3.500000, E 139.150000; 1000 to 1500 meters, February 18, 1939; L.J. Toxopeus; 1 ♂ paratype, NBC, Leiden, Papuasia, New Guinea, Irian Jaya: Rattan Camp; S 3.500000, E 139.150000; 1000 to 1500 meters, February 18, 1939; L.J. Toxopeus

***Notredamia* Skejo, Deranja & Adžić, 2020**

Notredamia dora Skejo, Deranja & Adžić, 2020, 1 ♀ holotype, MNHN, Paris, Southwestern Pacific, New Caledonia: Dumbéa, Mount Koghi; S 22.177409, E 166.508104; 500 meters, February 10, 1994; L. Desutter-Grandcolas

***Potua* Bolívar, 1887**

Potua coronata coronata Bolívar, 1887, 1 ♂ syntype, NHRS, Stockholm, Malesia, Malaya, Peninsular Malaysia: Malacca; N 2.190031, E 102.247726, Staudinger; 1 ♂ syntype, NMW, Vienna Museum, Malesia, Borneo, Sarawak: Sarawak; N 1.553278, E 110.359214, Stevens; 1 ♀ syntype, NMW, Vienna Museum, Malesia, Borneo, Sarawak: Sarawak; N 1.553278, E 110.359214, Higgins

Potua coronata sumatrensis Bolívar, 1898, 1 ♀ syntype, MCSN, Genoa, Malesia, Sumatera: Si-Rambé, December 01, 1890 to March 31, 1891; E. Modigliani; 1 ♀ not a type, SMTD,

Dresden, Malesia, Sumatera: Lampongs, Wai Lima; S 5.047930, E 104.877030, November 01, 1921 to December 31, 1921; Karny & Siebers

Potua morbillosa (Walker, 1871), 1 ♂ holotype, BMNH, London NH Mus, Malesia, Borneo, Sarawak; 1 ♂ not a type, NHRS, Stockholm, Malesia, Borneo, Sarawak: O. Borneo, Pajau River, Mjöberg; 1 ♀ not a type, NHRS, Stockholm, Malesia, Borneo, Sarawak: O. Borneo, Pajau River, Mjöberg

Potua sabulosa Hancock, 1915, 1 ♂ holotype, ANSP, Philadelphia, Indian Subcontinent, India, Maharashtra: Satara District, Venna Valley, Medina; 762 to 1067 meters, April 17, 1912 to April 23, 1912; F.H. Gravely

***Acmophyllum* Karsch, 1890**

Acmophyllum undulatum Karsch, 1890, 1 ♀ holotype, MfN, West-Central Tropical Africa, Zaire: Democratic Republic of Congo, between Kwako and Kimpoko; 1 ♀ not a type of a synonym
Acmophyllum nigropunctatum Bolívar, 1905, NHRS, Stockholm, West-Central Tropical Africa, Cameroon, Sjöstedt

***Astyalus* Rehn, 1938**

Astyalus tessmanni (Günther, 1938), 1 ♀ holotype, MfN, West-Central Tropical Africa, Cameroon: environs of Uam, Bosum, May 04, 1914; G. Tessmann; 1 ♀ paratype, MfN, West Tropical Africa, Ghana: Kete Krachi; N 7.811000, W 0.051500, October 01, 1900 to October 31, 1900; Mischlich; 1 ♂ paratype, SDEI, SDEI Müncheberg, West Tropical Africa, Ivory Coast: Dimbroko; N 6.660898, W 4.715151; 1 ♀ syntype, SMTD, Dresden, West-Central Tropical Africa, Cameroon: environs of Uam, Bosum, May 04, 1914; G. Tessmann, 1 ♂ paratype, SMTD, Dresden, West Tropical Africa, Ivory Coast: Dimbroko; N 6.660898, W 4.715151

***Cladoramus* Hancock, 1907**

Cladoramus crenulatus Hancock, 1907, 1 ♀ holotype, UMO, Oxford, South Tropical Africa, Zambia: East Loangwa, Petauke; S 14.242669, E 31.322321, December 20, 1904; Neave, S. A.

***Morphopoides* Rehn, 1930**

Morphopoides coriaceum Rehn, 1930, 1 ♀ holotype, BMNH, London NH Mus, West-Central Tropical Africa, Cameroon: near Moyamba; N 8.157235, E 12.437500, February 23, 1925

Morphopoides folipes (Hancock, 1909), 1 ♂ holotype of synonym *Morphopus burri* Rehn, 1930, BMNH, London NH Mus., South Tropical Africa, Angola: Moxico district, Upper Luena valley, May 17, 1927; Burr, M.; 1 ♂ unspecified primary type, UMO, Oxford, South Tropical Africa, Zimbabwe: Salisbury, Mashonaland; S 17.793643, E 31.073322; 1524 meters, November 11, 1905; Marshall, Guy

Morphopoides madagascariensis Günther, 1939, 1 ♂ paratype, SMTD, Dresden, Western Indian Ocean, Madagascar: southwest, Ambovomne; S 25.170772, E 46.089206, January 01, 1901 to December 31, 1901; J. Decorse; 1 ♂ holotype, MNHN, Paris, Western Indian Ocean, Madagascar: Nossi Bé, Sambirano

Morphopoides tessmanni Günther, 1939, 1 ♂ holotype, MfN, West-Central Tropical Africa, Central African Republic: Bosum [Bozoum], Ouham river area; N 6.316700, E 16.383300, April 17, 1914; G. Tessmann; 1 ♀ paratype, MfN, West Tropical Africa, Togo: Kete-Kratji, October 01, 1900 to October 31, 1900; Mischlich.

***Morphopus* Bolívar, 1905**

Morphopus acmophylloides Günther, 1939, 1 ♀ syntype, SMTD, Dresden, West-Central Tropical Africa, Gabon: Mayumbe, Lundu; S 3.430400, E 10.652100, March 21, 1924; A. Collart; 1 ♀ syntype, MRAC, Tervuren KMMA, West-Central Tropical Africa, Zaire: Mayumbe, Bula Naku, August 22, 1924.

Morphopus phyllocerus (Bolívar, 1887), 1 ♀ holotype, NMW, Vienna Museum, West-Central Tropical Africa, Gabon, Higgins; 1 ♀ not a type, NBC, Leiden, West Tropical Africa, Nigeria: Oyakama (Port Harcourt); N 4.857687, E 7.013977, January 01, 1982 to January 31, 1982; Santini, L.

***Pantelia* Bolívar, 1887**

Pantelia horrenda (Walker, 1871), 1 ♀ holotype, BMNH, London NH Mus., West Tropical Africa, Sierre Leone; 1 ♀ not a type, MCSN, Genoa, West Tropical Africa, Guinea-Bissau: Bolama; N 11.141698, W 16.143133, June 01, 1899 to December 31, 1899; Fea, L.

***Seyidotettix* Rehn, 1938**

Seyidotettix swahili Rehn, 1939, 1 ♀ holotype, ANSP, Philadelphia, East Tropical Africa, Kenya: Seyidie Province, Mazeras; S 3.964400, E 39.547500, November 01, 1921 to November 30, 1921.

***Tettilobus* Hancock, 1909**

Tettilobus pelops (Walker, 1871), 1 ♂ holotype, BMNH, London NH Mus, Indian Subcontinent, Sri Lanka; 1 ♀ holotype of synonym *Tettilobus spinifrons* Hancock, 1909, UMO, Oxford, Indian Subcontinent, Sri Lanka.

Tettilobus prashadi Günther, 1938, 1 ♂ syntype, SMTD, Dresden, Indian Subcontinent, India, Kerala: Kavalai; N 10.000000, E 76.000000; 400 to 915 meters, September 24, 1914 to September 27, 1914; F.H. Gravely: 1 ♀ syntype, SMTD, Dresden, Indian Subcontinent, India, Kerala: Forest Tramway mile 10 to 14, September 28, 1914 to September 29, 1914; F.H. Gravely; 1 ♀ syntype, MHNG, Geneva Museum, Indian Subcontinent, India, Kerala: Forest Tramway mile 10 to 14, September 28, 1914 to September 29, 1914; F.H. Gravely.

Tettilobus trishula Skejo, Bhaskar & Stermšek, 2020, 1 ♀ holotype, MNCN, Madrid Mus., Indian Subcontinent, India: Western Ghats, P. Castets.

***Trachytettix* Stål, 1876**

Trachytettix alatus Bolívar, 1908, 1 ♂ not a type, MCSN, Genoa, West Tropical Africa, Guinea-Bissau: Bolama; N 11.141698, W 16.143133, June 01, 1899 to December 31, 1899; Fea, L.

Trachytettix scaberrimus scaberrimus Stål, 1876, 1 ♂ holotype, NHRS, Stockholm, Southern Africa, Namibia: Damaraland; S 22.253889, E 15.190833, De Vylder; 1 ♀ not a type, MCSN, Genoa, East Tropical Africa, Uganda: Bussu Busoga, May 01, 1909 to May 31, 1909; Bayon, E.

***Trypophyllum* Karsch, 1890**

Trypophyllum glabrifrons Karsch, 1890, 1 ♂ holotype, MfN, West-Central Tropical Africa, Zaire: Democratic Republic of Congo, between Kwako and Kimpoko.

***Xerophyllum* Fairmaire, 1846**

Xerophyllum cortices Buckton, 1903, 1 ♂ holotype of synonym *Xerophyllum minor* Buckton, 1903, BMNH, London NH Mus., West Tropical Africa, Nigeria: Rio Nigro, Ogruga; 1 ♀ syntype, BMNH, London NH Mus., West Tropical Africa, Nigeria: Rio Nigro, Ogruga.

Xerophyllum platycorys platycorys (Westwood, 1839), 1 ♂ syntype, BMNH, London NH Mus., West Tropical Africa, Sierre Leone; 1 ♀ syntype, BMNH, London NH Mus., West Tropical Africa, Sierre Leone.

3.3.4. Cladonotinae genera with no tribal placement

***Afrolarcus* Günther, 1979**

Afrolarcus aequalis (Karsch, 1890), 1 ♂ holo type, MfN, West-Central Tropical Africa, Cameroon: Kribi; N 2.940500, E 9.906500.

Afrolarcus inaequalis (Karsch, 1890), 1 ♂ holotype, MfN, West-Central Tropical Africa, Cameroon: Kribi; N 2.940500, E 9.906500.

***Austrohancockia* Günther, 1938**

Austrohancockia kwangtungensis (Tinkham, 1936), 1 ♀ not a type, MfN; 1 ♂ not a type, ZIN, St. Petersburg, Lao Cai Prov., Sa Pa District, Fan Si Pan Mt., 22°18'59''N, 103°49'16''E, 1200 m, 12–25 May 1999, N. Orlov

Austrohancockia orlovi Storozhenko, 2016, 1 ♀ holotype, ZIN, St. Petersburg, Indo-China, Vietnam: Hai Duong Prov., Chi Linh District, near Chi Linh, October 01, 1997 to October 31, 1997; N. Orlov

Austrohancockia platynota platynota (Karny, 1915), 1 ♀ syntype, SDEI, SDEI Müncheberg, Eastern Asia, Taiwan: Sokutu, Banshoryo District, June 22, 1912, H. Sauter; 1 ♂ not a type, MfN, Eastern Asia, Taiwan: Chip Chip, H. Sauter

***Cota* Bolívar, 1887**

Cota saxosa Bolívar, 1887, 1 ♀ holotype, NMW, Vienna Museum, Western South America, Peru, Staudinger

***Epitettix* Hancock, 1907**

Epitettix dammermanni Günther, 1939, 1 ♀ holotype of, SMTD, Dresden, Malesia, Jawa: Idjen, Blawan; S 7.916700, E 112.916700; 950 meters, June 07, 1924; Dammermann

Epitettix emarginatus (Haan, 1843), 1 ♀ holotype of *Acridium (Tetrix) emarginatum* Haan, 1843, NBC, Leiden, Papuasia, New Guinea; 1 ♂ not a type, BPBM, Honolulu Museum, Papuasia, New Guinea, Irian Jaya: Vogelkop, Bomberi, June 06, 1959; T. C. Maa

Epitettix fatigans Günther, 1938, 1 ♂ holotype, MfN, Papuasia, New Guinea, Papua New Guinea: East Sepik, Lordberg; S 4.633333, E 142.616667, November 29, 1912 to November 30, 1912; S.G. Bürgers; 1 ♀ paratype, MfN, Papuasia, New Guinea, Papua New Guinea: Regenber; S 4.870100, E 144.107000; 550 meters, May 01, 1913 to May 31, 1913; S.G. Bürgers

Epitettix humilicolus Günther, 1938, 1 ♂ holotype, MfN, Papuasia, New Guinea, Papua New Guinea: East Sepik, main camp near Malu; S 4.233333, E 142.850000, March 01, 1912 to April 30, 1912; S.G. Bürgers; 1 ♀ not a type, MfN, Papuasia, New Guinea, Papua New Guinea: East Sepik, main camp near Malu; S 4.233333, E 142.850000, August 03, 1912; S.G. Bürgers; S.G. Bürgers.

Epitettix lativertex Günther, 1938, 1 ♀ holotype, MfN, Papuasia, New Guinea, Papua New Guinea: East Sepik, Lordberg; S 4.633333, E 142.616667, December 02, 1912 to December 04, 1912; S.G. Bürgers.

Epitettix obtusus Storozhenko & Dawwrueng, 2014, 1 ♀ holotype, ZIN, St. Petersburg, Indo-China, Thailand: Khao Yai National Park; N 14.295278, E 101.626111; 500 to 1000 meters, October 26, 2000 to November 04, 2000; A.V. Gorochoy & L.N. Anisyutkin.

Epitettix spheniscus Günther, 1974, 1 ♂ holotype, MNHN, Paris.

Epitettix tumidus Günther, 1938, 1 ♀ holotype, MfN, Papuasia, New Guinea, Papua New Guinea: East Sepik Province, Etappenberg; S 4.633333, E 142.466667; 800 meters, November 16, 1912 to November 18, 1912; S.G. Bürgers.

***Eurymorphopus* Hancock, 1907**

Eurymorphopus boliviensis Tumbrinck, 2014, 1 ♀ holotype, MHNG, Geneva Museum, Southwestern Pacific, New Caledonia; 2 ♀ 2 ♂ not a type, NBC, Leiden, Southwestern Pacific, New Caledonia: Nouméa; S 22.277583, E 166.446440, Fauvel.

Eurymorphopus cunctatus (Bolívar, 1887), 1 ♂ syntype, ISNB, Brussels, Southwestern Pacific, New Caledonia; 1 ♂ syntype, NMW, Vienna Museum, Southwestern Pacific, New Caledonia, Andrée.

Note: Syntypes have different levels of anterior protrusion of vertex. Needs to be investigated if the specimens belong to the same species of *E. cunctatus*.

Eurymorphopus dubius Günther, 1974, 1 ♂ holotype, BMNH, London NH Mus, Western Indian Ocean, Mauritius: Port Louis District, Le Pouce; S 20.202300, E 57.526000; 492 meters, January 05, 1935; Lawrence, R. F.

***Hippodes* Karsch, 1890**

Hippodes conradti Günther, 1938, 1 ♀ holotype, MfN, West-Central Tropical Africa, Cameroon: Johann Albrechtshöhe; N 4.653946, E 9.415133, January 01, 1896 to January 31, 1896; L. Conradt.

Hippodes vicarius Karsch, 1890, 1 ♀ syntype, MfN, West-Central Tropical Africa, Zaire: Democratic Republic of Congo, between Kwako and Kimpoko, R. Büttner; 1 ♀ not a type, MfN, West-Central Tropical Africa, Cameroon: Barombi Station; N 4.666700, E 9.383300, Preuss.

***Ichikawatettix* Tumbrinck, 2014**

Ichikawatettix exsertus (Günther, 1938), 1 ♀ holotype, MfN, Papuasia, New Guinea, Papua New Guinea: East Sepik Province, Etappenberg; S 4.633333, E 142.466667; 800 meters, November 02, 1912 to November 05, 1912; S.G. Bürgers; 1 ♂ not a type, MfN, Papuasia, New Guinea, Papua New Guinea: East Sepik Province, Etappenberg; S 4.633333, E 142.466667; 800 meters, November 02, 1912 to November 05, 1912; S.G. Bürgers.

Ichikawatettix kleinertae Tumbrinck, 2014, 1 ♀ holotype, BPBM, Honolulu Museum, Papuasia, New Guinea, Irian Jaya: Bodem; S 1.966667, E 138.733333, July 07, 1959 to July 17, 1959; T.C. Maa; 1 ♂ not a type, ZFMK, Bonn, Papuasia, New Guinea, Irian Jaya: Bodem; S 1.966667, E 138.733333, July 07, 1959 to July 17, 1959; T.C. Maa.

***Ingrischitettix* Tumbrinck, 2014**

Ingrischitettix mountabilalaensis Tumbrinck, 2014, 1 ♂ holotype, BPBM, Honolulu Museum, Papuasias, New Guinea, Papua New Guinea: Morobe Prov., Finisterre Mts., Mt. Abilala; S 5.831678, E 146.173233; 2743 meters, November 19, 1964 to November 22, 1964; M.E. Bacchus; 1 ♀ paratype, BPBM, Honolulu Museum, Papuasias, New Guinea, Papua New Guinea: Morobe Prov., Finisterre Mts., Mt. Abilala; S 5.831678, E 146.173233; 2743 meters, November 19, 1964 to November 22, 1964; M.E. Bacchus.

***Microthymochares* Devriese, 1991**

Microthymochares pullus Devriese, 1991, 1 ♀ holotype, MNCN, Madrid Mus., Western Indian Ocean, Madagascar: Perinet; S 18.927913, E 48.414220, December 01, 1932 to December 31, 1932.

***Nesotettix* Holdhaus, 1909**

Nesotettix cheesmanae Günther, 1938, 1 ♀ holotype, BMNH, London NH Mus., Southwestern Pacific, New Caledonia: Bourail; S 21.567696, E 165.483970, December 01, 1930 to December 31, 1930; L.E. Cheesman.

Nesotettix samoensis Holdhaus, 1909, 1 ♀ holotype, NMW, Vienna Museum, Southwestern Pacific, Samoa, Samoa: Upolu; S 13.920898, W 171.747265, Reckinger.

***Pelusca* Bolívar, 1912**

Pelusca schoutedeni Günther, 1939, 1 ♀ paratype, SMTD, Dresden, West-Central Tropical Africa, Zaire: Tshuapa, Yolo; S 0.558682, E 21.829727, June 01, 1937 to June 30, 1937; Buckinck.

***Planotettix* Tumbrinck, 2014**

Planotettix buergersi Tumbrinck, 2014, 1 ♂ holotype, MfN, Papuasia, New Guinea, Papua New Guinea: East Sepik Province, Quellenlager; S 4.383333, E 142.783333; 980 meters, August 13, 1912 to August 16, 1912; S.G. Bürgers; 1 ♂ paratype, ZFMK, Bonn, Papuasia, New Guinea, Papua New Guinea: East Sepik Province, Wewak; S 3.583800, E 143.656900; 2 to 30 meters, October 13, 1957; J. L. Gressitt.

Planotettix planus Tumbrinck, 2014, 1 ♂ holotype, BPBM, Honolulu Museum, Papuasia, New Guinea, Papua New Guinea: Telefomin; S 4.133333, E 141.583333; 1700 meters, August 08, 1963; R. Straatman.

***Pseudepitettix* Zheng, 1995**

Pseudepitettix pimkarnae Storozhenko & Dawwrueng, 2014, 1 ♀ holotype, Kasetsart, Indo-China, Thailand: Saraburi Province, environs of Wat Phra Phutthabat; N 14.717900, E 100.789300; 50 to 150 meters, July 06, 2013; P. Dawwrueng & P. Pawangkhanant.

Pseudepitettix torulosinota (Zheng & Lin, 2016), 1 ♀ holotype, Shaanxi Normal, China, China South-central, Yunnan: Cangyuan (Mengleng); N 23.723324, E 99.264247, April 18, 2012; Chunchang Li.

***Pseudohyboella* Günther, 1938**

Pseudohyboella weylandiana Günther, 1938, 1 ♀ holotype, MfN, Papuasia, New Guinea, Irian Jaya: Weyland Mountains; S 3.871518, E 135.871134; 1500 meters, January 01, 1931 to December 31, 1931; G. Stein; 1 ♂ not a type, BPBM, Honolulu MuseumPapuasia, New Guinea, Irian Jaya: S Geelvink Bay, Nabire; S 3.366667, E 135.483333; 0 to 30 meters, July 02, 1962 to July 09, 1962; J. L. Gressitt.

***Stegaceps* Hancock, 1913**

Stegaceps brevicornis Hancock, 1913, 1 ♀ holotype, ANSP, Philadelphia, Malesia, Borneo, Sarawak: Kabong; N 1.813994, E 111.121040, June 01, 1900 to June 30, 1900.

***Tepperotettix* Rehn, 1952**

Tepperotettix reliqua Rehn, 1952, 1 ♀ holotype, MCZ, Harvard, Australia, New South Wales, New South Wales: McPherson Range, National Park; S 28.372080, E 153.037404; 914 to 1219 meters, March 11, 1932; P.J. Darlington; 1 ♀ not a type, AMS, Sydney, Australia, Queensland: Mt. Tambourine; S 27.880000, E 153.180000, December 20, 1961; McAlpine & Lossin; 1 ♂ not a type, MHNG, Geneva Museum, Australia, Queensland: McPherson Range, Lamington National Park, Mt. Merino; S 28.250000, E 153.200000; 1050 to 1100 meters, January 06, 1992; D. Burckhardt.

***Tetradinodula* Zha, 2017**

Tetradinodula bambusae Zha, 2017, 1 ♀ holotype, Huaibei, China, China South-central, Guizhou: Tongzi County, Baiqing Nature Reserve; N 28.869972, E 107.047739; 1906 meters, July 16, 2016; Ling-Sheng Zha.

***Thymochares* Rehn, 1929**

Thymochares exiguus Günther, 1974, 1 ♂ holotype, MNHN, Paris, Western Indian Ocean, Madagascar: Sambava-Distrikt, massif du Marojejy, Beodroka; 1200 meters, June 01, 1960 to June 30, 1960; P. Soga.

Thymochares galeatus Rehn, 1929, 1 ♀ holotype, BMNH, London NH Mus., Western Indian Ocean, Madagascar: Ambohimombo; S 20.716667, E 47.433333, January 01, 1894 to December 31, 1894; Forsyth-Major.

***Tondanotettix* Willemse, 1928**

Tondanotettix brevis (Haan, 1843), 1 ♀ holotype NBC, Leiden, Malesia, Sulawesi: Tondano; N 1.320536, E 124.942238.

Tondanotettix modestus Günther, 1937, 1 ♂ holotype, MfN, Malesia, Sulawesi: Ile Ile; 500 meters, November 01, 1930 to December 31, 1930; G. Heinrich.

***Tuberfemurus* Zheng, 1992**

Tuberfemurus kanokwanae Storozhenko & Dawwrueng, 2014, 1 ♂ not a type, Coll. Tumbrinck, Indo-China, Thailand: Lampang, Doi Khun Tan; N 18.483333, E 99.300000; 900 to 950 meters, September 17, 1993; Ingrisich, S.

***Willemsetettix* Tumbrinck, 2014**

Willemsetettix missai Tumbrinck, 2014, 1 ♀ holotype, ISNB, Brussels, Papuasia, New Guinea, Papua New Guinea: Madang, Baiteta; S 5.016667, E 145.750000; 57 meters, July 06, 1995; Olivier Missa; 1 ♂ paratype, BPBM, Honolulu Museum, Papuasia, New Guinea, Papua New Guinea: Madang Province, Madang (Alpinia); S 5.216667, E 145.800000; 5 meters, October 28, 1958; J. L. Gressitt.

Willemsetettix willemsei Tumbrinck, 2014, 1 ♂ holotype, BPBM, Honolulu Museum, Papuasia, New Guinea: 40 km W of Jayapura [Hollandia], Genjam; S 2.766667, E 140.200000; 100 to 200 meters, March 01, 1960 to March 10, 1960; T.C. Maa

3.3.5. Subfamily Batrachideinae Bolívar, 1887

3.3.5.1. tribe Bufonidini Hancock, 1907

***Anaselina* Storozhenko, 2019**

Anaselina minor (Sjöstedt, 1921), 1 ♀ holotype, NHRS, Stockholm, Australia, Queensland: Herberton; S 17.377000, E 145.376600, Mjöberg

***Bufonides* Bolívar, 1898**

Bufonides antennatus Bolívar, 1898, 1 ♂ holotype, MCSN, Genoa, Papuasia, New Guinea, Papua New Guinea: Fly River; 1 ♀ paralectotype, MCSN, Genoa, Papuasia, New Guinea, Papua New Guinea: Fly River, January 01, 1876 to December 31, 1877; L. M. D'Albertis; 1 ♀ paralectotype, MNCN, Madrid Mus., Papuasia, New Guinea, Irian Jaya: Paumomu River, Loria, November 01, 1892 to December 31, 1892. Notes: 1 ♂ holotype should be labeled as lectotype on OSF.

Bufonides sellatus Hinton, 1940, 1 ♀ holotype, BMNH, London NH Mus., Papuasia, New Guinea: Humbolt Bay, Pukusam District, West of Tami River, June 01, 1937 to June 30, 1937; W. Stüber; 1 nymph not a type, MfN, Papuasia, New Guinea, Papua New Guinea: Regenber; S 4.870100, E 144.107000; 550 meters, May 08, 1913 to May 15, 1913; S.G. Bürgers; 1 ♀ paratype, BMNH, London NH Mus., Papuasia, New Guinea: Humbolt Bay, Pukusam District, West of Tami River, June 01, 1937 to June 30, 1937; W. Stüber

Bufonides uvarovi Hinton, 1940, 1 ♂ holotype, BMNH, London NH Mus., Papuasia, New Guinea, Papua New Guinea: Kokoda; S 8.877778, E 147.737500; 360 to 400 meters, June 01, 1933 to June 30, 1933; L.E. Cheesman; 1 ♀ paratype, BMNH, London NH Mus., Papuasia, New Guinea, Papua New Guinea: Kokoda; S 8.877778, E 147.737500; 360 to 400 meters, October 01, 1933 to October 30, 1933; L.E. Cheesman

***Paraselina* Storozhenko, 2019**

Paraselina brunneri (Bolívar, 1887), 1 ♀ lectotype, NMW, Vienna Museum, Australia, New South Wales, New South Wales: Sydney; S 33.880433, E 151.207547, Frauenfeld

***Vingselina* Sjöstedt, 1921**

Vingselina crassa Sjöstedt, 1921, 1 ♀ holotype, NHRS, Stockholm, Australia, Queensland, Queensland: Colosseum; S 24.369428, E 151.543630, Mjöberg

3.3.6. Subfamily Tetriginæ Rambur, 1838

***Coptottigia* Bolívar, 1912**

Coptottigia cristata Bolívar, 1912, 1 ♀ syntype, BMNH, London NH Mus., Western Indian Ocean, Seychelles: Mahé Island; S 4.666700, E 55.466700, May 01, 1905 to December 31, 1905; Gardiner, J. S.; 1 ♂ syntype, BMNH, London NH Mus., Western Indian Ocean, Seychelles: Mahé Island; S 4.666700, E 55.466700

3.3.7. Subfamily Metrodorinae Bolívar, 1887

***Hildegardia* Günther, 1974**

Hildegardia mauritiicola Günther, 1974, 1 ♂ holotype, BMNH, London NH Mus., Western Indian Ocean, Mauritius: Les Mares, December 30, 1934; Lawrence, R. F.; 1 ♀ allotype, BMNH, London NH Mus., Western Indian Ocean, Mauritius: Les Mares, December 30, 1934; Lawrence, R. F.

Hildegardia mauritiivaga Günther, 1974, 1 ♀ holotype, BMNH, London NH Mus., Western Indian Ocean, Mauritius: Port Louis District, Le Pouce; S 20.202300, E 57.526000; 492 meters, January 05, 1935; Lawrence, R. F.; 1 ♂ allotype, BMNH, London NH Mus., Western Indian Ocean, Mauritius: Port Louis District, Le Pouce; S 20.202300, E 57.526000; 492 meters, January 05, 1935; Lawrence, R. F.

3.3.8. Subfamily Scelimeninae Bolívar, 1887

***Scelimena* Serville, 1838**

subspecies *Scelimena producta producta* (Serville, 1838), 1 ♀ holotype, MNHN, Paris, Malesia, Jawa; 1 ♀ not a type, MfN, Malesia, Jawa: Soekaboemi [Sukabumi]; S 6.933900, E 106.918300, January 01, 1893 to December 31, 1893; H. Fruhstorfer; 1 ♂ not a type, MfN, Malesia, Jawa: Soekaboemi [Sukabumi]; S 6.933900, E 106.918300, January 01, 1893 to December 31,

1893; H. Fruhstorfer.

Notes: specimens collected in 1893 were identified by K. Günther.

3.4. Software and hardware used for cladistic analysis

Cladograms were made in Mesquite version 3.6 (build 917) and iTOL v6 (Interactive Tree Of Life) an online tool for the display, annotation and management of phylogenetic and other trees.

Figures depicting specimens were altered using MSPaint version 6.3.

The Computer used was laptop Acer Aspire V17 Nitro—Intel® Core™ i5-4210H Processor 2.90 GHz, 8,00 GB RAM. Specifications are given to clarify the methodology in the section below (section 3.4.).

3.5. Methodology for obtaining the cladograms

Character matrix (Fig. 27. and 28.) was obtained by filling in an empty matrix in Microsoft Excel. Microsoft Excel was used due to it being the simplest and most elegant solution for handling a great amount of data in the shape of matrix at once. Matrix consists of the first column having all of the species of Cladonotinae all of which have their dedicated row. Each subsequent column corresponds to one character which then with each of it's rows correspond to each species' row, thus making matrix of species' characters. Then, by carefully analyzing photographs of specimens and writing states of characters (see Table 1. and section 3.1.) I filled the matrix with states for each character used for each species. If available, multiple specimens (section 3.3.) were consulted in order to decrease the chances of any ambiguity of characters seen in the photographs. When the matrix was filled, the next step was exporting the matrix to Mesquite. It was done by firstly making the empty matrix in Mesquite consisting of 118 species (rows) and 99 characters (columns). Species names were then copied from the Excel and pasted to the first column of Mesquite matrix. States of characters were copied from the Excel to the Mesquite matrix thus filling the whole matrix with the character data. Matrix in Mesquite was then translated to cladograms in the following way: Analysis > Tree Inference > Cluster Analysis. As a source of distances in cluster analysis the distances from character matrix were chosen. Uncorrected distances were chosen as a way to calculate the distances from character matrix. This was done because other options for calculating the distances are used for other types of data (DNA and protein data). The clustering method chosen

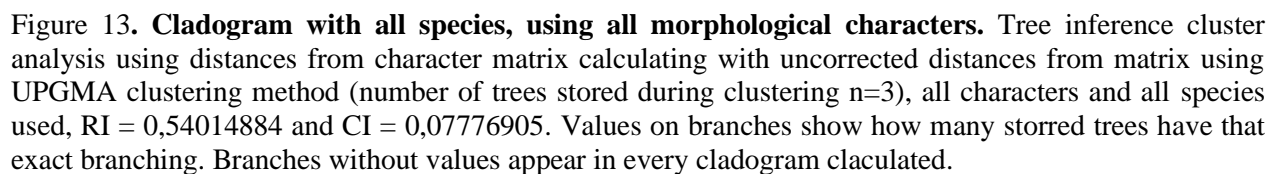
was UPGMA. Maximum number of equally good stored trees was set to a maximum value which my laptop (see section 3.3.) could calculate. Number of trees stored ranged from 3 to 20,000, depending on the complexity of the matrix. The highest number of trees the laptop could calculate was used in making cladograms, with the upper limit of 20,000 which was not exceeded due to lack of additional informativeness when increasing given number of the trees stored. When the trees were calculated, node values were set to display frequency of branchings in stored trees. RI and CI were then calculated by clicking on Analysis:Tree > Values for Current tree... > choosing Consistency index and Retention index for matrix. Ancestral states were obtained by clicking on Analysis:Tree > Trace Character History > Parsimony Ancestral States. Reconstructions of ancestral states on the trees are given in the Supplement. Trees were then exported in Newick's format and displayed in iTOL.

3.6. Methodology for obtaining Figures 24. and 25. (variability of tarsal pulvilli and FM projection)

I examined all available photographs of all 256 living species of Cladonotinae from OSF and cropped the desired morphological traits into collage depicting just a portion of true variability of those characters. Tarsal pulvilli and FM projections showed in Figures 24. and 25. were chosen on the basis of having more prominent traits showing the extremes of every distinct attribute of those characters. By showing noticeable and recognizable differences of those characters between a few species, I was able to adequately demonstrate the variability of these characters of the whole subfamily to just 2 figures.

4. Results

Fig. 13.-21. show cladograms obtained by analysing species' characters as described in section 3. Materials and methods. Cladograms in Fig. 14.-20. were obtained primarily for their RI and CI value (Table 5.), while cladogram in Fig. 13. (equivalent to cladogram in Fig. 21.) was obtained also for its topology. Cladogram in Fig. 21. shows taxonomy of species by color-coding specific tribes and subfamilies. Those results were thoroughly discussed in section 5. Discussion.



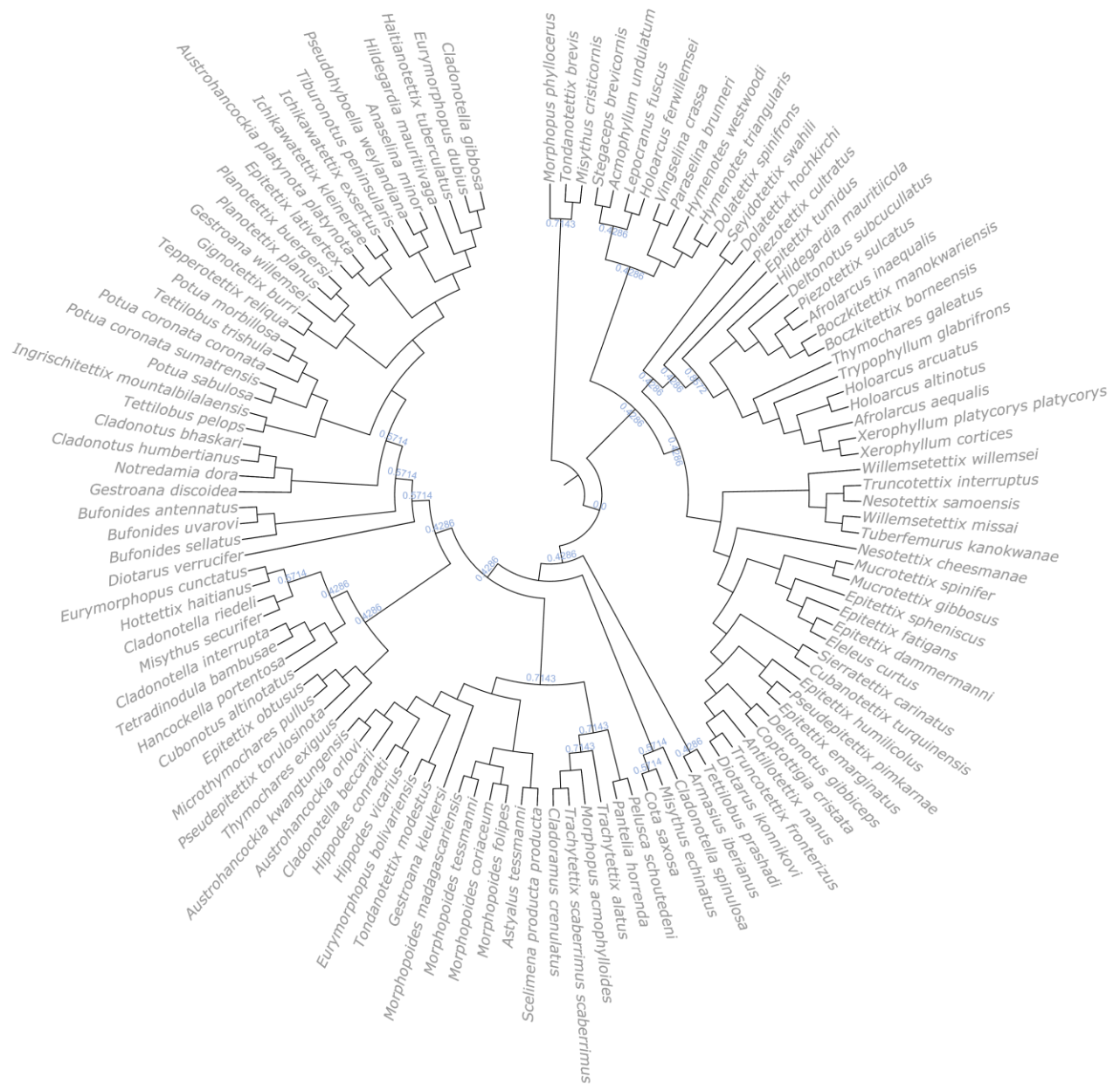


Figure 16. **Cladogram with all species, using only pronotum characters.** Tree inference cluster analysis using distances from character matrix calculating with uncorrected distances from matrix using UPGMA clustering method (number of trees stored during clustering $n=7$), only pronotum characters were used, all species used, $RI = 0,60273973$ and $CI = 0,09156627$. Values on branches show how many stored trees have that exact branching. Branches without values appear in every cladogram calculated.

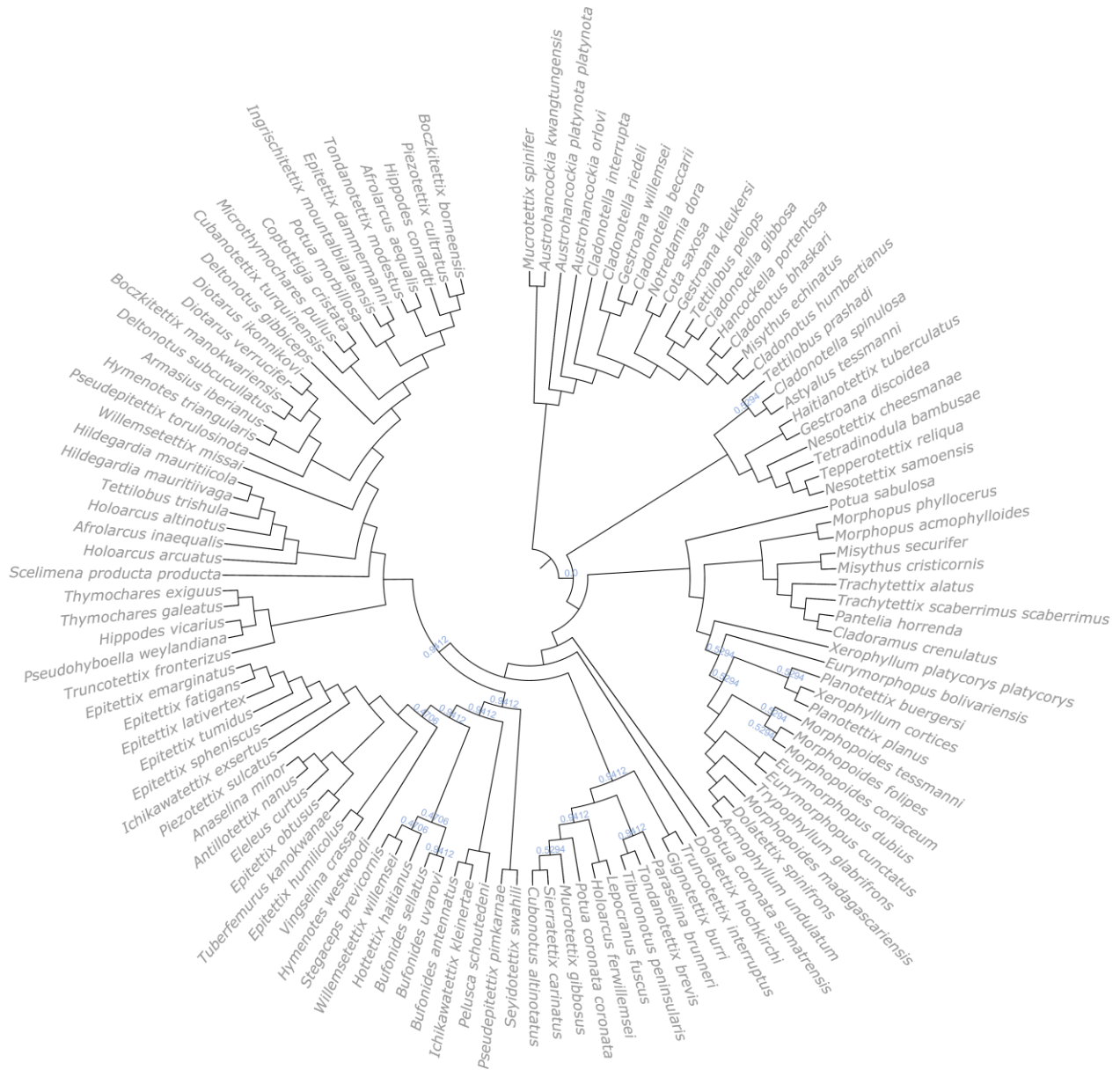


Figure 17. **Cladogram with all species, using only leg characters.** Tree inference cluster analysis using distances from character matrix calculating with uncorrected distances from matrix using UPGMA clustering method (number of trees stored during clustering $n=17$), only leg characters were used, all species used, $RI = 0,73369565$ and $CI = 0,12107623$. Values on branches show how many stored trees have that exact branching. Branches without values appear in every cladogram calculated.

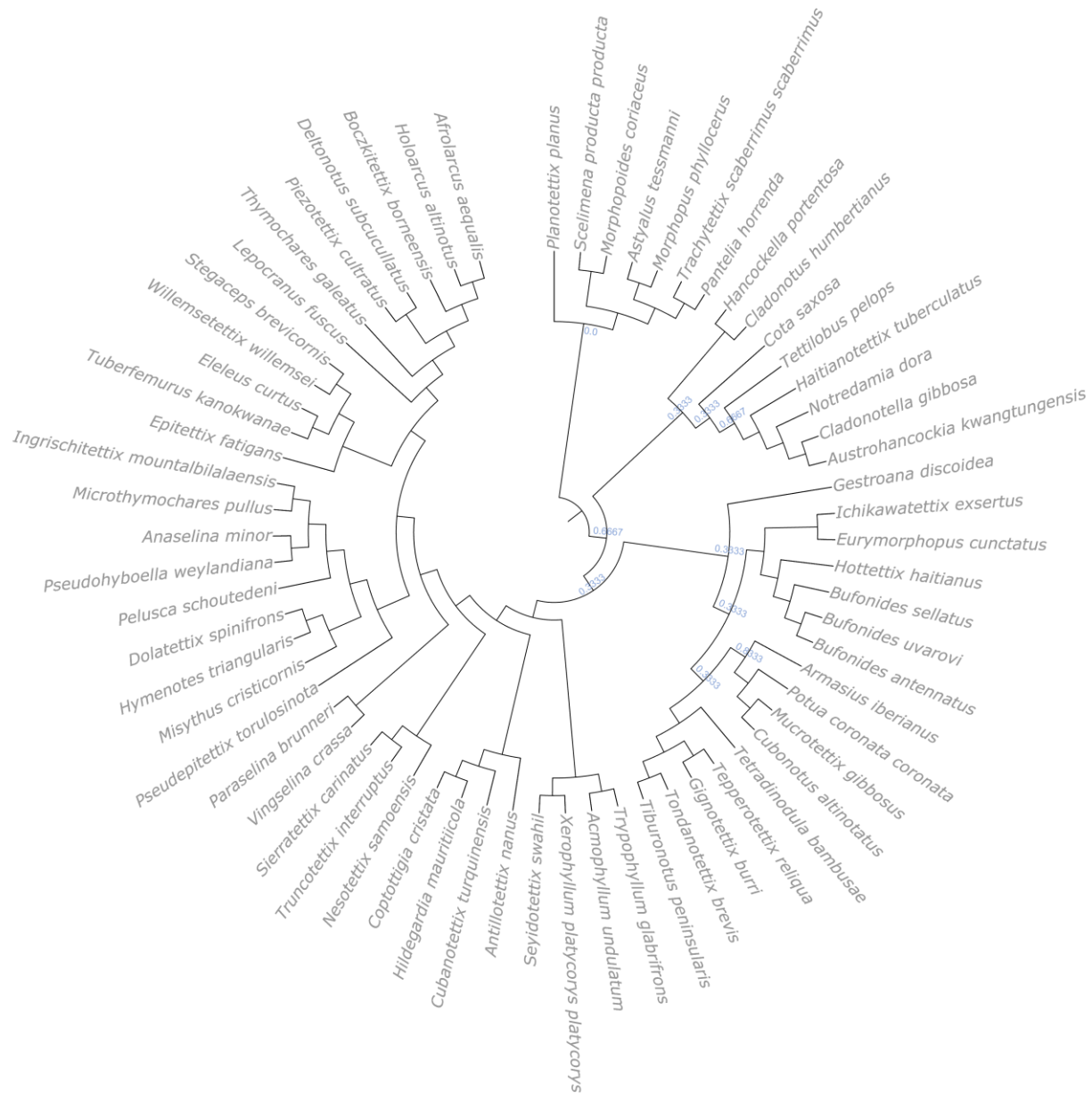


Figure 18. **Cladogram with only type species, using all morphological characters without projections.** Tree inference cluster analysis using distances from character matrix calculating with uncorrected distances from matrix using UPGMA clustering method (number of trees stored during clustering $n=100$), all characters without projections were used, type species used (*Epitettix fatigans* Günther, 1938 and *Pseudepitettix torulosinota* (Zheng & Lin, 2016) are not type species), $RI = 0,47323704$ and $CI = 0,12056738$. Values on branches show how many stored trees have that exact branching. Branches without values appear in every cladogram calculated.



Figure 19. **Cladogram with all apterous species out of South America, using all morphological characters without projections.** Tree inference cluster analysis using distances from character matrix calculating with uncorrected distances from matrix using UPGMA clustering method (number of trees stored during clustering $n=20000$), all characters without projections were used, type species used, species with tegmina except genus *Scelimena* omitted, South American species omitted, $RI = 0,47281713$ and $CI = 0,2039801$. Values on branches show how many many stored trees have that exact branching. Branches without values appear in every cladogram claculated.



Figure 20. **Cladogram with only type species, using all morphological characters.** Tree inference cluster analysis using distances from character matrix calculating with uncorrected distances from matrix using UPGMA clustering method (number of trees stored during clustering $n=4$), all characters were used, type species used (*Epitettix fatigans* Günther, 1938 and *Pseudepitettix torulosinota* (Zheng & Lin, 2016) are not type species), $RI = 0,47054323$ and $CI = 0,12515803$. Values on branches show how many stored trees have that exact branching. Branches without values appear in every cladogram calculated.

- subfamily Cladonotinae Bolívar, 1887 (including Cladonotinae genera without tribal placement)
- tribe Cladonotini Bolívar, 1887
- tribe Mucrotettigini Cadena-Castaneda & Silva, 2019
- tribe Xerophyllini Günther, 1979
- subfamily Batrachideinae Bolívar, 1887
- subfamily Metrodorinae Bolívar, 1887
- subfamily Tetriginae Rambur, 1838
- subfamily Scelimeninae Bolívar, 1887
- unassigned genera

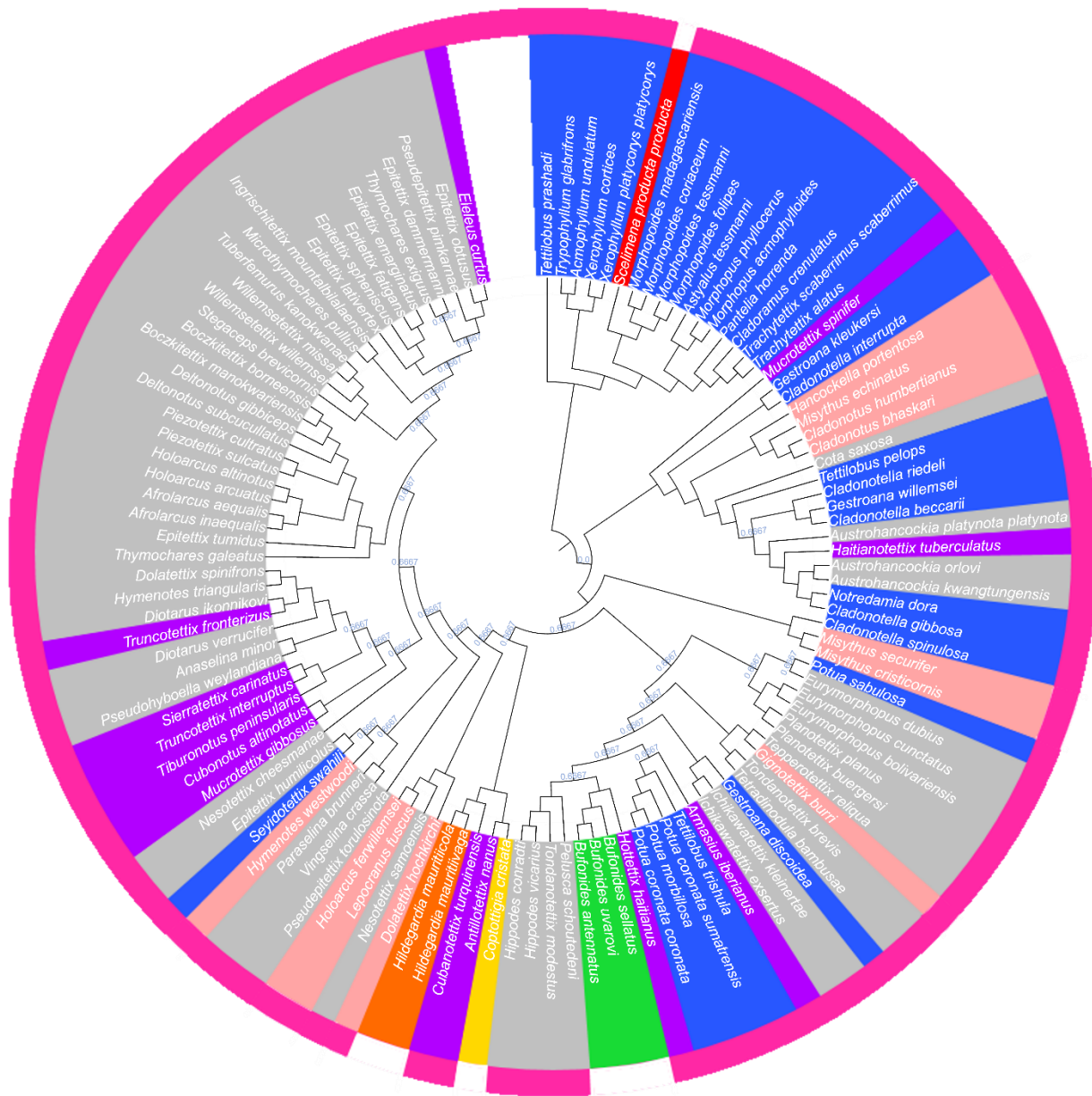


Figure 21. **Visualization of tribes and subfamilies on cladogram.** Cladogram topologically equivalent to cladogram on Fig 13. Tribes of Cladonotinae and other subfamilies shown to emphasise non-holophyly of Cladonotinae when making cladogram based on morphology—the basis for defining today's subfamilies.

Fig. 22. and Tables 2.-4. show how characters map on obtained cladogram (Fig 13.). Species bearing certain characetrts are shown with black squares denoting existance of that characters in that species. This result was obtained in order to discover which characters did computer program weighted more in forming clades.

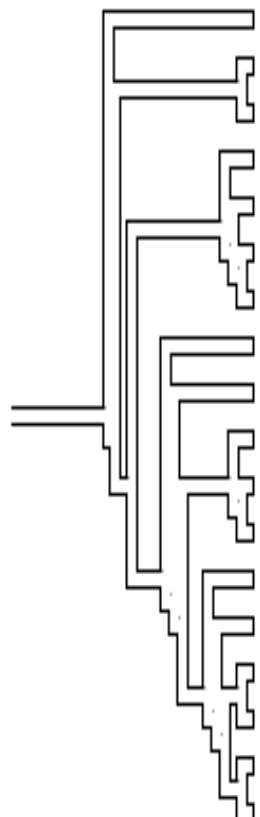


Figure 22. **Depiction of subsections of cladogram used to display character states of species on cladogram.** Division of cladogram (A) topologically equivalent to cladogram on Fig 13. for the purpose of presentation of results. Subsections (B-G) used to show results in Tables 2.-4. Red arrow on cladogram A points to place of splitting of cladogram into smaller subcladograms.

Table 2. **Combined visualisation of cladogram and states of head characters.** Table of head character states annotated on cladogram of the topology equivalent to the Fig 13. for the purpose of better visualization of characters based on which program grouped species into clades. Black squares denote state „1“ (existence) of character. The first row denotes number of characters of that column. Red color matches the color of characters in Table 1., meaning those are head characters.

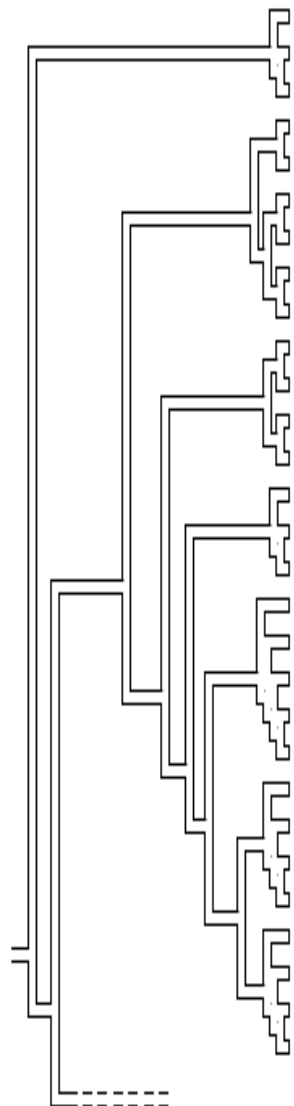
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>Tettilobus prashadi</i>																																
<i>Acmophyllum undulatum</i>																																
<i>Trypophyllum glabrifrons</i>																																
<i>Xerophyllum cortices</i>																																
<i>Xerophyllum platycorys platycorys</i>																																
<i>Scelimena producta producta</i>																																
<i>Morphopoides coriaceum</i>																																
<i>Morphopoides madagascariensis</i>																																
<i>Morphopoides folipes</i>																																
<i>Morphopoides tessmanni</i>																																
<i>Astyalus tessmanni</i>																																
<i>Morphopus acmophylloides</i>																																
<i>Morphopus phyllocerus</i>																																
<i>Pantelia horrenda</i>																																
<i>Cladoramus crenulatus</i>																																
<i>Trachytettix alatus</i>																																
<i>Trachytettix scaberrimus scaberrimus</i>																																

Table 2. (continued) **Combined visualisation of cladogram and states of head characters.**



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>Mucrotettix spinifer</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Cladonotella interrupta</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Gestroana kleukersi</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Hancockella portentosa</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Misythus echinatus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Cladonotus bhaskari</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Cladonotus humbertianus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Cota saxosa</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Tettilobus pelops</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Cladonotella riedeli</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Cladonotella beccarii</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Gestroana willemsei</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Austrohancockia platynota platynota</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Haitianotettix tuberculatus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Austrohancockia kwangtungensis</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Austrohancockia orlovi</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Cladonotella gibbosa</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Notredamia dora</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■

Table 2. (continued) **Combined visualisation of cladogram and states of head characters.**



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>Cladonotella spinulosa</i>			■	■	■			■		■	■			■								■		■	■		■	■	■	■	■	■
<i>Misythus cristicornis</i>			■	■	■		■	■		■	■			■	■					■		■		■	■		■	■	■	■	■	■
<i>Misythus securifer</i>			■	■	■			■		■	■			■	■							■		■	■		■	■	■	■	■	■
<i>Eurymorphopus dubius</i>		■	■							■			■		■		■	■			■	■			■	■				■		■
<i>Potua sabulosa</i>			■							■		■		■	■		■	■	■		■		■		■	■	■		■	■	■	■
<i>Eurymorphopus bolivariensis</i>			■	■	■							■		■				■		■	■					■		■		■	■	
<i>Eurymorphopus cunctatus</i>			■	■	■							■		■				■		■	■					■		■		■	■	
<i>Planotettix buergersi</i>			■	■									■	■	■		■	■		■	■					■		■		■		■
<i>Planotettix planus</i>				■						■			■	■	■		■	■		■	■					■		■		■		■
<i>Gignotettix burri</i>		■	■	■	■			■		■		■		■	■			■		■	■			■	■	■		■	■	■	■	■
<i>Tepperotettix reliqua</i>		■	■	■	■					■			■	■	■			■	■	■	■					■		■	■	■	■	■
<i>Tetradinodula bambusae</i>			■							■		■		■	■		■	■		■	■				■	■		■		■	■	■
<i>Tondanotettix brevis</i>			■	■	■					■			■	■	■		■	■		■	■				■	■	■		■	■	■	■
<i>Gestroana discoidea</i>		■	■	■	■								■	■	■		■	■		■				■	■	■	■		■	■	■	■
<i>Ichikawatettix exsertus</i>			■	■	■								■	■	■			■		■				■	■		■				■	
<i>Ichikawatettix kleinertae</i>			■	■	■								■	■	■		■	■		■				■	■		■		■		■	
<i>Armasius iberianus</i>			■	■	■					■		■		■	■			■		■	■				■	■	■		■	■	■	■
<i>Tettilobus trishula</i>			■	■	■					■			■	■	■	■		■		■				■	■	■		■		■		■
<i>Potua coronata coronata</i>			■	■	■		■			■		■		■	■			■		■	■				■	■	■		■	■	■	■
<i>Potua coronata sumatrensis</i>			■	■	■		■					■		■	■			■		■	■				■	■	■		■	■	■	■
<i>Potua morbillosa</i>			■	■	■		■					■		■	■			■		■	■				■	■	■		■	■	■	■
<i>Hottettix haitianus</i>			■	■	■		■	■		■	■			■	■					■	■				■	■		■	■	■	■	■
<i>Bufonides sellatus</i>			■	■	■							■		■	■		■			■		■	■		■	■		■	■	■	■	■
<i>Bufonides antennatus</i>			■	■	■							■		■	■		■			■	■			■	■		■	■	■	■	■	■
<i>Bufonides uvarovi</i>			■	■	■							■		■	■		■			■	■			■	■		■	■	■	■	■	■
<i>Pelusca schoutedeni</i>		■	■	■		■				■	■			■	■		■					■		■	■	■		■	■	■	■	■
<i>Tondanotettix modestus</i>			■	■		■				■		■		■			■	■		■	■				■	■		■	■	■	■	■
<i>Hippodes conradti</i>		■	■	■	■	■				■		■		■	■		■	■				■		■	■		■	■	■	■	■	■
<i>Hippodes vicarius</i>		■	■	■	■	■				■	■			■	■		■	■				■		■	■		■	■	■	■	■	■

Table 2. (continued) **Combined visualisation of cladogram and states of head characters.**

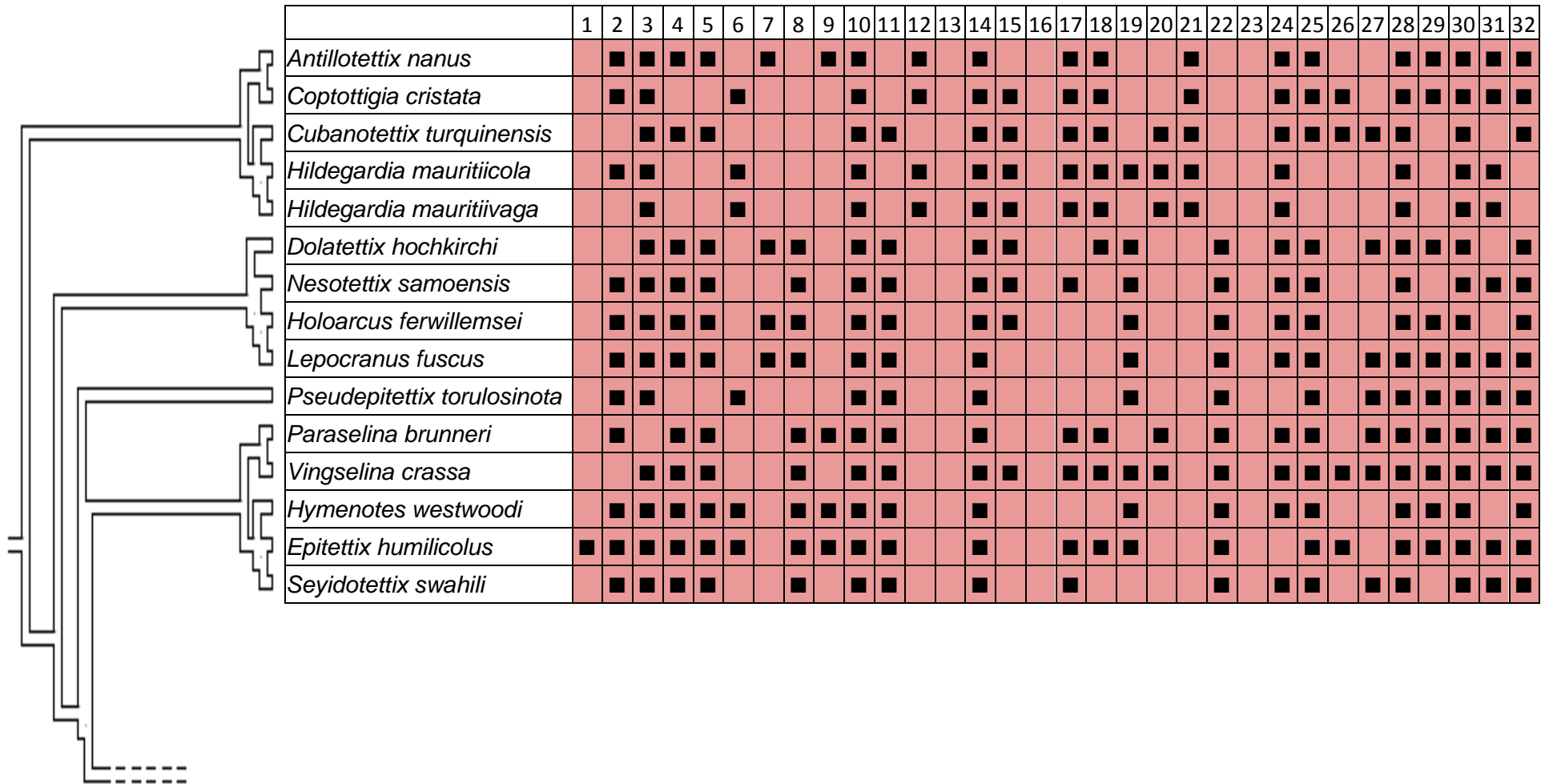
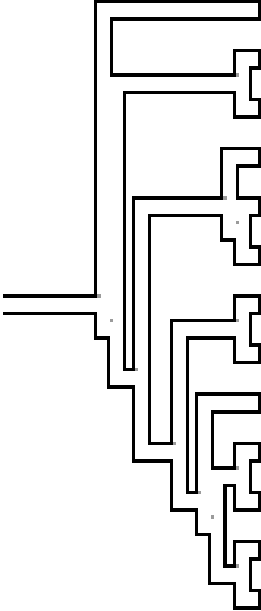
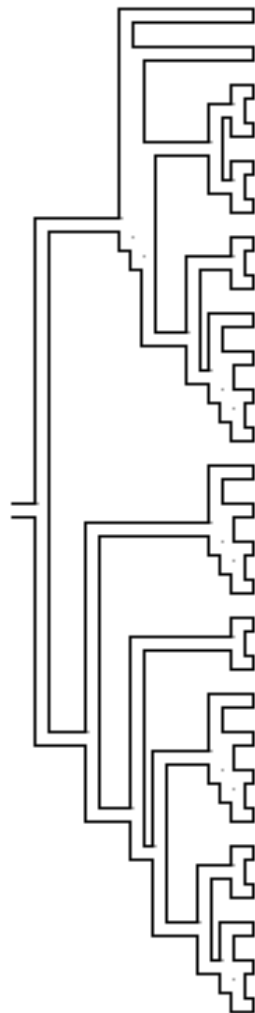


Table 2. (continued) **Combined visualisation of cladogram and states of head characters.**



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>Nesotettix cheesmanae</i>			■	■	■			■			■			■					■			■		■	■		■	■	■	■	■	■
<i>Cubonotus altinotatus</i>			■	■	■			■			■			■	■				■	■		■			■	■	■	■	■	■		■
<i>Mucrotettix gibbosus</i>			■	■	■			■			■			■	■				■		■	■		■	■			■	■	■		■
<i>Tiburonotus peninsularis</i>			■	■	■			■				■		■					■		■	■		■	■		■	■	■	■		■
<i>Sierratettix carinatus</i>			■	■	■			■		■		■		■	■			■	■	■	■		■	■	■		■	■	■	■	■	■
<i>Truncotettix interruptus</i>			■	■	■			■		■		■		■	■							■		■	■		■	■	■	■		■
<i>Anaselina minor</i>			■	■	■			■		■	■			■					■	■		■			■			■	■	■	■	■
<i>Pseudohyboella weylandiana</i>			■	■	■		■	■		■	■			■	■				■	■		■		■	■	■			■	■	■	■
<i>Diotarus verrucifer</i>			■	■	■		■	■		■	■			■					■			■		■	■		■	■	■	■		■
<i>Diotarus ikonnikovi</i>			■	■	■		■	■		■	■			■					■			■		■		■	■	■	■	■		■
<i>Truncotettix fronterizus</i>			■	■	■			■		■	■			■					■	■		■		■	■		■	■	■	■		■
<i>Dolatettix spinifrons</i>			■	■	■			■			■			■								■		■	■		■	■	■	■	■	■
<i>Hymenotes triangularis</i>			■	■	■	■		■		■	■			■					■			■			■		■	■	■	■	■	■

Table 2. (continued) **Combined visualisation of cladogram and states of head characters.**



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>Thymochares galeatus</i>		■	■			■				■	■			■	■		■	■	■			■			■			■	■	■	■	■
<i>Epitettix tumidus</i>	■	■	■	■	■	■		■		■	■			■					■			■						■	■	■	■	■
<i>Afrolarcus aequalis</i>		■	■	■	■	■		■	■	■	■			■					■			■		■	■			■	■	■	■	■
<i>Afrolarcus inaequalis</i>		■	■	■	■	■		■	■	■	■			■					■			■		■	■			■	■	■	■	■
<i>Holoarcus altinotus</i>		■	■	■	■	■		■		■	■			■				■	■			■		■	■			■	■	■	■	■
<i>Holoarcus arcuatus</i>		■	■	■	■	■		■		■	■			■					■			■		■	■			■	■	■		■
<i>Piezotettix cultratus</i>			■	■	■		■	■		■	■			■					■			■				■	■	■	■	■	■	■
<i>Piezotettix sulcatus</i>			■	■	■	■		■		■	■			■					■			■				■		■	■	■	■	■
<i>Deltonotus subcucullatus</i>		■	■	■	■		■	■		■	■			■			■	■	■			■			■			■	■	■		■
<i>Deltonotus gibbiceps</i>		■	■	■	■		■			■	■			■	■			■	■			■			■	■	■	■	■	■		■
<i>Boczkitettix borneensis</i>			■	■	■		■			■	■			■	■			■	■			■			■	■		■	■	■	■	■
<i>Boczkitettix manokwariensis</i>		■	■	■	■		■	■		■	■			■	■			■	■			■			■	■		■	■	■	■	■
<i>Stegaceps brevicornis</i>			■	■	■					■	■			■	■			■	■	■		■			■			■	■	■	■	■
<i>Willemsetettix willemsei</i>			■	■	■		■	■		■	■			■	■			■		■		■		■	■	■		■	■	■	■	■
<i>Tuberfemurus kanokwanae</i>		■	■	■	■		■			■	■			■	■					■	■			■	■	■		■	■	■		■
<i>Willemsetettix missai</i>		■	■	■	■	■				■	■			■	■				■	■	■		■		■	■	■		■	■	■	■
<i>Ingrischitettix mountabilalaensis</i>		■	■	■	■					■	■			■	■		■	■	■	■	■			■	■			■	■		■	■
<i>Microthymochares pullus</i>		■	■	■	■		■			■	■			■	■		■	■	■	■	■	■			■			■	■	■	■	■
<i>Epitettix lativertex</i>	■		■	■	■		■			■	■			■	■		■	■	■	■		■			■			■	■	■	■	■
<i>Epitettix spheniscus</i>		■	■	■	■		■			■	■			■	■		■	■	■	■		■			■			■		■	■	■
<i>Epitettix emarginatus</i>		■	■	■	■	■				■	■			■	■		■	■	■			■			■			■				■
<i>Epitettix fatigans</i>	■	■	■	■	■	■				■	■			■	■		■	■	■	■		■			■	■		■	■	■	■	■
<i>Epitettix dammermanni</i>		■	■	■	■	■		■		■	■			■	■		■	■	■			■			■	■		■			■	■
<i>Thymochares exiguus</i>		■	■	■		■				■	■			■	■		■	■	■			■			■	■		■	■	■	■	■
<i>Pseudepitettix pimkarnae</i>		■	■	■	■	■		■		■	■			■	■			■	■	■		■			■		■		■	■	■	■
<i>Eleleus curtus</i>		■	■	■	■		■			■	■			■	■					■		■		■	■			■	■	■	■	■
<i>Epitettix obtusus</i>		■	■	■	■	■				■	■			■	■		■	■		■		■		■	■			■	■	■	■	■

Table 3. **Combined visualisation of cladogram and states of pronotum characters.** Table of pronotum character states annotated on cladogram of the topology equivalent to the Fig 13. for the purpose of better visualization of characters based on which program grouped species into clades. Black squares denote state „1“ (existence) of character. The first row denotes number of characters of that column. Blue color matches the color of characters in Table 1., meaning those are pronotum characters.

		3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	7		
		3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
	<i>Tettilobus prashadi</i>	■	■	■		■				■		■	■			■						■								■							■		
	<i>Acmophyllum undulatum</i>				■	■	■		■	■		■	■	■	■							■								■									
	<i>Trypophyllum glabrifrons</i>					■			■	■	■			■	■							■																■	
	<i>Xerophyllum cortices</i>					■	■		■	■	■			■			■					■								■								■	
	<i>Xerophyllum platycorys platycorys</i>					■	■		■	■	■			■			■					■								■								■	
	<i>Scelimena producta producta</i>	■	■	■	■	■	■	■	■	■		■	■			■						■	■	■	■					■		■							
	<i>Morphopoides coriaceum</i>	■	■	■		■	■	■	■	■		■				■						■	■	■	■					■		■							
	<i>Morphopoides madagascariensis</i>	■	■	■	■	■	■	■	■	■		■				■						■	■	■	■					■									
	<i>Morphopoides folipes</i>	■	■	■		■	■	■	■	■		■			■							■	■	■	■					■		■							
	<i>Morphopoides tessmanni</i>	■	■	■		■	■		■	■		■				■						■	■	■	■					■									
	<i>Astyalus tessmanni</i>		■	■	■	■	■	■	■	■		■	■		■							■	■	■	■					■									
	<i>Morphopus acmophylloides</i>		■	■	■		■		■	■		■	■		■							■	■							■		■							
	<i>Morphopus phyllocerus</i>	■	■	■	■	■		■	■		■	■		■								■	■	■	■	■	■	■			■	■	■						
	<i>Pantelia horrenda</i>		■	■	■		■		■	■		■	■	■					■					■						■							■	■	
	<i>Cladoramus crenulatus</i>		■	■			■		■	■		■	■			■						■	■							■							■		
	<i>Trachytettix alatus</i>		■	■			■		■	■		■	■									■	■	■	■	■	■	■		■		■	■				■		
	<i>Trachytettix scaberrimus scaberrimus</i>		■	■			■		■	■		■	■		■							■								■							■		

Table 3. (continued) **Combined visualisation of cladogram and states of pronotum characters.**

	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	7		
	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
<i>Mucrotettix spinifer</i>	■	■	■		■	■		■		■						■														■								■
<i>Cladonotella interrupta</i>		■	■		■	■		■			■	■				■			■				■	■					■		■	■						
<i>Gestroana kleukersi</i>	■	■	■		■	■	■	■			■	■				■			■				■	■	■	■	■		■									
<i>Hancockella portentosa</i>	■	■	■			■		■			■	■						■					■	■	■				■		■	■						■
<i>Misythus echinatus</i>						■		■			■	■	■	■			■						■						■								■	
<i>Cladonotus bhaskari</i>					■	■		■			■	■				■	■						■	■					■							■	■	
<i>Cladonotus humbertianus</i>					■	■		■			■	■				■			■				■	■					■							■	■	
<i>Cota saxosa</i>	■					■		■			■	■				■		■					■	■					■								■	
<i>Tettilobus pelops</i>	■	■	■		■			■			■	■										■	■	■						■		■					■	
<i>Cladonotella riedeli</i>	■	■	■		■	■		■			■	■		■			■		■										■									
<i>Cladonotella beccarii</i>	■	■	■	■		■		■			■	■				■	■						■	■	■	■			■		■							
<i>Gestroana willemsei</i>	■	■	■	■	■	■		■			■	■		■			■						■	■						■	■							
<i>Austrohancockia platynota platynota</i>		■	■		■	■		■			■	■				■	■						■	■					■	■								
<i>Haitianotettix tuberculatus</i>	■	■	■		■	■		■			■	■				■		■											■		■							
<i>Austrohancockia kwangtungensis</i>	■	■	■		■	■		■			■	■				■	■						■	■	■					■								
<i>Austrohancockia orlovi</i>	■	■	■		■	■		■			■	■				■	■						■	■	■					■								
<i>Cladonotella gibbosa</i>	■	■	■		■	■		■			■	■				■	■						■							■								
<i>Notredamia dora</i>	■	■			■	■		■			■	■				■	■						■	■						■							■	■

Table 3. (continued) **Combined visualisation of cladogram and states of pronotum characters.**

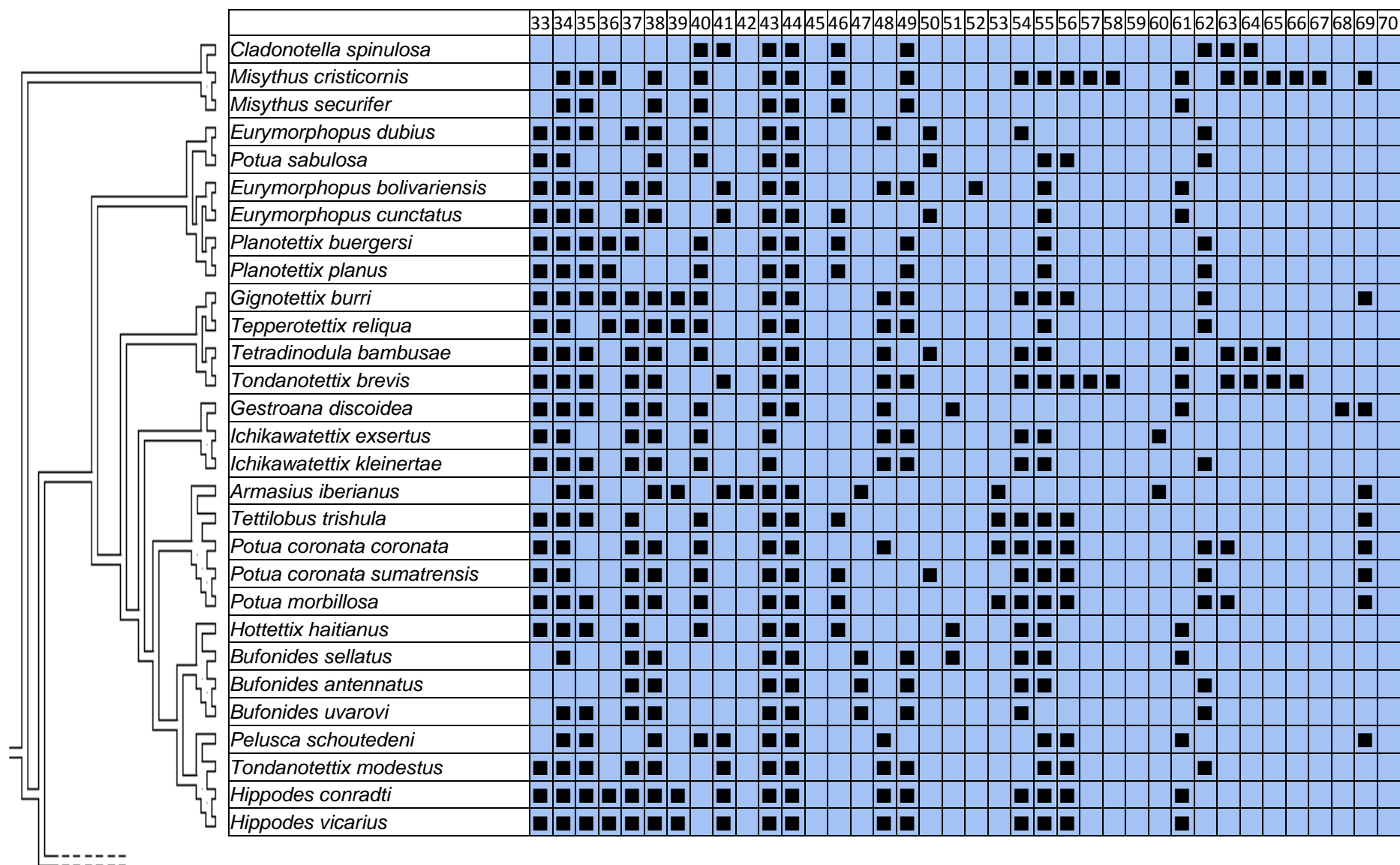
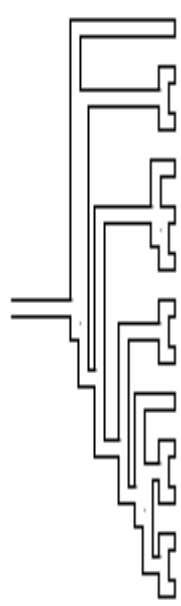


Table 3. (continued) **Combined visualisation of cladogram and states of pronotum characters.**

		3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	7		
		3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
	<i>Antillotettix nanus</i>	■	■	■		■	■		■		■				■			■												■								■	■
	<i>Coptottigia cristata</i>		■	■			■		■		■			■				■	■											■								■	
	<i>Cubanotettix turquinensis</i>		■	■	■	■	■		■		■			■	■						■											■						■	
	<i>Hildegardia mauritiicola</i>					■	■		■		■			■				■				■										■						■	
	<i>Hildegardia mauritiivaga</i>	■	■	■		■	■		■			■	■	■				■				■									■							■	
	<i>Dolatettix hochkirchi</i>				■				■		■				■	■															■							■	
	<i>Nesotettix samoensis</i>		■	■	■					■								■	■																			■	
	<i>Holoarcus ferwillemsei</i>					■				■		■	■	■				■					■								■							■	
	<i>Lepocranus fuscus</i>						■			■		■	■	■				■	■												■							■	
	<i>Pseudepitettix torulosinota</i>	■	■	■	■	■			■			■	■					■		■											■								
	<i>Paraselina brunneri</i>		■				■						■	■	■				■													■						■	
	<i>Vingselina crassa</i>		■			■	■					■	■	■	■				■													■							
	<i>Hymenotes westwoodi</i>								■				■	■	■							■		■								■						■	
	<i>Epitettix humilicolus</i>		■			■			■		■				■				■												■								
	<i>Seyidotettix swahili</i>					■			■		■			■	■				■																			■	■

Table 3. (continued) **Combined visualisation of cladogram and states of pronotum characters.**



	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	7
	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
<i>Nesotettix cheesmanae</i>		■				■		■		■					■					■									■								■	
<i>Cubonotus altinotatus</i>	■	■	■		■	■		■			■				■							■							■			■	■				■	
<i>Mucrotettix gibbosus</i>	■	■	■		■	■		■		■						■				■								■									■	
<i>Tiburonotus peninsularis</i>		■	■			■			■		■	■				■	■																				■	
<i>Sierratettix carinatus</i>		■	■		■	■		■	■				■	■			■														■						■	
<i>Truncotettix interruptus</i>		■	■						■	■						■	■																				■	
<i>Anaselina minor</i>		■	■		■	■		■				■				■	■														■						■	
<i>Pseudohyboella weylandiana</i>		■	■			■		■			■	■				■	■															■					■	
<i>Diotarus verrucifer</i>		■	■		■	■		■			■	■				■	■						■	■	■	■		■									■	
<i>Diotarus ikonnikovi</i>		■	■		■	■		■		■			■	■			■											■									■	
<i>Truncotettix fronterizus</i>		■	■			■		■		■				■			■											■									■	
<i>Dolatettix spinifrons</i>		■	■					■			■	■	■									■															■	
<i>Hymenotes triangularis</i>		■	■		■			■				■	■	■								■															■	

Table 3. (continued) **Combined visualisation of cladogram and states of pronotum characters.**

	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	7	
	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
<i>Thymochares galeatus</i>																																						
<i>Epitettix tumidus</i>																																						
<i>Afrolarcus aequalis</i>																																						
<i>Afrolarcus inaequalis</i>																																						
<i>Holoarcus altinotus</i>																																						
<i>Holoarcus arcuatus</i>																																						
<i>Piezotettix cultratus</i>																																						
<i>Piezotettix sulcatus</i>																																						
<i>Deltonotus subcucullatus</i>																																						
<i>Deltonotus gibbiceps</i>																																						
<i>Boczkittettix borneensis</i>																																						
<i>Boczkittettix manokwariensis</i>																																						
<i>Stegaceps brevicornis</i>																																						
<i>Willemsetettix willemsei</i>																																						
<i>Tuberfemurus kanokwanae</i>																																						
<i>Willemsetettix missai</i>																																						
<i>Ingrischitettix mountalbilalaensis</i>																																						
<i>Microthymochares pullus</i>																																						
<i>Epitettix lativertex</i>																																						
<i>Epitettix spheniscus</i>																																						
<i>Epitettix emarginatus</i>																																						
<i>Epitettix fatigans</i>																																						
<i>Epitettix dammermanni</i>																																						
<i>Thymochares exiguus</i>																																						
<i>Pseudepitettix pimkarnae</i>																																						
<i>Eleleus curtus</i>																																						
<i>Epitettix obtusus</i>																																						

Table 4. **Combined visualisation of cladogram and states of leg and wing characters.** Table of legs and wings character states annotated on cladogram of the topology equivalent to the Fig 13. for the purpose of better visualization of characters based on which program grouped species into clades. Black squares denote state „1“ (existence) of character. The first row denotes number of characters of that column. Green and yellow colors matche the color of characters in Table 1., meaning those are leg and wing characters.

	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
<i>Tettilobus prashadi</i>	■		■	■		■		■		■	■		■	■						■	■	■							
<i>Acmophyllum undulatum</i>		■	■		■	■		■	■	■		■	■		■					■	■	■	■	■	■	■		■	■
<i>Trypophyllum glabrifrons</i>	■	■	■		■	■		■	■	■		■	■		■					■	■	■		■		■		■	■
<i>Xerophyllum cortices</i>	■		■			■		■	■	■			■		■							■				■		■	
<i>Xerophyllum platycorys platycorys</i>	■	■			■	■		■	■				■		■							■		■	■	■		■	
<i>Scelimena producta producta</i>	■	■	■		■	■			■	■		■	■							■	■	■				■		■	■
<i>Morphopoides coriaceum</i>		■	■			■		■	■	■			■		■					■		■	■			■		■	■
<i>Morphopoides madagascariensis</i>		■	■		■	■		■	■	■		■	■		■					■	■	■	■	■	■	■		■	■
<i>Morphopoides folipes</i>	■	■	■			■		■	■	■			■		■					■		■	■	■	■	■		■	■
<i>Morphopoides tessmanni</i>		■	■			■		■	■	■		■	■		■					■		■	■	■	■	■		■	■
<i>Astyalus tessmanni</i>			■	■		■	■	■		■	■		■	■	■							■	■	■	■	■		■	■
<i>Morphopus acmophylloides</i>			■			■		■		■			■		■						■	■		■	■	■		■	■
<i>Morphopus phyllocerus</i>			■			■		■		■			■		■						■	■	■	■	■			■	■
<i>Pantelia horrenda</i>	■		■			■		■		■			■		■									■	■	■			
<i>Cladoramus crenulatus</i>	■		■			■		■		■			■		■								■	■	■	■		■	■
<i>Trachytettix alatus</i>			■			■		■		■			■		■								■	■	■	■		■	■
<i>Trachytettix scaberrimus scaberrimus</i>	■		■			■		■		■			■		■								■	■	■	■		■	■

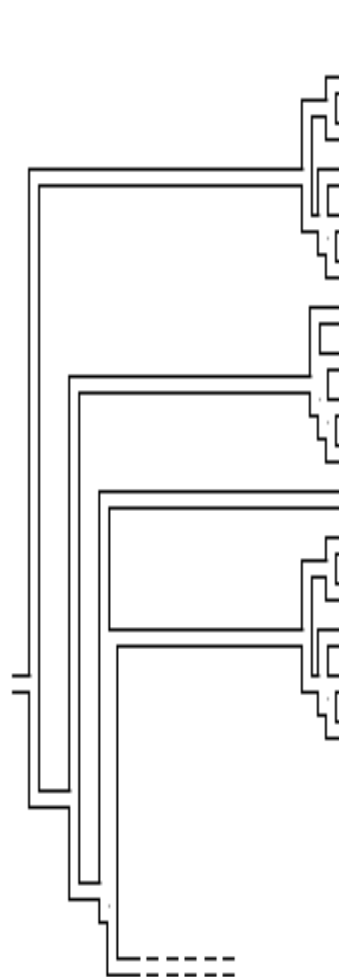
Table 4. (contoniued) **Combined visualisation of cladogram and states of leg and wing characters.**

	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
<i>Mucrotettix spinifer</i>	■			■					■	■				■			■		■			■		■	■	■			
<i>Cladonotella interrupta</i>																■	■	■	■			■	■			■			
<i>Gestroana kleukersi</i>	■															■	■	■	■			■		■	■				
<i>Hancockella portentosa</i>	■															■	■	■	■		■		■	■	■	■			
<i>Misythus echinatus</i>	■															■	■	■	■							■			
<i>Cladonotus bhaskari</i>	■															■	■	■	■			■	■	■	■	■			
<i>Cladonotus humbertianus</i>																■	■	■	■			■		■	■	■			
<i>Cota saxosa</i>																■	■	■	■					■	■				
<i>Tettlobus pelops</i>	■															■	■	■	■			■		■	■	■			
<i>Cladonotella riedeli</i>	■															■	■	■	■		■			■	■				
<i>Cladonotella beccarii</i>	■															■	■	■	■		■			■		■			
<i>Gestroana willemsei</i>	■															■	■	■	■		■			■	■	■			
<i>Austrohancockia platynota platynota</i>												■	■			■	■	■				■		■	■	■			
<i>Haitianotettix tuberculatus</i>				■			■				■			■								■		■	■				
<i>Austrohancockia kwangtungensis</i>	■			■							■						■		■			■		■	■	■			
<i>Austrohancockia orlovi</i>	■													■		■	■		■			■		■	■	■			
<i>Cladonotella gibbosa</i>	■															■	■	■	■			■		■	■	■			
<i>Notredamia dora</i>																■	■	■	■					■	■	■			

Table 4. (contoniued) **Combined visualisation of cladogram and states of leg and wing characters.**

	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	
<i>Cladonotella spinulosa</i>	■		■	■		■	■			■	■		■	■									■		■	■	■			
<i>Misythus cristicornis</i>	■		■			■				■			■									■		■	■	■	■			
<i>Misythus securifer</i>	■		■			■				■			■									■		■	■	■	■			
<i>Eurymorphopus dubius</i>			■		■	■		■	■				■		■															
<i>Potua sabulosa</i>	■	■	■		■	■				■	■		■										■	■			■			
<i>Eurymorphopus boliviariensis</i>	■	■	■		■	■		■	■						■					■	■		■		■	■	■			
<i>Eurymorphopus cunctatus</i>		■	■		■	■		■	■	■			■		■						■	■	■		■	■				
<i>Planotettix buergersi</i>		■	■			■		■	■	■			■	■	■						■		■							
<i>Planotettix planus</i>		■	■			■		■	■	■			■		■								■				■			
<i>Gignotettix burri</i>		■	■				■			■			■										■	■	■	■	■		■	
<i>Tepperotettix reliqua</i>	■	■	■				■			■	■			■							■	■	■	■	■	■	■			
<i>Tetradinodula bambusae</i>	■	■	■				■				■			■								■	■		■	■	■			
<i>Tondanotettix brevis</i>		■	■				■		■	■				■								■	■	■	■	■	■			
<i>Gestroana discoidea</i>		■	■		■	■					■			■									■		■	■	■			
<i>Ichikawatettix exsertus</i>		■			■				■			■									■	■	■		■	■				
<i>Ichikawatettix kleinertae</i>		■	■		■	■		■	■			■										■								
<i>Armasius iberianus</i>	■	■	■		■	■			■	■		■	■								■		■	■	■	■	■			
<i>Tettilobus trishula</i>	■	■	■		■	■			■	■		■	■										■							
<i>Potua coronata coronata</i>	■	■	■				■		■	■		■	■									■	■	■		■	■			
<i>Potua coronata sumatrensis</i>	■	■	■				■		■	■		■	■									■	■							
<i>Potua morbillosa</i>		■	■		■	■			■	■		■	■								■	■	■		■	■				
<i>Hottettix haitianus</i>		■	■		■		■		■	■		■										■	■		■	■	■			
<i>Bufonides sellatus</i>		■	■		■				■	■		■		■								■	■		■	■	■			
<i>Bufonides antennatus</i>		■	■		■	■			■			■										■	■		■	■				
<i>Bufonides uvarovi</i>		■			■				■			■		■								■	■		■	■	■			
<i>Pelusca schoutedeni</i>		■	■		■	■			■	■		■									■	■	■		■	■			■	
<i>Tondanotettix modestus</i>		■	■		■	■			■	■		■	■									■	■		■	■	■			
<i>Hippodes conradti</i>	■	■	■		■	■			■	■		■	■								■	■	■		■	■	■			
<i>Hippodes vicarius</i>	■	■	■		■				■	■		■									■	■	■		■	■	■			

Table 4. (contoniued) **Combined visualisation of cladogram and states of leg and wing characters.**



	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
<i>Antilotettix nanus</i>		■	■		■	■			■			■								■	■			■	■	■			
<i>Coptottigia cristata</i>		■	■		■	■			■	■		■	■							■	■	■		■	■	■	■		
<i>Cubanotettix turquinensis</i>		■	■		■	■			■	■		■	■								■	■		■	■	■	■		
<i>Hildegardia mauritiicola</i>	■	■	■		■	■			■	■		■	■									■		■	■	■	■		
<i>Hildegardia mauritiivaga</i>	■	■	■		■	■																■		■	■				
<i>Dolatettix hochkirchi</i>		■	■						■	■		■	■				■		■		■		■	■	■	■			
<i>Nesotettix samoensis</i>	■	■	■				■			■	■		■	■						■	■	■	■	■	■				
<i>Holoarcus ferwillemsi</i>	■	■	■				■		■	■		■	■								■	■		■	■	■	■		
<i>Lepocranus fuscus</i>		■	■				■		■	■		■	■		■						■	■				■	■		
<i>Pseudepitettix torulosinota</i>	■	■	■		■				■	■		■	■								■	■	■	■	■	■	■		
<i>Paraselina brunneri</i>		■	■				■		■	■		■		■							■		■		■	■			
<i>Vingselina crassa</i>		■			■				■			■	■									■		■	■				
<i>Hymenotes westwoodi</i>	■	■			■				■			■									■	■	■	■	■	■			
<i>Epitettix humiliculus</i>		■			■				■			■	■							■	■	■		■	■	■	■		
<i>Seyidotettix swahili</i>		■			■			■	■			■	■		■					■	■	■							

Table 4. (contoniued) **Combined visualisation of cladogram and states of leg and wing characters.**

	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
<i>Nesotettix cheesmanae</i>	■	■	■		■	■					■			■						■	■	■	■	■	■	■			
<i>Cubonotus altinotatus</i>	■	■	■				■		■	■		■	■							■	■	■	■	■	■	■			
<i>Mucrotettix gibbosus</i>	■	■	■						■	■		■	■				■			■	■	■				■			
<i>Tiburonotus peninsularis</i>		■	■				■		■	■		■		■							■	■	■	■	■	■			
<i>Sierratettix carinatus</i>		■	■				■		■	■		■	■							■	■	■	■	■	■	■			
<i>Truncotettix interruptus</i>		■			■		■		■	■		■	■							■		■	■	■	■	■			
<i>Anaselina minor</i>		■	■		■	■			■			■																	
<i>Pseudohyboella weylandiana</i>	■	■	■		■				■	■		■									■	■	■		■	■	■	■	
<i>Diotarus verrucifer</i>	■	■	■		■	■			■	■		■	■								■	■	■	■	■	■	■		
<i>Diotarus ikonnikovi</i>	■	■	■		■	■			■	■		■	■								■	■	■	■	■	■	■		
<i>Truncotettix fronterizus</i>	■	■	■		■		■		■	■		■		■							■	■	■	■	■	■	■		
<i>Dolatettix spinifrons</i>																													
<i>Hymenotes triangularis</i>	■	■	■		■	■			■	■		■	■								■		■	■	■	■	■		

Table 4. (contoniued) **Combined visualisation of cladogram and states of leg and wing characters.**

	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
<i>Thymochares galeatus</i>	■	■	■		■				■	■		■								■	■	■	■	■	■	■			
<i>Epitettix tumidus</i>		■			■				■			■								■	■	■		■	■				
<i>Afrolarcus aequalis</i>		■	■		■	■			■	■		■	■								■	■		■	■	■			
<i>Afrolarcus inaequalis</i>		■	■		■	■			■			■	■									■		■	■	■			
<i>Holoarcus altinotus</i>		■	■		■	■			■	■		■										■		■	■	■			
<i>Holoarcus arcuatus</i>	■	■	■		■	■			■	■		■									■	■		■	■	■	■		
<i>Piezotettix cultratus</i>	■	■	■		■	■			■	■		■	■																
<i>Piezotettix sulcatus</i>	■	■			■				■			■								■	■	■		■	■	■			
<i>Deltonotus subcucullatus</i>	■	■	■		■	■			■	■		■	■							■	■	■	■	■	■	■	■		
<i>Deltonotus gibbiceps</i>	■	■	■		■	■			■			■	■							■	■	■		■	■	■			
<i>Boczkittettix borneensis</i>	■	■	■		■	■			■	■		■	■								■	■		■	■	■			
<i>Boczkittettix manokwariensis</i>	■	■	■		■	■			■	■		■	■							■	■	■	■	■	■	■	■		
<i>Stegaceps brevicornis</i>		■			■		■		■			■									■	■				■		■	■
<i>Willemsetettix willemsei</i>		■			■		■														■	■	■			■			
<i>Tuberfemurus kanokwanae</i>		■			■	■			■											■	■	■		■	■	■			
<i>Willemsetettix missai</i>		■			■	■			■	■		■	■							■	■	■	■	■	■	■			
<i>Ingrischitettix mountalbilalaensis</i>		■	■		■	■			■	■		■	■							■	■	■		■	■	■			
<i>Microthymochares pullus</i>		■	■		■	■			■	■		■	■							■	■	■				■	■		
<i>Epitettix lativertex</i>		■			■				■			■																	
<i>Epitettix spheniscus</i>		■			■				■			■								■	■	■		■	■	■	■		
<i>Epitettix emarginatus</i>		■			■				■			■								■	■	■		■	■	■			
<i>Epitettix fatigans</i>		■			■				■			■								■	■	■		■	■	■			
<i>Epitettix dammermanni</i>		■	■		■	■			■	■		■	■							■	■	■		■	■	■			
<i>Thymochares exiguus</i>	■	■	■		■				■	■		■								■	■	■	■	■	■	■			
<i>Pseudepitettix pimkarnae</i>	■	■			■	■			■			■	■							■	■	■	■	■	■	■	■		
<i>Eleleus curtus</i>									■			■								■	■			■	■	■			
<i>Epitettix obtusus</i>		■			■	■			■			■								■	■	■		■	■	■			

Table 5. **Table of retention and consistency indices of cladograms (Fig. 13.-20.)** First row denotes which species were used in the making of cladograms, and first column denotes what characters were used. Species used: „All spp.“—all 119 species used; „Type“—only type species used (65 species used, see Fig. 18); „Reduced“—greatly reduced number of species (38 species used, see Fig. 19). Characters used: „All ch.“—all characters used (99 characters used); „No projections“—all characters without projections used (85 characters used, characters number 54 to 67 omitted); „Head“—only head characters used (32 characters used); „Pronotum“—only pronotum characters used (38 characters used); „Legs“—only legs characters used (27 characters used).

	All spp.	Type	Reduced
All ch.	RI = 0,54014884 CI = 0,07776905	RI = 0,47054323 CI = 0,12515803	
No projections	RI = 0,55089559 CI = 0,07637017	RI = 0,47323704 CI = 0,12056738	RI = 0,47281713 CI = 0,2039801
Head	RI = 0,65513126 CI = 0,09968847		
Pronotum	RI = 0,60273973 CI = 0,09156627		
Legs	RI = 0,73369565 CI = 0,12107623		

Fig. 23.-25. were made to visually show diversity of specific characters. This was done after examining dozens of species and hundreds of specimens; patterns or lack of them became obvious and they had to be shown. Those collages (Fig. 23.-25.) make discussion about whole analysis easier and more comprehensible.

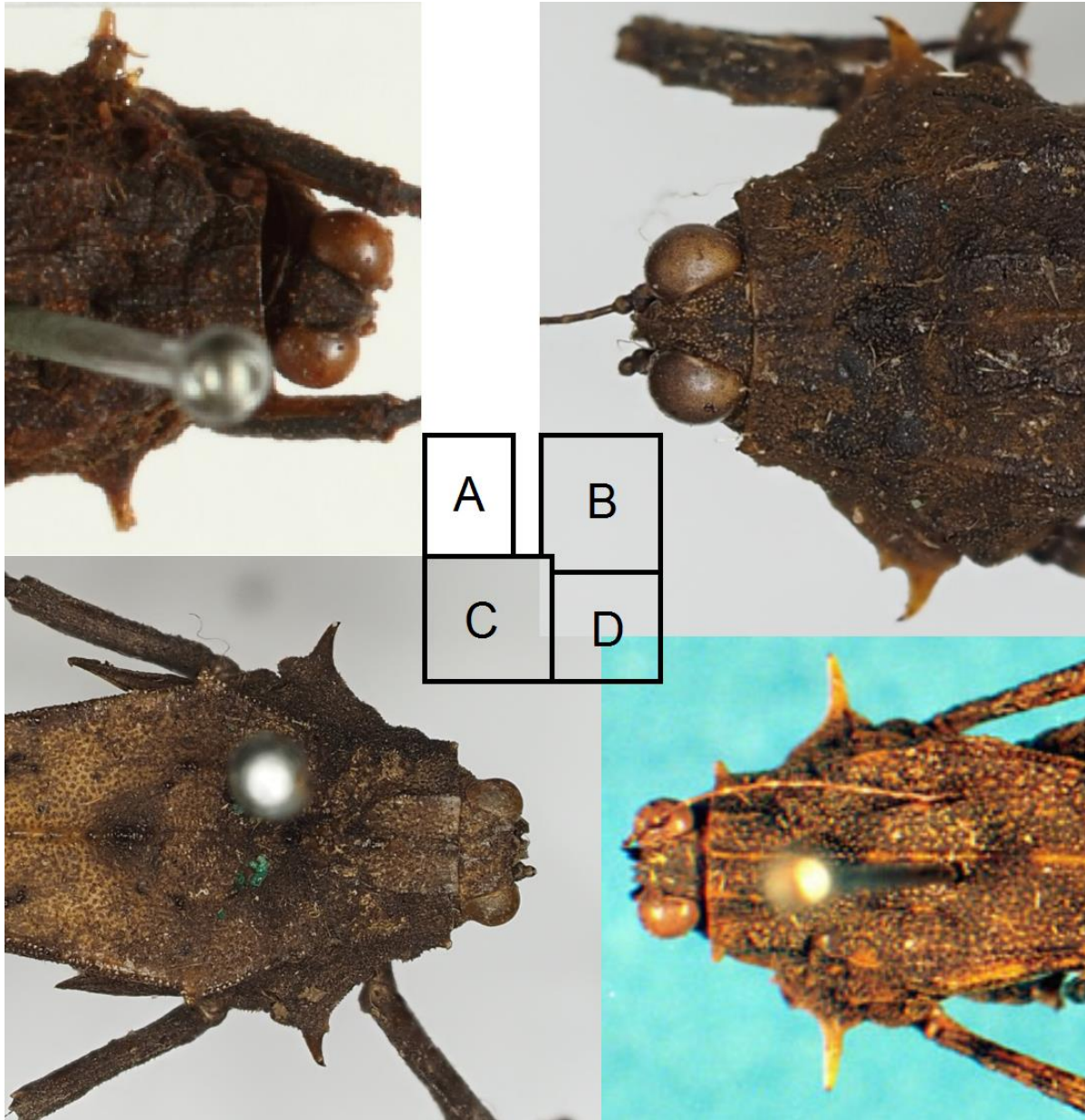


Figure 23. **Example of character (VL, ventrolateral projection) that exhibits at least superficial homology between genera.** (A) *Tefrinda palpata* (Stål, 1877), male, dorsal view (holotype). Source: © Naturhistoriska Riksmuseet Stockholm (NHRS), photo Josef Tumbrinck. (B) *Euscelimena logani* (Hancock, 1904), male (paratype), dorsal view. Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck. (C) *Platygavialidium productum* (Walker, 1871), female, dorsal view (syntype). Source: © The Natural History. (D) *Scelimena melli* Günther, 1938, female, dorsal view (holotype). Source: © Sigfrid Ingrisch, DORSA. Museum, London (BMNH), photo Josef Tumbrinck.



Figure 24. **Variability of FM (frontomedial projection) in various Cladonotinae genera.** (A) *Acmophyllum undulatum* Karsch, 1890, female, lateral view (holotype). Source: © Sigfrid Ingrisch, DORSA. (B) *Cladonotella gibbosa* (Haan, 1843), female, lateral view (syntype). Source: © Nederlands Centrum voor Biodiversiteit, Leiden, photo Josef Tumbrinck. (C) *Bufonides sellatus* Hinton, 1940, female, lateral view (paratype). Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck, flipped horizontally. (D) *Tettilobus trishula* Skejo, Bhaskar & Stermšek, 2020. Source: Bhaskar et al. (2020), flipped horizontally. (E) *Stegaceps brevicornis* Hancock, 1913, female, lateral view (holotype). Source: © Jason Weintraub, Academy of Natural Sciences, Philadelphia. (F) *Cladoramus crenulatus* Hancock, 1907, female, lateral view. Source: © Museo Civico di Storia Naturale "Giacomo Doria" (MCSN), Genova, photo Josef Tumbrinck. (G) *Holoarcus ferwillemse* Tumbrinck, 2014, female, lateral view (paratype). Source: © Nederlands Centrum voor Biodiversiteit, Leiden, photo Josef Tumbrinck. (H) *Potua coronata sumatrensis* Bolívar, 1898, female, lateral view (syntype) Source: © Museo Civico di Storia Naturale "Giacomo Doria" (MCSN), Genova, photo Josef Tumbrinck.



Figure 25. **Variability of tarsi in Cladonotinae.** (A) *Boczkitettix borneensis* (Günther, 1935), female, lateral view, Source: © Nederlands Centrum voor Biodiversiteit, Leiden, photo Josef Tumbrinck. (B) *Boczkitettix manokwariensis* Tumbrinck, 2014 male, lateral view, Source: © Bernice P. Bishop Museum, Honolulu, photo Josef Tumbrinck. (C) *Cladonotella spinulosa* Tan, Tumbrinck, Baroga-Barbecho & Yap, 2019, Source: Tan et al. (2019). (D) *Cota saxosa* Bolívar, 1887, female, lateral view (holotype), Source: © Naturhistorisches Museum Wien (NMW), Vienna, Austria, photo Josef Tumbrinck. (E) *Diotarus ikonnikovi* Bey-Bienko, 1935, male, lateral view, Source: © Ming Kai Tan. (F) *Diotarus verrucifer* Stål, 1877, male, lateral view (holotype), Source: © Naturhistoriska Riksmuseet Stockholm (NHRS), photo Josef Tumbrinck. (G) *Epitettix humilicolus* Günther, 1938, female, lateral view (from locus typicus). Source: © Museum für Naturkunde, Berlin (MFN), photo Josef Tumbrinck. (H) *Gestroana willemsei* Tumbrinck, 2014, female, lateral view (paratype). Source: © Nederlands Centrum voor Biodiversiteit, Leiden, photo Josef Tumbrinck. (I) *Hildegardia mauritiivaga* Günther, 1974, female, lateral view (holotype). Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck. (J) *Holoarcus arcuatus* (Haan, 1843), female, lateral view. Source: © Nederlands Centrum voor Biodiversiteit, Leiden, photo Josef Tumbrinck. (K) *Hymenotes westwoodi* (Bolívar, 1887), female, lateral view. Source: © Naturhistoriska Riksmuseet Stockholm (NHRS), photo Josef Tumbrinck. (L) *Thymochares galeatus* Rehn, 1929, female (holotype), lateral view. Source: © The Natural History Museum, London (BMNH), photo Josef Tumbrinck.

5. Discussion

In science, it is necessary to firmly stand on the shoulders of giants that came before us, said Bernard of Chartres, a twelfth-century French Neo-Platonist philosopher, scholar, and administrator (Trojan 2004). The giants are all scientists who left us knowledge about the world without which we would not be able to conduct our research. One of the great living tetrigidologists, Dr. Josef Tumbrinck paved the way for Cladonotinae research by publishing a revision of the subfamily Cladonotinae (Tumbrinck 2014). Even though he made the biggest revision of the subfamily and proved his expertise numerous times, he made some mistakes that quickly got noticed by other scientists, in this case, Josip Skejo (Tumbrinck & Skejo 2017). Seeing that even highly regarded experts can make mistakes in their field, I decided to briefly step down from the giant's shoulders and investigate the problems of the subfamily of Cladonotinae by myself. That being the reason for temporarily ignoring most of the previously accumulated knowledge on Cladonotinae apomorphies, or as they are called „good characters“ (Grant 1962). In this master's thesis I gave an unbiased view on characters that can be used in distinguishing species from species and genera from genera. The unbiased view was accomplished by wisely *de novo* forming sets of the “good characters” and analysing them in a comprehensive character matrix.

5.1. Discussion about methodology: Traits omitted from analysis of which value still needs to be tested

5.1.1. FL, FM, PML, PL

This paragraph is an indirect continuation of paragraph 1.6. In my opinion, there is only problem with aforementioned way of describing morphology, and it is the high risk of those traits being non-homologous between species. Without sufficient amounts of genetic data for every species and deep knowledge of embryology and development of each species, it is practically impossible to determine homologous characters between distantly related species of Tetrigidae. I think that even with the said knowledge of homologies, understanding the homology of said traits is very difficult to achieve. In practice that means having species from numerous genera bearing something that could be regarded as, for example, FM. Structures in those cases look completely different and under closer inspection are composed of different parts of an animal (Fig. 24). FM

projection is a trait that shows no “obvious homology”, unlike, for example, VL projection in members of the tribe Scelimenini (subfamily Scelimeninae) (Fig. 23).

Considering what was said, I omitted FM from the analysis. Following the same scientific logic, characters FL, PML, and PL were also omitted from the analysis.

5.1.2. Tarsal pulvilli

Tarsal pulvilli exhibit great variability from species to species. If one were to arrange photographs of tarsal pulvilli of all Tetrigidae, or even just all Cladonotinae, a spectrum of different shapes, sizes, degrees of pointiness, direction of growth, and many other characteristics would be evident. This was clearly showed in collage depicting just a fraction of variability in pulvilli of hind tarsi (Fig. 25). Efforts to sort or describe them in any meaningful way showed counterproductive because they greatly vary morphology.

Because of the impracticality of using the morphology of pulvilli as a character, I omitted them from the analysis.

5.2. Discussion about methodology: Problem of small sizes of specimens when describing the morphology of Tetrigidae

“... the pronotal and other embellishments which have been used to distinguish species [of Cladonotinae] seem to be very variable in form and may not provide taxonomically reliable specific character.”, Blackith (1992) cited Kevan (1966). This is the only time a tetrigidologist has pointed to a problem of understanding the morphology of specimen even when it is inspected personally by tetrigidologist as long and detailed as needed. I agree with Kevan on multiple levels. The similar fact I noticed is that with body lengths often shorter than 20 millimeters, it is hard to determine what fine anatomical structures the specimen really bears, and which are anomalies formed by damaging the soft exoskeleton shortly after they molt or damage to the exoskeleton the specimen got during its lifetime. This problem gets even harder to resolve when there is only one available specimen. For example, when describing position between topmost margin of compound eyes and vertex, scientists are observing the individual under magnification of over 30x and said distances

are in the range of 0 to 200 micrometers (Fig. 26). Mistakes in interpretation of what is observed can easily occur when dealing with such small morphological formations observed under a binocular stereo microscope. This is an important fact to point because even a high-resolution photographs of an individual can bring disagreement on the reality of morphology of specimens if the definition of a given character is not agreed upon. Even if a character is well defined and can be used by multiple scientists who will get the same results, the character in question may not be homologous between distantly related species, for example when comparing species from different subfamilies, thus making the results of those research at least partially faulty. This whole problem appeared obvious to me while examining all available specimens by hand or from photos and noticing that sometimes, for reasons unknown to me, I would interpret morphology of a specimen differently if examined more than once or sometimes I simply wouldn't understand the topology of morphology of specimen. After consulting with colleagues and mentors, the same problem occurred to them. This problem is not in the scope of this paper, but is important to acknowledge its existence and have it in mind when conducting future research.

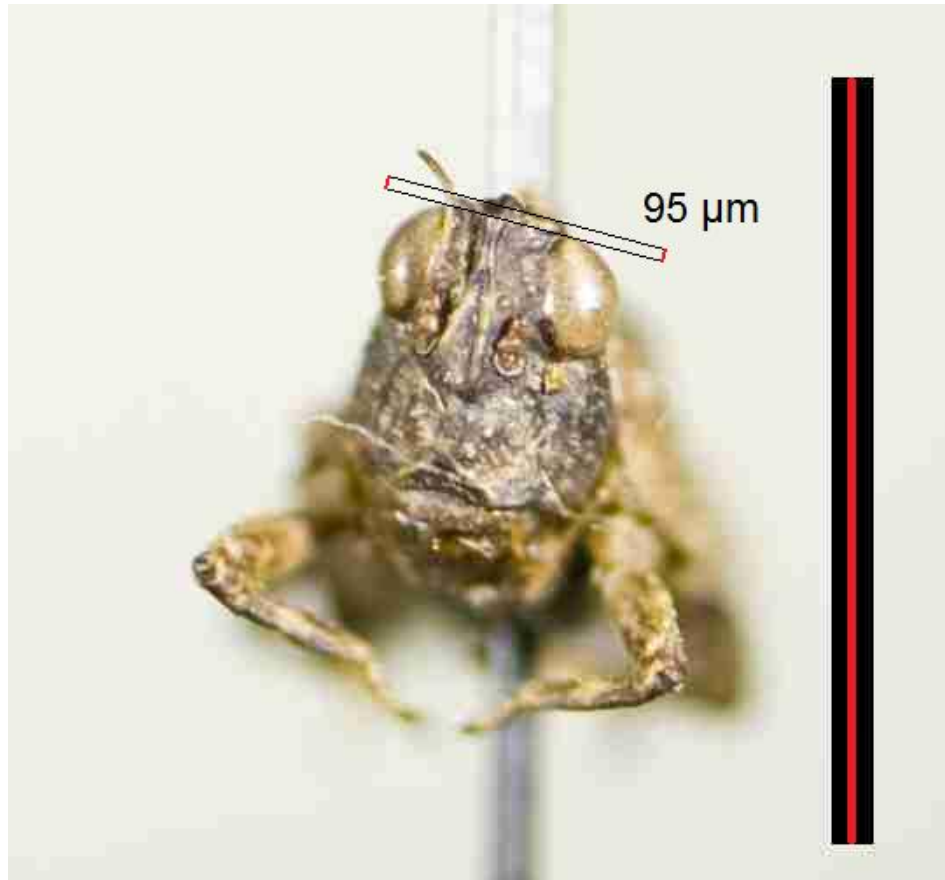


Figure 26. **Example of how the low quality of the photograph and tiny sizes of observed characters contributes to the confusion about real morphology of specimens.** Frontal view of *Microthymochares pullus* Devriese, 1991. Shown distance is between topmost margin of compound eyes and vertex. Mistakes about the morphology of specimens sometimes depend on a few dozen micrometers, which can inadvertently happen to anyone measuring the specimen. Black and red stripe on the right is 5 mm long (435px), the distance between the top margin of the compound eye and vertex is 0,095 mm (8px high, 2px wide = 8,24px diagonal). Photograph edited in Paint v6.3. Source: © Josip Skejo, Copyright Josip Skejo & MNCN Madrid.

5.3. Discussion on Retention indices and Consistency indices shown in the results

Results show no significant change in the relative amount of apparent homoplasy and synapomorphies if projections of pronotum were included or not in the analysis (using all characters: RI = 0,54014884, CI = 0,07776905; using no projections: RI = 0,55089559, CI = 0,07637017 (see Table 2.)). That means that some projections are homologous between the species and some are not, and the ratio of homologies vs. homoplasies among pronotal projections is the same as in all other characters used in the analysis.

Using type species of each genus lowers the RI (RI = 0,5440658 vs. RI = 0,47054323), but

increases the CI (CI = 0,0783848 vs. CI = 0,12515803) in comparison to analysis of more species from each genera. This shows that among type species there are relatively less synapomorphies. This is to be expected because by removing really similar species, in this case from the same genus, we end up with species all from different genera. In this way we removed terminal branches that had more similarities among themselves than with sister clades, resulting in a cladogram deprived of sub-general similarities.

On the other hand, when all but type species were removed from the analysis, CI was greater, meaning the cladogram was less “homoplastic”. This neatly shows that a lot of species of Cladonotinae subfamily are placed in genera they do not belong to. Another way of interpreting that result is that Cladonotinae are a subfamily almost as old as Tetrigidae themselves, and that they accumulated more than 200 million years of synapomorphies which now seem like homoplasies due to extinction of many “branches in between” today's living genera. That result can be seen both when pronotal projections are taken into analysis and when they are not used in analysis. I expect this hypothesis will be disproven in future by doing molecular analyses of the subfamily.

The two cladograms made without pronotal projections, which show no value in Cladonotinae determination, present one interesting result. The cladograms are the ones made by removing all but type species, and cladogram made by eliminating all but type species and all species widely considered not to be Cladonotinae, meaning those with wings, and those from South America (“Reduced”). The more Cladonotinae species are removed, the results show that characters exhibit less homoplasies (CI=0,07637017 → CI=0,12056738 → CI=0,2039801). That “Reduced” cladogram shows an increase in CI value, which was an expected result, but one interesting result is that those winged Cladonotinae were grouped together on the basis of many other characters (see supplement: Character history of characters 16, 17, 41, 53, 61, 76, 78, 83, and 85). That means that species considered not to be Cladonotinae have characters relatively less homoplastic in nature than other members of Cladonotinae. In other words, those Cladonotinae that are widely thought to belong to some other subfamilies appear to really be members of some other subfamily and are good candidates for further research of their true taxonomic placement. And not only those species, but the cladogram consisting of only type species shows that all Cladonotinae species added to Cladonotinae genera after the type species show the same pattern. This paints a picture about Cladonotinae as a subfamily in which scientists would place a new genus or species

not on the basis of similarities with other Cladonotinae, but on the basis of differences with every other subfamily. Today Cladonotinae is a subfamily filled with species bearing the biggest variability of morphology of all subfamilies. This is enabling scientists to describe a new species of unique morphology and place it within Cladonotinae. Now when the subfamily consists of a lot of unofficially non-Cladonotinae species, it is easy to justify the placement of a new unique genera or species that bears little similarities with any of the subfamilies to the Cladonotinae.

By comparing cladograms made with only one group of characters we can see that the most informative characters are the characters of legs (RI = 0,73369565, CI = 0,12107623). Second best are head characters, which are traditionally the most used characters to determine whether a species belongs to the Cladonotinae subfamily (RI = 0,65513126, CI = 0,09968847). The least informative of the three are pronotal characters (RI = 0,60273973, CI = 0,09156627).

Cladistic analysis gives lower values of CI when more taxa and characters are used in analysis. My results show a pattern of rising CI value when less taxa and characters are included, but that does not make results less significant. That is because the values of the CI do not fall by much when removing taxa and characters from a matrix that has enough taxa and characters included in the analysis (e. g. >35 taxa and >40 characters). Adding characters in the analysis with more than 60 characters, lowers the value of CI by an insignificant amount (Archie 1989). This supports the explanation of why the CI value did not drop after removing pronotal projections from the analysis.

Everything said above can be explained by two other hypotheses - great extinctions within the subfamily or much greater mutation rates within Cladonotinae. If we assume that all taxonomic placement of today's Cladonotinae is correct, that would imply that Cladonotinae as a group evolved at the time when the rest of Tetrigidae branched off other Orthoptera 224 million years ago in the Upper Triassic period (Song et al. 2015). This implication comes from the fact that the variability of morphology of Cladonotinae is almost as great as variability of morphology of all other Tetrigidae combined. Hypothetical early branching of Cladonotinae would mean that Cladonotinae are a basal group of Tetrigidae. Then, if the premise about extinction of a big part of Cladonotinae were true, thus leaving today a holophyletic subfamily with evolutionarily branches far and few, that would then imply that all Cladonotinae alive today branched off other Cladonotinae in a span of a few million years, assuming that the rate of morphological changes are more or less constant through time. This would result in a subfamily of never-considered proportions and, my

thoughts are that it would be almost impossible to prove that even with modern genetic analysis. Second hypothesis would explain the morphological differences between Cladonotinae as a product of their much bigger mutation rates which gave Cladonotinae morphological differences we see today. Personally, I do not think those hypotheses are true, they were given just to show that alternatives to Cladonotinae simply having many misassigned species are very unlikely.

5.4. Reasons not to abolish current characters used

Even though the homology of characters between species may not be yet proven, we should still use all previously used characters. What needs to be changed is how scientists view them—not as a sign of homology between species, but as a precise way of conveying morphological characters into words. In today's time when high quality photographs are a norm in every taxonomic paper, we still need a consistent way to describe morphology of a specimen. This cannot be done by descriptive depiction of a specimen, but it must be done in some way so any potential confusion about the right way of interpreting morphology of specimens from given photographs can be resolved. The best way to avoid any confusion is by keeping today's system of characters tetrigidologists already agreed upon. By doing so, and by treating those characters simply as tools for clearly describing morphology, a lot of future misplacements of taxa could be avoided.

5.5. Comments on the results of „Combined visualisation of cladogram and states of characters“ (Table 2.-4.)

5.5.1. Characters best used for genera/species keys of Cladonotinae subfamily

Results show that some characters are more sporadically present in species analyzed than other characters. Under the assumption that the resulting cladogram somewhat shows the real evolutionary relations between Cladonotinae, we can deduce that those characters can be used in differentiating one genus from another, or one species in the genus from another within the same genus. Whether it is better to use character for distinguishing genera or species can be inferred by looking at the tables of character states (see Table 2.-4. and optionally Supplement for different visualisation of the same results). If character is present in a few species of many genera, then those

characters are better for distinguishing one species from another from the same genus. If the character is present in all species from a few genera, then those characters are better for distinguishing one genus from another. Thus, characters which show great potential for being used in species keys are characters number 7, 12, 27, 36, 46, 50, 62, 63, 64, 65, 77, 81, 84 and 97 (see supplement). Best of those are: (1) morphology of carinas of middle and frontal femur, (2) location of humeral angles in comparison to lateral lobes, mid and hind leg coxa, (3) and morphology of apex of lateral lobes of paranota.

5.5.2. Characters revealing potential natural clades

Cladogram of character history shows that some characters strongly correlate with specific holophyletic clades given by analysis, meaning all or most species in that clade possess that character, and at the same time, no or few species outside of the clade possess that character. Those characters are numbers 8, 21, 22, 23, 26, 41, 45, 50, 53, 54, 55, 61, 69, 72, 73, 75, 76, 78, 79, 82, 86, 87, 88, 89, 98, and 99 (see supplement). Best of those characters, meaning, those which show very clearly that the clade can be recognised on it's basis are: (1) the shape of vertex in frontal view, (2) height of vertex in lateral view, (3) morphology of posterior end of pronotum, (4) morphology of carinas of femurs, (5) and existence of tegmina and alae.

Those characters had enough “evolutionary weight” to give the program that analyzed the character matrix enough information to calculate those species as closely related. This does not necessarily mean those species are closely related, it only means they are, in this case, morphologically most similar. It also means that, if the problem is holistically looked upon, those characters can shed light on characters which can nudge the research of experts in the right direction. Thus making those characters the focus of further research into evolutionary relations and taxonomic validity of the subfamily Cladonotiane. Such a way of finding new insights in the problem of Cladonotinae taxonomy is likely to bring new and important discoveries.

5.5.3. Characters specific for clade consisting of type genus of subfamily Cladonotinae

Characters that clearly define clade where the type species of type genus of Cladonotinae is situated (*Cladonotus humbertianus*) are characters number 86, 87, 88 and 89. Those characters are the existence of dentiform spines on the dorsal and ventral side of the front and middle femurs, explained further in chapter 5.5.6.

5.5.4. Head characters

Head characters show variation of results. Some characters, for example, position of eyes in relation to vertex, or protrusion of vertex before the compound eye show clear groupings of clades. While some other characteristics, such as straightness of facial carinae after bifurcation show no signs of being correlated to some monophyletic clade. This is as valuable of a result as any other would be. Results shows us that some characters considered good for determining Cladonotinae from other subfamilies, such as wide scutellum, meaning wider than scapus, gives us no new knowledge about taxonomy of species we are analysing, because, as results show, there are other subfamilies bearing the same characteristics, in this case, every Batrachideinae used in analysis. By carefully considering all the results, we can change the way head characters are used in Cladonotinae taxonomy. High frontal costa bifurcation (2), high antennal grooves (6), antennal grooves very far apart (8), eyes below the vertex (11), vertex protruded before the compound eye (19), bulging vertex (22), and extremely wide scutellum (27) together all relatively clearly group one specific clade of, what is today considered Cladonotinae. These characters correlate to many other pronotal and leg characters, and I think are a good sign for species not belonging to the Cladonotinae subfamily.

5.5.5. Pronotum characters and wings

Characters of pronotum show good signs of being useful as they are today used. Some, for example morphology of both anterior and posterior part of the pronotum and morphology of median carinae, show clear groupings throughout the resulting cladograms. Pronotum is the most variable part of the morphology of Cladonotinae species and as such needs to be further analyzed to reduce further misuse of pronotum characters in taxonomy as explained in chapter 5.4.

5.5.6. Leg characters

As it is clear from the analysis, leg characters had an important role in determining which species belongs to which clade. Many monophyletic groups can be observed by looking at the distribution of given leg characters on resulting cladograms, especially clade in which type genus of Cladonotinae subfamily (*Cladonotus*) is situated. Historically, the morphology of legs, excluding tibiae and basic morphometry, was often dismissed for distinguishing Tetrigidae species, and Cladonotinae for that matter (e.g. Storozhenko 2012, Storozhenko 2013, Zheng, Li

& Lin 2012). More emphasis was given to pronotum and head characters. Those characters had variability between species which was easier to define. For example, the existence of leaf-like median carinae or wide scutellum were more practical characters to use than to make sense of the practically infinite variability of morphology of leg carinae.

There are no known functions of Cladonotinae legs except locomotion and as a surface for colours and patterns for cryptic mimicry. That is why I assume that characters of legs do not change much through evolution as other more multi-purpose body parts do. For example, pronotum would change as an answer to greater or lesser needs for wing usage; eye position would change as an answer to changes in predators inhabiting their living area, etc. Legs of what is today considered Cladonotinae are almost always positioned very wide in relation to the body (Cigliano et al. 2021). Morphology of legs does not impede walking or jumping, so the only suspected purpose of their morphology would be to seem less noticeable to predators. I hypothesise that when any cryptic pattern emerges, for example leaf-like, undulating or spiky femurs, and when those patterns get fixated in populations, it tells us that those patterns were selected by natural selection, thus confirming that they work and that they are really helping individuals to survive. Because Cladonotinae live only in tropical environments which do not change much even during the ice ages, constant ecological factors contribute in making their morphology constant through time. Combining the never changing environment with fixation of cryptic morphology which obviously does a trick, I come to the conclusion that looking in morphology of legs, especially femurs, is a great way for determining evolutionary relations of Cladonotinae.

After looking at photos of hundreds Cladonotinae species for hundreds of hours, I firmly believe that, despite the impracticality of using the morphology of legs in general as a tool for determining evolutionary relations between species, the key to understanding the taxonomy of Cladonotinae lays in leg morphology. Further research of deeper correlations between characters and clades is undoubtedly needed, but this thesis clearly shows that the problem of Cladonotinae taxonomy is slowly but surely coming to an end.

Even though the resulting cladogram does not mean those cladistic relations are completely valid, it shows that, if morphology could give us answers, the answers will probably come in the shape of leg morphology.

5.5.7. The importance of the results

Results in this thesis are obtained by analyzing only the morphology of species, unlike previous works which used only molecular data to determine phylogenetic relations between Cladonotinae species. Molecular data can only tell us which species or specimens form a single clade, not the reason for their grouping in one clade. Using molecular data to find out the potential problems in systematics of any taxonomical group can only tell us whether this group is mono- or polyphyletic, without giving scientists any further guidance on how to fix potential taxonomical misplacements of species. Even though I think molecular data should always be considered when investigating phylogenetic relations, morphology will always be more practical and will always give us more profound answers to problems of systematics. Those previous works did indirectly use morphology in their research in the sense that they used already known descriptions of species' morphology. This still means that the results and discussion of those research would be the same whether the species they analyzed had descriptions justified by their morphology or not, because no one used morphological data to infer any result. This thesis uses only morphology to obtain the results, meaning I was using the same type of data which was used to form the Cladonotinae subfamily (Bolívar 1887). All Cladonotinae species were described by their morphology, not by means of molecular data. This thesis shows that characters used to justify the placement of new species in Cladonotinae are not good for forming a monophyletic clade. This could only be done by making cladograms solely using morphological data. Firstly, I had to make cladograms solely using morphological data. Then, I had to see which if any parts of their morphology correlates with cladograms having more or less homoplastic characters. Then, I had to see which characters did the program found to be of most importance when assigning species to specific clades. And only then I could deduce what characters are good for determining whether a species belongs to Cladonotinae or not. That step enabled me to see that Cladonotinae today are not consistent with the morphological classification of the Bolívar's Cladonotinae of the 19th century (Bolívar 1887)—the Cladonotinae for which we can certainly claim are Cladonotinae on the basis of them being described first (International Commission on Zoological Nomenclature (ICZN) —Article 23. Principle of Priority) (Ride 1999) and on the basis of them bearing a lot of morphological similarities, unlike Cladonotinae today. Summing up everything said, I claim that not only

Cladonotinae species are wrongly taxonomically assigned, but that we fundamentally do not know how to correct those taxonomical mistakes without a lot of future research.

5.5.8. Final word

All those results should be considered as guidelines for further research using molecular data, and not the final saying on the evolutionary informativeness of analysed characters. Cladistic analysis can only partially resolve the true taxonomy of any clade, and in this case of Cladonotinae subfamily, analysis showed a lot of problems and a lot of potential solutions to those problems. There is still a great amount of work needed to make a good set of characters which will serve as a tool for describing new Cladonotinae species. Until then, this thesis will light the path for future research, helping any future scientist with answering the question of Cladonotinae taxonomy.

6. Conclusion

1. Cladonotinae are a subfamily littered with species wrongly assigned to Cladonotinae justified by numerous homoplastic characters.
2. Leg characters are showing good signs of being diagnostic characters for true Cladonotinae.
3. Historically, the most used character of the widely forked frontal costa (wide scutellum) is not a good character for diagnosing Cladonotinae species.
4. No character historically used should be abandoned in future research of Cladonotinae. Every single one has its place in the process of diagnosing species of Cladonotinae.

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8. Supplement

Table 6. **Alphabetical list of species used in the analysis.** Species are numerated to show the number of species used in the analysis.

1	<i>Acmophyllum undulatum</i> Karsch, 1890
2	<i>Afrolarcus aequalis</i> (Karsch, 1890)
3	<i>Afrolarcus inaequalis</i> (Karsch, 1890)
4	<i>Anaselina minor</i> (Sjöstedt, 1921)
5	<i>Antillotettix nanus</i> Perez-Gelabert, 2003
6	<i>Armasius iberianus</i> Perez-Gelabert & Yong, 2014
7	<i>Astyalus tessmanni</i> (Günther, 1938)
8	<i>Austrohancockia kwangtungensis</i> (Tinkham, 1936)
9	<i>Austrohancockia orlovi</i> Storozhenko, 2016
10	<i>Austrohancockia platynota platynota</i> (Karny, 1915)
11	<i>Boczkitettix borneensis</i> (Günther, 1935)
12	<i>Boczkitettix manokwariensis</i> Tumbrinck, 2014
13	<i>Bufonides antennatus</i> Bolívar, 1898
14	<i>Bufonides sellatus</i> Hinton, 1940
15	<i>Bufonides uvarovi</i> Hinton, 1940
16	<i>Cladonotella beccarii</i> (Bolívar, 1898)
17	<i>Cladonotella gibbosa</i> (Haan, 1843)
18	<i>Cladonotella interrupta</i> (Bolívar, 1898)
19	<i>Cladonotella riedeli</i> Tumbrinck, 2014
20	<i>Cladonotella spinulosa</i> Tan, Tumbrinck, Baroga-Barbecho & Yap, 2019
21	<i>Cladonotus bhaskari</i> Tumbrinck, Deranja, Adžić, Pavlović & Skejo, 2020
22	<i>Cladonotus humbertianus</i> Saussure, 1862
23	<i>Cladoramus crenulatus</i> Hancock, 1907
24	<i>Coptottigia cristata</i> Bolívar, 1912
25	<i>Cota saxosa</i> Bolívar, 1887
26	<i>Cubanotettix turquinensis</i> Perez-Gelabert, Hierro & Otte, 1998
27	<i>Cubonotus altinotatus</i> Perez-Gelabert, Hierro & Otte, 1998
28	<i>Deltonotus gibbiceps</i> (Bolívar, 1902)
29	<i>Deltonotus subcucullatus</i> (Walker, 1871)
30	<i>Diotarus ikonnikovi</i> Bey-Bienko, 1935
31	<i>Diotarus verrucifer</i> Stål, 1877
32	<i>Dolatettix hochkirchi</i> Tumbrinck, 2014

- 33 *Dolatettix spinifrons* Hancock, 1907
- 34 *Eleleus curtus* Bolívar, 1887
- 35 *Epitettix dammermanni* Günther, 1939
- 36 *Epitettix emarginatus* (Haan, 1843)
- 37 *Epitettix fatigans* Günther, 1938
- 38 *Epitettix humilicolus* Günther, 1938
- 39 *Epitettix lativertex* Günther, 1938
- 40 *Epitettix obtusus* Storozhenko & Dawwrueng, 2014
- 41 *Epitettix spheniscus* Günther, 1974
- 42 *Epitettix tumidus* Günther, 1938
- 43 *Eurymorphopus bolivariensis* Tumbrinck, 2014
- 44 *Eurymorphopus cunctatus* (Bolívar, 1887)
- 45 *Eurymorphopus dubius* Günther, 1974
- 46 *Gestroana discoidea* (Bolívar, 1898)
- 47 *Gestroana kleukersi* Tumbrinck, 2014
- 48 *Gestroana willemsei* Tumbrinck, 2014
- 49 *Gignotettix burri* Hancock, 1909
- 50 *Haitianotettix tuberculatus* Perez-Gelabert, Hierro & Otte, 1998
- 51 *Hancockella portentosa* (Kirby, 1914)
- 52 *Hildegardia mauritiicola* Günther, 1974
- 53 *Hildegardia mauritiivaga* Günther, 1974
- 54 *Hippodes conradti* Günther, 1938
- 55 *Hippodes vicarius* Karsch, 1890
- 56 *Holoarcus altinotus* Hancock, 1909
- 57 *Holoarcus arcuatus* (Haan, 1843)
- 58 *Holoarcus ferwillemsei* Tumbrinck, 2014
- 59 *Hottettix haitianus* Perez-Gelabert, Hierro & Otte, 1998
- 60 *Hymenotes triangularis* Westwood, 1837
- 61 *Hymenotes westwoodi* Bolívar, 1887
- 62 *Ichikawatettix exsertus* (Günther, 1938)
- 63 *Ichikawatettix kleinertae* Tumbrinck, 2014
- 64 *Ingrischitettix mountalbilalaensis* Tumbrinck, 2014
- 65 *Lepocranus fuscus* Devriese, 1991
- 66 *Microthymochares pullus* Devriese, 1991
- 67 *Misythus cristicornis* (Walker, 1871)
- 68 *Misythus echinatus* (Stål, 1877)
- 69 *Misythus securifer* (Walker, 1871)
- 70 *Morphopoides coriaceum* Rehn, 1930

71	<i>Morphopoides folipes</i> (Hancock, 1909)
72	<i>Morphopoides madagascariensis</i> Günther, 1939
73	<i>Morphopoides tessmanni</i> Günther, 1939
74	<i>Morphopus acmophylloides</i> Günther, 1939
75	<i>Morphopus phyllocerus</i> (Bolívar, 1887)
76	<i>Mucrotettix gibbosus</i> Perez-Gelabert, Hierro & Otte, 1998
77	<i>Mucrotettix spinifer</i> Perez-Gelabert, Hierro & Otte, 1998
78	<i>Nesotettix cheesmanae</i> Günther, 1938
79	<i>Nesotettix samoensis</i> Holdhaus, 1909
80	<i>Notredamia dora</i> Skejo, Deranja & Adžić, 2020
81	<i>Pantelia horrenda</i> (Walker, 1871)
82	<i>Paraselina brunneri</i> (Bolívar, 1887)
83	<i>Pelusca schoutedeni</i> Günther, 1939
84	<i>Piezotettix cultratus</i> (Stål, 1877)
85	<i>Piezotettix sulcatus</i> (Stål, 1877)
86	<i>Planotettix buergersi</i> Tumbrinck, 2014
87	<i>Planotettix planus</i> Tumbrinck, 2014
88	<i>Potua coronata coronata</i> Bolívar, 1887
89	<i>Potua coronata sumatrensis</i> Bolívar, 1898
90	<i>Potua morbillosa</i> (Walker, 1871)
91	<i>Potua sabulosa</i> Hancock, 1915
92	<i>Pseudepitettix pimkarnae</i> Storozhenko & Dawwrueng, 2014
93	<i>Pseudepitettix torulosinota</i> (Zheng & Lin, 2016)
94	<i>Pseudohyboella weylandiana</i> Günther, 1938
95	<i>Scelimena producta producta</i> (Serville, 1838)
96	<i>Seyidotettix swahili</i> Rehn, 1939
97	<i>Sierratettix carinatus</i> Perez-Gelabert, Hierro & Otte, 1998
98	<i>Stegaceps brevicornis</i> Hancock, 1913
99	<i>Tepperotettix reliqua</i> Rehn, 1952
100	<i>Tetradinodula bambusae</i> Zha, 2017
101	<i>Tettilobus pelops</i> (Walker, 1871)
102	<i>Tettilobus prashadi</i> Günther, 1938
103	<i>Tettilobus trishula</i> Skejo, Bhaskar & Stermšek 2020
104	<i>Thymochares exiguus</i> Günther, 1974
105	<i>Thymochares galeatus</i> Rehn, 1929
106	<i>Tiburonotus peninsularis</i> Perez-Gelabert, Hierro & Otte, 1998
107	<i>Tondanotettix brevis</i> (Haan, 1843)
108	<i>Tondanotettix modestus</i> Günther, 1937
109	<i>Trachytettix alatus</i> Bolívar, 1908

- 110 *Trachytettix scaberrimus scaberrimus* Stål, 1876
- 111 *Truncotettix fronterizus* Perez-Gelabert, Hierro & Otte, 1998
- 112 *Truncotettix interruptus* Perez-Gelabert, Hierro & Otte, 1998
- 113 *Trypophyllum glabrifrons* Karsch, 1890
- 114 *Tuberfemurus kanokwanae* Storozhenko & Dawwrueng, 2014
- 115 *Vingselina crassa* Sjöstedt, 1921
- 116 *Willemsetettix missai* Tumbrinck, 2014
- 117 *Willemsetettix willemsei* Tumbrinck, 2014
- 118 *Xerophyllum cortices* Buckton, 1903
- 119 *Xerophyllum platycorys platycorys* (Westwood, 1839)

Ancestral state reconstructions using parsimony reconstruction are available on this link: https://drive.google.com/drive/folders/1MN2n_QrUFVhScpvkRFx8wHAlsnKbEu4?usp=sharing

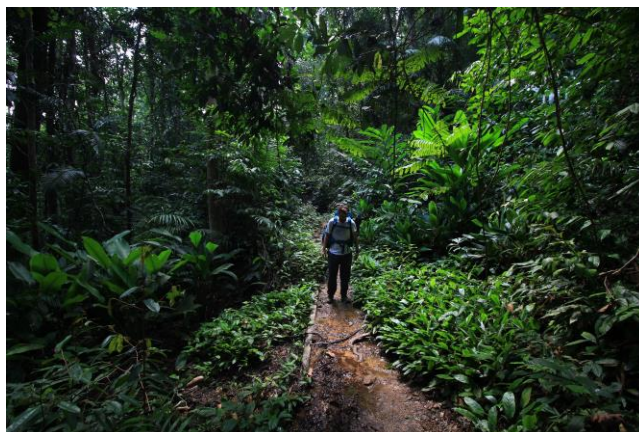
Pictures are named according to the number of state (see Table 1.) that picture represents.

Black line showing state “1” (meaning existence) of each given character of hypothetical ancestors and recent species. Cladograms below are of the same topology as the cladogram in Fig. 13. and are represented by Tables 2.-4. in the Results section.

Pictures are given just as an alternative way of visualising characters and states given in Tables 2.-4.

Curriculum vitae

Name and surname: Maks Deranja
Citizenship: Croatian
Date of birth: 8. 12. 1996.
Sex: M
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EDUCATION

2003-2011 Primary School Ivan Mažuranić, Zagreb
2011-2015 XV. Gymnasium, Zagreb
2015-2018 Bachelor's degree, University of Zagreb, Faculty of Science, Department of Biology, Biology, Zagreb
2018-2021 Master's degree, University of Zagreb, Faculty of Science, Department of Biology, Experimental Biology, module Zoology

LECTURES AND POPULARIZATION OF SCIENCE

2012-2013 The „Coacervates“ project—Working in a lab environment under the mentorship of Mihaela Marceljak Ilić, a biology teacher at XV. Gymnasium, Zagreb, and holding a public lecture on the subject as a part of the Gifted Students Program of XV. Gymnasium
2013-2014 The „Memory“ project—Working in a lab environment under the mentorship of Mihaela Marceljak Ilić, a biology teacher at XV. Gymnasium, Zagreb, and holding a public lecture on the subject as a part of the Gifted Students Program of XV. Gymnasium
2015 „Igra vjerojatnosti“ („Probability Game“) Workshop—Workshop aiming to bring mathematics, especially statistics, closer to primary school students as a part of the exhibition for popularization of science “I love Mathematics”, under the mentorship of two math teachers, Marina Ninković and Vesna Ovčina, 12.3.2015.

- 2019** „Diversity of insects of Croatian peat bogs“—Public seminar for middle school and high school students under the mentorship of Ass. prof. Andreja Brigić as a part of college course „Biodiversity of Croatian Fauna“
- 2019** „Evolution, Phylogeny, & Tetrigidae identification“ Workshop—Held a total of 15 hours in workshops for students of Institute of Biological Sciences, Faculty of Science, University of Malaya, Kuala Lumpur, conducted in English, 5.8.2019.–9.8.2019.
- 2019** Public lecture „Peninsular Malaysia—forgotten biodiversity hot-spot“ („Poluotočna Malezija—zaboravljeno žarište bioraznolikosti“) as a part of BIOMs' popular-science lectures at Faculty of Science, Department of Biology, Zagreb.
- 2021** Public lecture „Istraživanje skakavaca i zrikavaca Jadranskih otoka“ („Research of Grasshoppers and Crickets of the Adriatic Islands“) as a part of SiSB (Students' Symposium) lectures at Faculty of Science, Zagreb.

PUBLICATIONS

1. Adžić, K., Deranja, M., Franjević, D., & Skejo, J. (2020). Are Scelimeninae (Orthoptera: Tetrigidae) monophyletic and why it remains a question?. *Entomological News*, 129(2), 128-146.
2. Skejo, J., Deranja, M., & Adžić, K. (2020). Pygmy Hunchback of New Caledonia: Notredamia dora gen. n. et sp. n.—A new cladonotin (Caelifera: Tetrigidae) genus and species from Oceania. *Entomological News*, 129(2), 170-185.
3. Tumbrinck, J., Deranja, M., Adžić, K., Pavlović, M., & Skejo, J. (2020). Cockscomb-shaped twighopper, Cladonotus bhaskari sp. n., a new and rare pygmy grasshopper species from Sri Lanka (Orthoptera: Tetrigidae: Cladonotinae). *Zootaxa*, 4821(2), 333-342.
4. Adžić, K., Deranja, M., Pavlović, M., Tumbrinck, J., Skejo, J. (2021). Endangered Pygmy Grasshoppers (Tetrigidae). In DellaSala, D. & Goldstein, M. I.(Eds.). *Imperiled: The Encyclopaedia of Conservation* (pp. 1-11). Oxford: Elsevier. doi:10.1016/B978-0-12-821139-7.00046-5
5. Kasalo, N., Deranja, M., Adžić, K., Sindaco, R., Skejo, J. (in press). A nameless species of Scaria (Batrachideinae: Batrachideini) from Peru discovered on iNaturalist. *Journal of Orthoptera Research*.

PROJECTS AND INTERNATIONAL COLLABORATIONS

- 2020-2021** Leader of the international project „Grasshoppers and Crickets of the Adriatic Islands“ focused on improving the OSF (Orthoptera Species File) database in a period of two years.

VARIOUS EXTRACURRICULAR ACTIVITIES

- 2018** Assistant to teaching assistant—Assisted in a total of 90 hours in hours in a practical course of Biological Evolution
- 2018** Assistant to teaching assistant—Assisted in a total of 90 hours in hours in a practical course of Evolutionary Biology
- 2018** Laboratory Skill Training under the mentorship of dr. sc. Damjana Franjević; “*Evolution, taxonomy, and biogeography of subfamily Cladonotinae*”
- 2019** Assistant to teaching assistant—Assisted in a total of 45 hours in hours in a practical course of Evolutionary Biology
- 2019** Laboratory Skill Training under the mentorship of dr. sc. Damjana Franjević; “*Evolution, taxonomy, and biogeography of subfamily Scelimeninae*”

FIELDWORK

- 2019** 20 days (15.7.2019.–4.8.2019.) of exploring Malaysian jungles and rainforest to study a family of Tetrigidae and 5 days (5.8.2019.–9.8.2019.) of work on Malaysian entomological collections (Collections visited: Khalid Mahmood collection on Universiti Kebangsaan Malaysia, Kuala Lumpur, and collection of University of Malaya, Kuala Lumpur)
- 2020** 39 days (1.6.2020.–19.6.2020. and 15.7.2020.–3.8.2020.) of exploring Croatian islands (Vis, Lastovo, Hvar, Biševo, Korčula) to study Orthoptera in general. Field work financed by international project „*Grasshoppers and Crickets of the Adriatic Islands*“
- 2021** 58 days (1.6.2021.–28.6.2021, 13.7.2021.–8.8.2021., and 5.9.2021.–7.9.2021.) of exploring Croatian islands (Molat, Dugi otok, Kaprije, Žirje, islands of NP Kornati, Ugljan, Pašman and Olib) to study Orthoptera in general. Field work financed by international project „*Grasshoppers and Crickets of the Adriatic Islands*“

SCHOLARSHIP

- 2017-2018** Scholarship for students in STEM fields

FIELDS OF INTEREST

Evolution, phylogeny, taxonomy, systematics, and ecology of Orthoptera of Croatia and the rest of the world with an emphasis on the family of Tetrigidae, conservation and exploration of tropical areas and encouraging and accomplishing international collaborations.