Towards animal phylogeny through diversity of methods

Contents

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Preface

Systematics is increasingly in demand today. Ambitious programs like the "Systematics Agenda 2000" and the foundation of new societies (e. g. the "Gesellschaft für Biologische Systematik" in Germany) reflect the newly growing interest. One of the main reasons for this trend lies in the development of attractive new methodologies. The past decades have seen the advent of cladistics as the method of choice for reconstructing phylogenies. Molecular techniques have amplified the possibilities for studying the relationships among organisms at all levels, from individuals to populations, species, and higher taxa. Advanced computer technology gives new possibilities for creating and transmitting results from systematic studies, for instance by establishing interactive identification keys on the internet. Systematics thus provides the key tools for describing and classifying the diversity of life which is fundamental to all aspects of biology. It now has also a great impact on many other research fields like pest management, medicine, pharmacy, genetics, or conservation.

The increasing diversity in systematic methods and techniques makes it more and more difficult for individual researchers, to keep pace with recent changes. In November 2000 we therefore organized a one day symposium to give a review of the most important methods in systematics. The symposium included contributions on biogeography, cladistics, molecular systematics, classification of fossils and applications of the internet for identification. The present volume comprises some of the papers given at the symposium. Unfortunately, it was not possible to publish these works prior to the establishment of our new journal "Contributions to Natural History" in 2003. However, the submitted manuscripts were not only reviewed, but also extensively revised, since their first submission.

Hannes Baur and Christian Kropf

Jumping plant-lice of the Paurocephalinae (Insecta, Hemiptera, Psylloidea): systematics and phylogeny

Daniel Burckhardt & David Mifsud

ABSTRACT

Much confusion exists with respect to the content and definition of the psyllid subfamily Paurocephalinae. Based on a cladistic analysis of 22 morphological characters (16 adult and 6 larval), the subfamily is redefined to comprise the following five valid genera: *Aphorma* (3 species), *Camarotoscena* (12 valid species, with 1 new synonymy), *Diclidophlebia* (= *Aconopsylla, Haplaphalara, Paraphalaroida, Sinuonemopsylla* and *Woldaia;* 24 species), *Paurocephala* (52 species) and *Syntomoza* (= *Anomoterga* and *Homalocephala;* 7 species). The tribe Diclidophlebiini is synonymised with the subfamily Paurocephalinae. The seven new generic synonymies produce 25 new species combinations. A key to genera for adults and fifth instar larvae is presented. In their revised definitions the genera exhibit relatively restricted distributions and host ranges: *Aphorma:* Palaearctic, Oriental - Ranunculaceae; *Camarotoscena:* Palaearctic - Salicaceae; *Diclidophlebia:* pantropical - Tiliaceae, Malvaceae, Sterculiaceae, Melastomataceae, Rhamnaceae, Ulmaceae and Euphorbiaceae; *Paurocephala:* Old World tropics - Moraceae, Urticaceae, Ulmaceae (all Urticales), Malvaceae, Sterculiaceae (all Malvales) and Clusiaceae (Theales); *Syntomoza:* Oriental, Afrotropical, Palaearctic - Flacourtiaceae, Salicaceae. The following taxa which have been referred to the Paurocephalinae are transferred to other taxa: *Atmetocranium* to the Calophyidae and *Primascena* to the Aphalaroidinae; *Pseudaphorma* is symonymised with *Aphalara,* and *P. astigma* with *A. polygoni;* the position of *Strophingia* is confirmed in the Strophingiinae.

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Introduction

Phytophagy is widespread among insects. Coevolution with their host plants contributed probably much to the present enormous species diversity of phytophagous insects. Coevolution can be seen as association by descent of the phytophages with their host plants. In this respect coevolution, or cospeciation

as it is termed more aptly in this context, is similar to historical biogeography and can be analysed with the methods of this field (Humphries et al. 1986; Brooks & McLennan 1991; Page 1993a, 1993b, 1995; Burckhardt 2003). A prerequisite for cospeciation studies is the availability of independently derived explicit phylogenetic hypotheses for the phytophages and the plants.

In this respect, a potentially significant taxon is the superfamily Psylloidea or jumping plant lice, comprising some 3000 described species of plant-sap feeding bugs (Burckhardt & Basset 2000). Psylloids are usually highly specific to their almost exclusively angiosperm hosts both at lower and higher taxonomic levels. A major drawback in using psylloids in cospeciation studies is the absence of a well-corroborated phylogenetic base in several groups. One taxon with a particularly confused history is the subfamily Paurocephalinae. Its content varies between authors, and there is no explicit phylogenetic hypothesis available of its internal relationships.

The confusion started when Crawford (1914a) erected *Paurocephala* for *P. psylloptera*, a species developing on *Ficus ulmifolia* (Moraceae), and noted a resemblance to *Pauropsylla* Rübsaamen, also associated with *Ficus* spp. In his monograph of the Psyllidae of the New World, Crawford (1914b) assigned both *Paurocephala* and *Pauropsylla* to the subfamily Pauropsyllinae. He added the two species *Paurocephala magnifrons* Crawford (currently placed in *Platycorypha* Tuthill, Psyllidae, possibly Psyllinae/Arytaininae) and *Psylla ilicis* Ashmead (currently placed in *Gyropsylla* Brethes, Psyllidae, Aphalarinae). In the same year Enderlein (1914) described *Agonoscena* and included *Agonoscena sauteri* Enderlein from Taiwan. Crawford (1920) suggested that *Agonoscena sauteri* might be synonymous with *Paurocephala psylloptera* but that *Agonoscena* might be a valid genus, as Enderlein had fixed *Psylla targionii* Lichtenstein as type species, which is not closely related to *P. psylloptera*.

In the following decades additional species have been added, usually characterised by the lack of genal processes and the presence of a pterostigma in the forewing. This combination of characters, however, does not indicate phylogenetic relationships, thus producing an extremely artificial classification. Several authors removed species from *Paurocephala* to other genera (e. g. Heslop-Harrison 1952, Loginova 1972, Hollis 1984, Brown & Hodkinson 1988) trying to make *Paurocephala* more homogenous. The subgenus *Thoracocorna* was established for *Paurocephala chonchaiensis* Boselli by Klimaszeski (1970) and later synonymised with *Paurocephala* Crawford by Loginova (1972). Hodkinson (1983, 1986a) concluded that *Paurocephala* is a large Old World genus, and that the few New World species probably belong to a separate genus. For diagnosing *Paurocephala*, Brown & Hodkinson (1988) used the presence of weakly sclerotised apical metatibial spurs, the basally thickened portion of the

distal segment of the aedeagus and the lack of basimetatarsal spurs. In this revised definition, *Paurocephala* included also a few New World species. Burckhardt (1996) in adding two species from Paraguay concluded that the phylogenetic significance of these characters is difficult to assess, and that the monophyly of *Paurocephala* remains debatable. Mifsud & Burckhardt (2002) redefined *Paurocephala* to include 51 named Old World species and, thus, confirmed Hodkinson's (1983, 1986a) view.

Similarly confusing are the discussions on the phylogenetic relationships of *Paurocephala*. Crawford (1914b) assigned *Paurocephala* together with *Pauropsylla*, *Heteropsylla* Crawford (now placed in Psyllidae, Ciriacreminae) and *Calophya* Löw (now placed in Calophyidae), to the Pauropsyllinae. Several authors including Mathur (1975) followed this concept. Vondráček (1957) included the Pauropsyllinae in the Aphalaridae, whereas Loginova (1972) treated the Pauropsyllini as tribe of the Carsidaridae. Heslop-Harrison (1952), in contrast, removed *Paurocephala* from the Pauropsyllinae to the Aphalarinae. Vondráček (1963a), who followed Heslop-Harrison's (1952) view, treated the aphalarids as a family and erected the tribe Paurocephalini for *Paurocephala* and *Camarotoscena* Haupt, the latter as subgenus of the former, in the subfamily Aphalaroidinae. Klimaszewski (1964) adopted a similar view but raised the group to subfamily level, Paurocephalinae, of the Aphalaridae. He included in the subfamily, among other genera, *Atmetocranium* Tuthill and *Syncoptozus* Enderlein.

Based on much sounder evidence, Hollis (1984) and White & Hodkinson (1985) confirmed the assignment of *Paurocephala* to the Aphalaridae. White & Hodkinson (1985) assigned *Paurocephala* and *Camarotoscena* to the Paurocephalinae. In a closely related subfamily, the Euphyllurinae, they included the Diclidophlebiini with *Diclidophlebia* Crawford, *Paraphalaroida* Loginova and *Haplaphalara* Uichanco, in addition to the tribes Euphyllurini with six genera including *Syntomoza* Enderlein, and the Ctenarytainini. The Euphyllurini are identical with the concept of Loginova (1973). Burckhardt (1991) synonymised the Ctenarytainini with the Spondyliaspidini.

The genus *Aphorma* Hodkinson, according to Heslop-Harrison (1949), "fitted" between *Aphalaroida* Crawford and *Paurocephala*. Burckhardt (1983), Burckhardt & Lauterer (1989) and Burckhardt & Bänziger (1995) suggested a close relationship to *Camarotoscena*. *Anomoterga* Klyver, *Aconopsylla* Tuthill & Taylor and *Homalocephala* Yang & Li were all referred to the Paurocephalinae, however, without detailed evidence (Hodkinson 1983; Morgan 1984; Yang & Li 1987). Conci & Tamanini (1985) erected the genus *Pseudaphorma* for a single male which they felt belongs to the Aphalaridae, Rhinocolinae or Paurocephalinae.

Brown & Hodkinson (1988) suggested that the monophyly of the subfamily Paurocephalinae sensu White & Hodkinson (1985) is doubtful and that it may ultimately prove necessary to include the Diclidophlebiini (genera *Diclidophlebia*, *Paraphalaroida* and *Haplaphalara*) and Togepsyllinae (*Togepsylla* Kuwayama and *Syncoptozus*). They transferred *Haplaphalara* to the Paurocephalinae, and concluded that Neotropical *Haplaphalara* form a homogeneous group, which may be generically distinct from the Old World species. *Woldaia* Brown & Hodkinson was put close to *Diclidophlebia* (Euphyllurinae, Diclidophlebiini). Burckhardt & Brown (1992) transferred *Woldaia* to the Paurocephalinae.

Using differences in the hindwing venation, Klimaszeski (1993) subdivided the family Aphalaridae sensu White & Hodkinson (1985) into the Aphalaridae (with Aphalarinae and Togepsyllinae) and Rhinocolidae (with Rhinocolinae, Aphalaroidinae, Bharatianinae (spelt Bhratianinae) and Strophingiinae (spelt Strophinginae)). Liviinae, Paurocephalinae and some Euphyllurinae are probably included in the latter family. Burckhardt & Lauterer (1997) showed that the characters for this family separation are trivial and synonymised the two.

Klimaszewski (1998) erected the genus *Primascena* for a fossil species in Dominican amber which he assigned to the Rhinocolidae, Paurocephalinae. According to the original drawings and the description, the taxon lacks genal processes and metabasitarsal spurs. Finally the genus *Sinuonemopsylla* Li & Yang (1991), which was referred to the Rhinocolinae, is included in the following considerations as it lacks basimetatarsal spurs.

The present paper revises and cladistically analyses the Paurocephalinae with the following aspects addressed in particular: monophyly, definition and content of Paurocephalinae; internal relationships of Paurocephalinae; relationships of Paurocephalinae with Togepsyllinae, Euphyllurinae sensu White & Hodkinson (1985), *Atmetocranium*, *Strophingia*, *Pseudaphorma* and *Primascena*. Host plants and distributions are examined to search for general patterns.

Material and Methods

Morphological terminology follows mostly Ossiannilsson (1992). Hollis (1976) is followed here in the usage of the terms “spurs” and “spines” in relation to the metatibia.

Material from following collections was examined: AMNH, American Museum of Natural History, New York; BAUC, Beijing Agricultural University, Beijing, China; BMNH, The Natural History Museum, London, UK; BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA; MHNG, Muséum d’histoire naturelle, Geneva, Switzerland; NCHU, National Chung Hsing University, Taiwan; NHMB,

Naturhistorisches Museum, Basel, Switzerland; OMNH, Osaka Museum of Natural History, Osaka, Japan; TULE, Tokyo University of Agriculture, Laboratory of Entomology, Japan; USNM, National Museum of Natural History, USDA, Beltsville, MD, USA.

The cladistic analyses were performed with WinClada 1.0 (Nixon 2002) and Hennig86 (Farris 1988), using the mh and bb* search options and successive weighting. A consensus tree was calculated with the nelsen command.

The aim of the analysis was to find monophyletic groupings among the species referred to the genera *Aconopsylla*, *Anomoterga*, *Aphorma*, *Camarotoscena*, *Diclidophlebia*, *Haplaphalara*, *Homalocephala*, *Paraphalaroida*, *Paurocephala*, *Paurocephala* (*Thoracocorna*), *Sinuonemopsylla* and *Woldaia*. The genera *Atmetocranium*, *Ctenarytaina*, *Euphyllura*, *Strophingia*, *Syncoptozus*, *Syntomoza* and *Togepsylla* were included in the analysis to see whether they exhibit close cladistic relationships to any of the above genera. *Rhinocola aceris* served as out-group. The species selected for the analysis are listed in Table 1. If possible the type species was selected (indicated with an asterisk in Table 1). In the few cases where the data for the type species were inclomplete (e.g. missing larvae), a species closely related to the type species was selected.

The characters used in the present analyses have partly been used previously to delimit genera or higher level taxa. Other characters come from an extensive morphological comparative analysis which is detailed in Mifsud (2001) and Mifsud & Burckhardt (2002). Characters, which are treated as unordered, are taken from adults (Table 2, characters 1–16) and the last larval instar (Table 2, characters 17–22).

Cladistics

The cladistic analysis resulted, after 2 iterations, in 18 most parsimonious trees (weighted characters: length 218, consistency index 72, retention index 91; unweighted characters: length 46, consistency index 58, retention index 85). Fig. 9 shows the consensus with character states mapped onto the tree with the fast character optimisation.

A monophyletic clade, which is defined here as the Paurocephalinae, is supported by characters 13 and 15. Character 13, a sclerotised patch with spines on the first visible abdominal tergite, is particularly noteworthy as it is unique within Psylloidea. The Paurocephalinae clearly split into 5 clades which are given generic rank here. *Aphorma* is the only of the five genera whose definition agrees with previous concepts. Both *Camarotoscena* and *Paurocephala* become more restricted, *Camarotoscena africana* and *C. unicolor* are more closely rela-

ted to species assigned to the genera *Syntomoza*, *Anomoterga* and *Homalocephala*, rather than to the remainder of *Camarotoscena*, and *Paurocephala* becomes restricted to Old World species. The content of *Syntomoza* and *Diclidophlebia*, on the other hand, is broadened to include species previously assigned to 4 and 7 genera respectively. Except for *Paurocephala*, which includes 4 monophyletic species groups (Mifsud & Burckhardt 2002), there is no resolution within the five genera. *Diclidophlebia* as defined here is diverse with respect to adult morphology (head, forewing, hind legs) which is in contrast to its homogenous larval morphology. Despite the wide range of adult morphology in *Diclidophlebia,* no infrageneric groupings are supported by the present analysis, in particular there is no support for a separation of the Old World from the New World taxa. Further studies will be necessary to elucidate the phylogenetic relationships within this genus of which, at most, half of the existing species are described up to now.

The cladistic analysis suggests a basal position of *Aphorma*, and a sister-group relationship of *Camarotocena* with an unresolved clade of *Syntomoza* + *Paurocephala* + *Diclidophlebia* (Fig. 9). The support of this grouping is, however, weak. A consequence of the phylogeny discussed here is the synonymy of Paurocephalinae and Diclidophlebiini.

The cladistic analysis places *Strophingia*, *Ctenarytaina*, *Euphyllura*, *Atmetocranium*, *Togepsylla* and *Syncoptozus* clearly outside the monophyletic Paurocephalinae. These genera are probably not close to the Paurocephalinae and more work is required to investigate their phylogenetic relationships.

Subfamily Paurocephalinae

Paurocephalini Vondraček, 1963a: 277. Type-genus: *Paurocephala* Crawford, 1914a.

Paurocephalinae; Klimaszewski 1964: 92; Bekker-Migdisova 1973: 108.

Diclidophlebiini Bekker-Migdisova, 1973: 100. Type-genus: *Diclidophlebia* Crawford, 1920. **Syn. n.**

Diagnosis. **Adult**. Genal cones absent; frons developed, exposed in *Camarotoscena* with parallel-sided margins, small trapezoidal in *Aphorma* and *Syntomoza*, small to moderately sized trapezoidal in *Paurocephala* and small to relatively large trapezoidal in *Diclidophlebia*. Coronal suture fully developed. Metacoxa rounded, with distinct meracanthus, small and apically rounded (Fig. 2E, F) to long, marginally curved or straight laterally (Fig. 2D) or horn-shaped (Fig. 2G); metatibia without basal spine, with an incomplete crown of 4–12 apical spurs (Fig. 2H–N), with (Fig. 2K) or without (Fig. 2M) apical widening. Basal metatarsus without black spurs. First visible abdominal tergite, laterally bearing a

patch with spinule-like microsculpture varying from relatively small and indistinct (Fig. 5F–I) to very large forming a finger-like anteriorly directed process (in some *Paurocephala* spp.). Forewing with costal break developed (Figs. 1, 2 A–C); pterostigma usually developed (absent in *Aphorma*, Fig. 1A). Male proctiger 1-segmented (Fig. 3E–I). Aedeagus 2 or sometimes indistinctly 3-segmented, apex of proximal portion more or less distinctly inflated with folds on the anterior face (Figs. 3I, 4H), apex of distal portion bulbose (Fig. 5H–N).

Fifth instar larva. Margin of forewing pads (Fig. 6E–G) and caudal plate (Fig. 7J–L) with sectasetae. Tarsal arolium short triangular to fan shaped (Fig. 7E–I). Outer circumanal ring usually consisting of a single row of pores (Fig. 7M–O) but in some *Paurocephala* species the circumanal ring is subdivided at irregular intervals or consists of multiple pores laterally. Additional pore fields present in all genera (Figs. 7M–O, 8) except for *Paurocephala* Crawford.

Discussion. The combination of the above listed characters diagnoses the subfamily Paurocephalinae within the superfamily Psylloidea. The following two characters are considered to be autapomorphies for the subfamily (Table 2, Fig. 9): first visible abdominal tergite bearing lateral patch of spinules, sometimes forming process (character 13-1), apex of proximal portion of aedeagus inflated with folds on the anterior face (character 15-1).

Key to Paurocephalinae genera

Adult

1 Forewing membrane with plate-like surface structures (Fig. 1A). Head angular anteriorly, vertex clearly delimited from genae. Frons elongate, parallel-sided. *Aphorma*

– Forewing membrane without plate-like surface structures. Head rounded anteriorly, vertex passing smoothly into genae. Frons rhomboidal or elliptical. 2

2 Head strongly inclined at about 90° to longitudinal body axis. *Syntomoza*

– Head almost horizontal or inclined but always at less than 90° to longitudinal body axis. 3

3 Head weakly inclined, at most, 45° to longitudinal body axis. Metascutellum forming a distinct horn. Hind legs long and slender. Old World. *Paurocephala*

– Character combination different. 4

4 Antenna about as long as head width. *Camarotoscena*

– Antenna at least 1.5 times as long as head width. *Diclidophlebia*

Fifth instar larva

1 Additional pore fields lacking. *Paurocephala*
– Additional pore fields present (Figs. 7M–O, 8). 2
2 Tibiae with massive peg-like spurs (Fig. 7D). *Syntomoza*
– Tibiae lacking peg-like spurs (Fig. 7A–C). 3
3 Antenna 9-segmented, flagellum bearing sectasetae (Fig. 6C). Extra pore fields on caudal plate widely distant from outer circumanal ring (Fig. 8). *Diclidophlebia*
– Antenna 7-segmented, flagellum lacking sectasetae (Fig. 6A, B). Extra pore fields on caudal plate near circumanal ring (Fig. 7M, N). 4
4 Sectasetae on abdominal dorsum relatively sparse (Fig. 7K). *Aphorma*
– Sectasetae on abdominal dorsum forming dense rows (Fig. 7L). *Camarotoscena*

Aphorma Hodkinson

Aphorma Hodkinson, 1974: 76. Type species: *Aphalara bagnalli* Laing, 1929, by original designation.

Description. **Adult**. Head weakly inclined from longitudinal body axis, directed fowards, without genal processes; vertex large subtrapezoidal, anteriorly more or less delimited to genae, sometimes anterior margin with tubercle, frons small trapezoidal. Frontal ocellus slightly hidden from above; genae strongly expanded at base on either side of clypeal apex, with transverse suture, separating each a subrectangular sclerite from the remainder of genae. Antennae about as long as head width; with each a subapical rhinarium on segments 4, 6, 8, and 9; segment 9 strongly inflated (Fig. 3D). Thorax flattened dorsally, pronotum relatively long and flat; propleurites rectangular, higher than wide, divided by diagonal suture. Parypterae forming large plates extending to posterior pronotal margin. Forewing membrane coriaceous (Fig. 1A), covered by tubercular surface structures, sometimes also with spinules; pterostigma lacking. Metacoxa with horn-shaped meracanthus. Metatibia relatively short and stout (Fig. 2H), without basal spine, slightly widening apically, bearing an incomplete crown of 6–9 sclerotised apical spurs. Metabasitarsus without black spurs. Male proctiger simple, tubular, more or less straight posteriorly (Fig. 3E); male paramere lamellar and simple (Fig. 4A); distal portion of aedeagus relatively short with rounded apical dilatation. Female genitalia cuneate (Fig. 5A).

Fifth instar larva. Antenna 7-segmented (Fig. 6A), rhinaria formula as 3577. Tarsal arolium large, triangular, petiolate with developed unguitractor (Fig. 7E).

Sectasetae present behind eye, sparse on wing pad margins and on abdomen laterally and dorsally. Anus ventral, outer circumanal ring consisting of a single row of pores, additional pore fields developed (Fig. 7M).

Comments. The genus has been revised by Burckhardt & Bänziger (1995) who recognised three valid described species in the Palaearctic and Oriental regions. Species develop, as far as known, on Ranunculaceae.

Camarotoscena Haupt

Camarotoscena Haupt, 1935: 228. Type species: *Rhinocola speciosa* Flor, 1861a, by original designation.

Description. Adult. Head down-curved, without genal processes; vertex subtrapezoidal and anteriorly passing smoothly into genae; frons developed, exposed, with parallel-sided margins. Frontal ocellus situated on anterior margin of head; genae small and rounded. Antennae slightly longer than head width; with each a subapical rhinarium on segments 4, 6, 8, and 9 (Fig. 3C); thorax curved dorso-laterally, pronotum relatively long and flat. Forewing membrane coriaceous (Fig. 1B, C), covered with surface spinules, often bearing dark pattern (Fig. 1B), pterostigma present. Metacoxa with horn-shaped meracanthus. Metatibia relatively short and stout (Fig. 2I), without basal spine, weakly widening apically, bearing an incomplete crown of 8–12 sclerotised apical spurs and 2–3 small unsclerotised spurs. Metabasitarsus without black spurs. Male proctiger simple, tubular, curved posteriorly (Fig. 3F); male paramere lamellar and simple (Fig. 4B); distal portion of aedeagus relatively short with rounded apical dilatation (Fig. 4H). Female genitalia cuneate (Fig. 5B, G).

Last instar larva. Antenna 7-segmented (Fig. 6B), rhinaria formula as 3577. Tarsal arolium relatively short triangular, petiolate with developed unguitractor (Fig. 7F). Sectasetae present on head and thorax dorsally, abdomen laterally and dorsally and reduced on wing pad margin. Caudal plate and wing pads with numerous long simple setae. Anus terminal or ventral, outer circumanal ring consisting of a single row of pores, additional pore fields developed (Fig. 7N).

Comments. The genus contains 12 Palaearctic species associated with *Populus* spp. (Salicaceae). Loginova (1975) revised the recent taxa and included *C. africana* and *C. unicolor* which are transferred here to *Syntomoza*.

Species catalogue

badia Loginova, 1965: 198. Distribution: Tajikistan. Host plant: *Populus tadzhikistanicus* (Salicaceae).

bianchii Loginova, 1975: 56. Distribution: Kyrgyzstan, Mongolia, Russia (East Siberia), Uzbekistan, Tajikistan. Host plant: *Populus laurifolia* (Salicaceae).

fulgidipennis Loginova, 1975: 57. Distribution: Armenia, Azerbaijan, Iran, Turkey. Host plant: *Populus* sp. (Salicaceae).

hoberlandti Vondraček, 1953: 445. Distribution: Iran, Iraq, Turkey, Turkmenistan. Host plant: *Populus nigra*, *P.* sp. (Salicaceae).

lauta Loginova, 1975: 56. Distribution: Azerbaijan. Host plant: *Populus* sp. (Salicaceae).

libera Loginova, 1975: 59. Distribution: Azerbaijan. Host plant: *Populus* sp. (Salicaceae).

pamirica Baeva, 1983: 256. Distribution: Tajikistan. Host plant: *Populus* sp. (Salicaceae).

personata Loginova, 1975: 58; *huashana* Li & Yang, 1989: 74, **syn. n**. Distribution: China (Shaanxi Province), Russia (East Siberia, Far East). Host plant: *Populus* sp. (Salicaceae). *Comment*: The examination of a ♀ parataype of *C. huashana* (BAUC) showed that this species is characterised by the long apical process of the female subgenital plate which is diagnostic for *C. personata*. The two species are, therefore, synonymised.

speciosa (Flor, 1861a: 526). Distribution: From Spain to Central Asia. Host plant: *Populus alba*, *P. nigra*, *P. pyramidalis* (Salicaceae).

subrubescens (Flor, 1861b: 411). Distribution: Croatia, France, Italy, Spain, Turkey. Host plant: *Populus robusta* (Salicaceae).

trjapitzini Loginova, 1968: 282. Distribution: Armenia. Host plant: *Populus* sp. (Salicaceae).

ujenci Klimaszewski, 1982: 3. Distribution: Mongolia. Host plant: *Populus diversifolia* (Salicaceae).

Diclidophlebia Crawford

Heteroneura Crawford, 1919: 152; nec Fallén, 1810. Type species: *Heteroneura oceanica* Crawford, 1919, by original designation and monotypy.

Diclidophlebia Crawford, 1920: 355; replacement name for *Heteroneura* Crawford.

Gyroza Enderlein, 1921: 122; replacement name for *Heteroneura* Crawford; objective junior synonym of *Diclidophlebia*.

Haplaphalara Uichanco, 1921: 260. Type species: *Aphalara dahli* Rübsaamen, 1905, by original designation. **Syn. n.**

Aconopsylla Tuthill & Taylor, 1955: 247. Type species: *Psylla sterculiae* Froggatt, 1901, by original designation. **Syn. n.**

Paraphalaroida Loginova, 1972: 851. Type species: *Paurocephala fremontiae* Klyver, 1930, by original designation. **Syn. n.**

Woldaia Brown & Hodkinson, 1988: 49. Type species: *Woldaia nebulosa* Brown & Hodkinson, 1988, by original designation and monotypy. **Syn. n.**

Sinuonemopsylla Li & Yang, 1991: 11. Type species: *Sinuonemopsylla excetrodendri* Li & Yang, 1991, by original designation and monotypy. **Syn. n.**

Description. **Adult**. Head weakly inclined from longitudinal body axis directed fowards, without genal processes; vertex subrectangular, smoothly passing into genae; frons small to relatively large. Antennae longer than head width; with each a subapical rhinarium on segments 4, 6, 8, and 9 (Fig. 3B),

sometimes a small subapical rhinarium present on segment 3. Thorax flattened to marginally curved dorsally, pronotum weakly inclined; propleurites narrow. Forewing membrane smooth (Fig. 1D–K), covered with surface spinules, sometimes forming distinct cellular pattern (Fig. 1H); forewing often with colour pattern (Fig. 1D, E, G); pterostigma developed, as long as or longer than half Rs vein. Metacoxa with short meracanthus almost straight laterally and rounded apically (Fig. 2E). Metatibia moderately long, without basal spine; with or without apical widening, bearing a crown of 4–12 often sclerotised apical spurs arranged as 3 + 1 (Fig. 2L), 4 + 2 and 8 slender unsclerotised setae (Fig. 2K), an incomplete crown of 7–9 black spurs (Fig. 2J) or 10–12 hardly sclerotized spurs (Fig. 2M). Metabasitarsus without black spurs. Male proctiger simple tubular, straight to globular posteriorly (Fig. 3G, H); male paramere robust, often short and complex (Fig. 4C, D, G); aedeagus 2 or 3-segmented with the terminal segment varying from relatively simple to complex (Fig. 4I–L). Female genitalia short (Fig. 5D), sometimes upturned apically (Fig. 5C).

Last instar larva. Antenna 9-segmented (Fig. 6C), rhinaria formula as 3578. Tarsal arolium triangular, distinctly petiolate with long unguitractor (Fig. 7H, I). Sectasetae present on antenna, behind eye, on wing pad margins, on legs, on abdomen laterally; dorsal sclerites with short lanceolate setae. Anus terminal, outer circumanal ring consisting of a single row of pores, additional pore fields developed forming semicircular to oval patterns (Fig. 8).

Comments. The genus *Diclidophlebia* contains 24 described species but numerous undescribed species are present in collections. The genus has a pantropical distribution and is associated with a variety of host families (Tiliaceae, Malvaceae, Sterculiaceae, Melastomataceae, Rhamnaceae, Ulmaceae and Euphorbiaceae).

Species catalogue

adelaidae (Braza & Calilung, 1981: 344), **comb. n.** from *Paurocephala*; *Haplaphalara*, Navasero & Calilung, 1998: 14. Distribution: Philippines. Host plant: *Diplodiscus paniculatus* (Tiliaceae).

crassiflagellata (Burckhardt, 1996: 79), **comb. n.** from *Paurocephala*. Distribution: Paraguay. Host plant unknown, perhaps *Luehea paniculata* (Tiliaceae).

dahli (Rübsaamen, 1905: 23), **comb. n.** from *Aphalara*; *Haplaphalara*, Uichanco 1921: 261; *Strophingia*, Crawford 1925: 40. Distribution: Bismark Archipelago, New Caledonia, Papua New Guinea, Philippines (Luzon). Host plant: *Thespesia* spp. (Malvaceae).

eastopi Vondraček, 1963b: 289. Distribution: Cameroon, Nigeria. Host plant: *Triplochiton scleroxylon* (Sterculiaceae).

excetrodendri (Li & Yang, 1991: 11), **comb. n.** from *Sinuonemopsylla*. Distribution: China (Guangxi). Host plant: *Excetrodendron hsienmu* (Tiliaceae).

fava (Brown & Hodkinson, 1988: 44), **comb. n.** from *Haplaphalara*. Distribution: Panama. Host plant: *Miconia argentea* (Melastomataceae).

fremontiae (Klyver, 1930: 111), **comb. n.** from Paurocephala; *Paraphalaroida,* Loginova 1972: 851. Distribution: USA (California). Host plant: *Fremontodendron californica* (Sterculiaceae).

grewiae (Kandasamy, 1986: 61) **comb. n.** from *Paurocephala*. Distribution: India. Host plant: *Grewia rotundifolia* (Tiliaceae).

harrisoni Osisanya, 1969: 71. Distribution: Central African Republic, Nigeria. Host plant: *Triplochiton scleroxylon* (Sterculiaceae).

heterotrichi (Caldwell & Martorell, 1952: 605), **comb. n.** from *Paurocephala*; *Haplaphalara*, Brown & Hodkinson 1988: 40. Distribution: Puerto Rico. Host plant: *Heterotrichum cymosum* (Melastomataceae).

lanceomedia (Brown & Hodkinson, 1988: 37), **comb. n.** from *Paurocephala*. Distribution: Panama. Host plant unknown.

longitarsata (Brown & Hodkinson, 1988: 42), **comb. n.** from *Haplaphalara*. Distribution: Panama. Host plant: *Miconia argentea* (Melastomataceae).

maculata (Crawford, 1919: 151), **comb. n.** from *Paurocephala*; *Haplaphalara*, Loginova 1972: 841. Distribution: Malaysia (Sabah), Singapore. Host plant unknown.

maculipennis (Brown & Hodkinson, 1988: 47), **comb. n.** from *Haplaphalara*. Distribution: Panama, Trinidad. Host plant: *Trema micrantha* (Ulmaceae).

menoni (Mathur, 1975: 50), **comb. n.** from *Paurocephala*; *Haplaphalara*, Hollis 1984: 28. Distribution: India. Host plant: *Grewia asiatica* (Tiliaceae).

nebulosa (Brown & Hodkinson, 1988: 49), **comb. n.** from *Woldaia*. Distribution: Panama. Host plant: *Luehea seemannii* (Tiliaceae).

oceanica (Crawford, 1919: 152). Distribution: Malaysia (Sabah), Philippines (Basilan, Luzon), Singapore. Host plant unknown.

paucivena (Brown & Hodkinson, 1988: 39), **comb. n.** from *Paurocephala*. Distribution: Guatemala, Panama. Host plant unknown.

paucipunctata (Brown & Hodkinson, 1988: 40), **comb. n.** from *Haplaphalara*. Distribution: Panama. Host plant: *Conostegia xalapensis* (Melastomataceae).

setinervis (Burckhardt, 1996: 78), **comb. n.** from *Paurocephala*. Distribution: Paraguay. Host plant unknown.

sterculiae (Froggatt, 1901: 255), **comb. n.** from *Psylla*; *Aconopsylla,* Tuthill & Taylor 1955: 247. Distribution: Australia (NSW, SA). Host plant: *Brachychiton* spp. (Sterculiaceae).

trimaculata (Mathur, 1975: 69), **comb. n.** from *Paurocephala*; *Haplaphalara*, Hollis 1984: 28. Distribution: India. Host plant: *Zizyphus jujuba* (Rhamnaceae).

tuxtlaensis (Conconi, 1972: 51), **comb. n.** from *Paurocephala*; *Haplaphalara*, Brown & Hodkinson 1988: 40. Distribution: Mexico. Host plant: *Conostegia xalapensis*, *Miconia* sp. (Melastomataceae).

xuani Messi in Messi et al., 1998: 233; *Camarotoscena* sp., Vondráček 1963a: 278. Distribution: Cameroon, Nigeria. Host plant: *Ricinodendron heudelotii* (Euphorbiaceae).

Following species probably also belongs to *Diclidophlebia*:

Haplaphalara durio Heslop-Harrison, 1952: 974; nomen nudum, Malaysia.

Paurocephala Crawford

Paurocephala Crawford, 1914a: 293. Type species: *Paurocephala psylloptera* Crawford, 1914a, by original designation.

Subgenus *Thoracocorna* Klimaszewski, 1970: 427. Type species: *P. chonchaiensis* Boselli, 1929, by original designation; synonymised with *Paurocephala* by Loginova 1972: 842.

Description. Adult. Head down-curved, without genal processes; frons small to moderate-sized trapezoidal. Antenna 8- to 10-segmented, shorter to longer than head width; with each a subapical rhinarium on segments 3, 4, 6, 7, segments 3, 5, 7, 8, or segments 4, 6, 8, 9. Thorax curved dorso-laterally, pronotum relatively long; metascutellum produced into horn-shaped structure. Forewing membrane smooth, often covered with surface spinules, rarely with dark pattern, pterostigma developed. Metacoxa with short to long meracanthus, margin curved or straight laterally. Metatibia short to moderately long, without basal spine, weakly widening apically, bearing an incomplete crown of 6–8 unsclerotised apical spurs. Metabasitarsus without black spurs. Male proctiger simple, tubular, often with distinct lateral plates posteriorly; male paramere lamellar to simple, often with stout or peg-like setae on inner surface; distal portion of aedeagus relatively short with rounded apical dilatation. Female genitalia cuneate, sometimes up-turned apically.

Last instar larva. Antenna 3-segmented, sometimes subdivided, flagellum rarely with distinct subdivisions; rhinaria formula, when 3-segmented, 3333. Tarsal arolium relatively short triangular to fan-shaped, basally expanded, petiolate with developed unguitractor. Sectasetae present on head, antenna, dorsal sclerites and wing pads. Anus ventral or terminal, circumanal ring simple without additional pore fields, if present, laterally connected to outer circumanal ring.

Comments. The genus has been revised by Mifsud & Burckhardt (2002) who recognised 51 species, and one species has been added by Navasero & Calilung (2001). *Paurocephala* is restricted to the Old World and is most diverse in the Oriental region (43 spp.) with some Afrotropical species. Host records include: Moraceae, Urticaceae, Ulmaceae (all Urticales), Malvaceae, Sterculiaceae (all Malvales) and Clusiaceae (Theales).

Syntomoza Enderlein

Syntomoza Enderlein, 1921: 117. Type species: *Euphyllura magna* Kuwayama, 1907, by original designation and monotypy.

Anomoterga Klyver, 1932: 93. Type species: *Anomoterga tahuata* Klyver, 1932, by original designation and monotypy. **Syn. n.**

Homalocephala YANG & LI, 1987: 54. Type species: *Homalocephala homali* YANG & LI, 1987, by original designation and monotypy. **Syn. n.**

Description. **Adult**. Head down-curved, without genal processes; vertex passing smoothly into genae; frons small trapezoidal. Frontal ocellus clearly visible from above. Antennae slightly longer than head width, segment 3 very long; with each a subapical rhinarium on segments 4, 6, 8, and 9 (Fig. 3A); thorax curved dorso-laterally, pronotum relatively long and flat. Forewing membrane smooth to rugose (Fig. 2A–C), covered with surface spinules, pterostigma developed, longer than half Rs vein. Metacoxa with short robust to horn-shaped meracanthus (Fig. 2G). Metatibiae relatively short and stout, slightly widening apically, without basal spine, bearing an incomplete crown of 9–11 sclerotised apical spurs and 2–3 small black stout setae (Fig. 2N). Metabasitarsus without black spurs. Male proctiger simple, tubular, curved posteriorly, bearing few setae on inner surface (Fig. 3I); male paramere lamellar to complex, widened apically (Fig. 4E, F); distal portion of aedeagus relatively short with rounded apical dilatation (Fig. 4M, N); male subgenital plate produced apically. Female genitalia long (Fig. 5E).

Last instar larva. Antenna 7-segmented (Fig. 6D), rhinaria formula as 3577. Tarsal arolium short fan-shaped with developed unguitractor (Fig. 7G). Sectasetae present on abdominal margin and on dorsum of caudal plate. Legs with massive spurs (Fig. 7D). Anus ventral, outer circumanal ring consisting of a single row of pores, additional pore fields forming oval patches (Fig. 7L, O).

Comments. The genus contains 7 species occurring in the Oriental, Afrotropical and Palaearctic regions. Host plants include Flacourtiaceae with one species associated with *Populus* (Salicaceae).

Species catalogue

africana (LOGINOVA, 1975: 55), **comb. n.** from *Camarotoscena*. Distribution: Ethiopia, Kenya, Uganda. Host plant: *Dovyalis abyssinica* (Flacourtiaceae).

homali (YANG & LI, 1987: 54), **comb. n.** from *Homalocephala*. Distribution: China (Fujian, Guangdong, Guangxi. Host plant: *Homalium hainanense* (Flacourtiaceae).

hsenpinensis (FANG & YANG, 1986: 137), **comb. n.** from *Anomoterga*. Distribution: (China (Fujian), Hong Kong, Taiwan, Vietnam. Host plant: *Homalium cochinchinensis* (Flacourtiaceae).

magna (KUWAYAMA, 1907: 151), from *Euphyllura,* Enderlein 1921: 117. Distribution: Korea, Japan. Host plant: *Idesia polycarpa*, *Xylosma congestum* (Flacourtiaceae); Klimaszewski (1973) and Loginova (1973) report also *Myroxylon japonicum* (Fabaceae) which is an unlikely host.

scolopiae YANG, 1984: 23. Distribution: Taiwan. Host plant: *Scolopia oldhamii* (Flacourtiaceae).

tahuata (KLYVER, 1932: 94), **comb. n.** from *Anomoterga*. Distribution: Marquesas Islands. Host plant unknown.

unicolor (LOGINOVA & PARFENTIEV, 1958: 99), **comb. n.** from *Camarotoscena*. Distribution: Afghanistan, Armenia, Iran, Kazakhstan, Kyrgyzstan, Mongolia, Uzbekistan, Tajikistan. Host plant: *Populus diversifolia*, *P. pruinosa* (Salicaceae).

Following species should be excluded from *Syntomoza* and the Paurocephalinae: *Syntomoza lebezia* HODKINSON, 1986b: 149. Distribution: Belize. In the head shape *S. lebezia* resembles *Metapsylla* spp. with which it may be related.

Phylogenetic implications

The Paurocephalinae can be diagnosed within the Psylloidea with adult and larval characters. The present revised definition differs from previous classifications. Based on the compact adult body form (Loginova 1973), and the presence of additional pore fields on the caudal plate in larvae respectively (White & Hodkinson 1985), *Syntomoza* and *Diclidophlebia* were assigned to the Euphyllurini/Euphyllurinae. These characters are clearly homoplasies. Our results confirm, in part, the suggestion of Brown & Hodkinson (1988) that the inclusion of the Diclidophlebiini (*Diclidophlebia*, *Paraphalaroida* and *Haplaphalara*) and Togepsyllinae (*Togepsylla* and *Syncoptozus*) may render the subfamily Paurocephalinae sensu White & Hodkinson (1985) more natural. The Diclidophlebiini are part of the Paurocephalinae in our analysis, the Togepsyllinae, however, are not. Similarities between the two subfamilies could not be substantiated with genuine synapomorphies. The position of Togepsyllinae as well as Euphyllurinae remains doubtful. Hodkinson (1986b) has pointed out that the Euphyllurini comprise a fairly heterogeneous collection of genera. The group may not be monophyletic even after removal of *Syntomoza*.

Four other taxa have been related to the Paurocephalinae: *Atmetocranium*, *Primascena subita*, *Pseudaphorma astigma* and *Strophingia*.

The monotypic New Zealand genus *Atmetocranium* has a highly autapomorphic morphology which makes it difficult to relate to other psylloid groups. The metatibia with an internal comb of apical spurs and the 1-segmented assymmetric larval antenna suggest a relationship with the Calophyidae to which it is transferred here.

Primascena subita KLIMASZEWSKI, 1998: 21, was described from a single male from Dominican amber. According to Klimaszewski's description the taxon lacks metabasitarsal spurs and exhibits a clypeus which is markedly pointed downwards. The examination of the holotype (AMNH) revealed that neither is true. The alleged clypeus is in fact part of the fore leg, the head being partly

destroyed. Both metabasitarsi have two sclerotised spurs. This clearly puts *Primascena* outside the Paurocephalinae. The metatibia has a crown of spaced apical spurs similar to those of some Aphalaroidinae to which it may belong.

Pseudaphorma astigma Conci & Tamanini, 1985: 350, was erected for a single male specimen which appears to be lost now (C. Conci pers. comm., M. Daccordi pers. comm.). From the description it is quite clear that the abdomen and genitalia do not belong to the same animal as the remaining parts. The description of the head, antenna, forewing, distribution of surface spinules and hind leg fits perfectly well *Aphalara polygoni* Foerster, the abdomen belongs without doubt to *Trioza remota* Foerster. Here we suggest following synonymies *Aphalara* = *Pseudaphorma*, **syn. n.**, and *Aphalara polygoni* Foerster = *Pseudaphorma astigma*, **syn. n.**

Strophingia is a small West Palaearctic genus which lacks autapomorphies of the groups such as Paurocephalinae, Rhinocolinae or Aphalaroidinae to which it has been related to. Our analysis is not informative in this respect.

Biogeography and host plants

The subfamily Paurocephalinae is predominantly pantropical with *Diclidophlebia* as sole New World representative. *Aphorma* and *Camarotoscena* are mostly Palaearctic with a few Oriental species restricted to Ranuculaceae and *Populus* spp. (Salicaceae) respectively. *Diclidophlebia* has 12 New World, 8 Indo-Australian, 3 Afrotropical and 1 Australian species. Host plant records are within the Malviflorae: Malvales (Malvaceae, Sterculiaceae, Tiliaceae), Urticales (Ulmaceae), Rhamnales (Rhamnaceae), Euphorbiales (Euphorbiaceae) and Myrtiflorae: Myrtales (Melastomataceae). *Syntomoza* includes 7 described species, 4 of which are Oriental, 2 Palaearctic and 1 Afrotropical. Host plants are within the family Flacourtiaceae, except for *S. unicolor* which is associated with *Populus* spp. (Saliaceae).

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Address of the authors:

Naturhistorisches Museum
Augustinergasse 2
CH-4001 Basel
Switzerland

RHI	**Rhinocola aceris* (Linnaeus)	0100010001100000000001
SPO	*Ctenarytaina eucalypti* (Maskell)	2000400000100000100002
EUP	*Euphyllura olivina* (Costa)	2000400000000000000001
STR	**Strophingia ericae* (Curtis)	0000010000000000210000
CAL	**Atmetocranium myersi* (Ferris & Klyver)	3121411001110000200000
TOG	*Togepsylla matsumurana* Kuwayama	1020?11001110000100000
TOG	*Syncoptozus mexicana* Hodkinson	1020???001110000100000
PAU	**Aconopsylla sterculiae* (Froggatt)	0001311000011011110002
PAU	*Anomoterga hsenpinensis* Fang & Yang	2001111000011010001001
PAU	*Aphorma clematidis* Burckhardt & Bänziger	1000000000011010000001
PAU	*A. lichenoides* (Puton)	1000000000011010??????
PAU	*Camarotoscena africana* Loginova	2001111000011010001001
PAU	*C. fulgidipennis* Loginova	0001100000011010000101
PAU	*C. speciosa* (Flor)	0001100000011010000101
PAU	*C. unicolor* Loginova & Parfentiev	2001111000011010001001
PAU	*Diclidophlebia eastopi* Vondraček	0001311000011011110002
PAU	**Haplaphalara dahli* (Rübsaamen)	0001311000011011110002
PAU	**Homalocephala homali* Yang & Li	2001111000011010?01001
PAU	**Paraphalaroida fremontiae* (Klyver)	0001311000011011110002
PAU	*Paurocephala artocarpae* Braza & Calilung	1001201010011010210000
PAU	*P. crassiflagellata* Burckhardt	0001311000011011??????
PAU	*P. gossypii* Russell	1001201010011010210000
PAU	*P. lanceomedia* Brown & Hodkinson	0001311000011011??????
PAU	*P. paucivena* Brown & Hodkinson	0001311000011011??????
PAU	**P. psylloptera* Crawford	1001201010011010210000
PAU	*P. pterospermi* Mifsud & Burckhardt	1001201010011010210000
PAU	**P.* (*Thoracocorna*) *chonchaiensis* Boselli	1001201010011010210010
PAU	**Sinuonemopsylla excetrodendri* Li & Yang	0001311000011011110002
PAU	*Syntomoza scolopiae* Yang	2001111000011010001001
PAU	**Woldaia nebulosa* Brown & Hodkinson	0001311000011011110002

Table 1. Matrix for adult and larval characters of selected members of Paurocephalinae (PAU), Euphyllurinae (EUP), Rhinocolinae (RHI), Spondyliaspidinae (SPO), Strophingiinae (STR), Togepsyllinae (TOG) (all Psyllidae) and Calophyidae (CAL) (Table 2, Fig. 9) (subfamilies as in present review, genera as previous to review). Asterisks indicate type species.

1. Head inclination 45–90° (0); 0–45° (1); 90° (2); >90° (3).
2. Rhinaria present on apex of antennal segments 4, 6, 8, and 9 (0); 4, 5, 6, 7, 8, 9 (1).
3. Coronal suture fully developed (0); largely reduced (1); completely reduced (2).
4. Vertex and genae separated by angle, lobes or processes (0); vertex passing smoothly into genae (1).
5. Frons elongate, parallel-sided (0); moderately wide, rhomboidal (1); elliptical (2); very wide, rhomboidal (3); reduced (4).
6. Clypeus pear-shaped (0); flattened (1).
7. Terminal setae on antennal segment 10 short (0); very long (1).
8. Pro- and mesothorax flat (0); with large conspicuous horns (1).
9. Metascutellum flat or weakly raised (0); horn-shaped (1).
10. Metacoxae with meracanthus (0); without meracanthus (1).
11. Metacoxae without (0); with a membranous process near trochanteral insertion (1).
12. Metabasitarsus with 2 sclerotised spurs (0); without spurs (1).
13. First visible abdominal tergite without (0); with sclerotised patch of spinules laterally (1).
14. Paramere simple (0); cleft apically (1).
15. Proximal portion of aedeagus simple apically (0); with a rim-like inflation apically (1).
16. Distal portion of aedeagus simple (0); complex (1).
17. Fifth instar larva with antenna 7- or 8-segmented (0); 9- or 10-segmented (1); 3-segmented (2).
18. Larva without sectasetae or lanceolate setae on antennal flagellum (0); with (1).
19. Larval mid and hind legs without (0); with massive peg-like setae (1).
20. Last instar larva with precaudal tergites not (0); bearing a row of densely spaced setae (incl. sectasetae) (1).
21. Last instar larva with outer circumanal ring consisting of a single row of pores (0); consisting of one row of pores which is expanded laterally (1).
22. Last instar larva without additional pore fields (0); with additional pore fields present, which are close to circumanal ring (1); with additional pore fields present, which are widely distant from circumanal ring (2).

Table 2. Characters of adult (1–16) and last instar larva (17–22) with character states of matrix in Table 1.

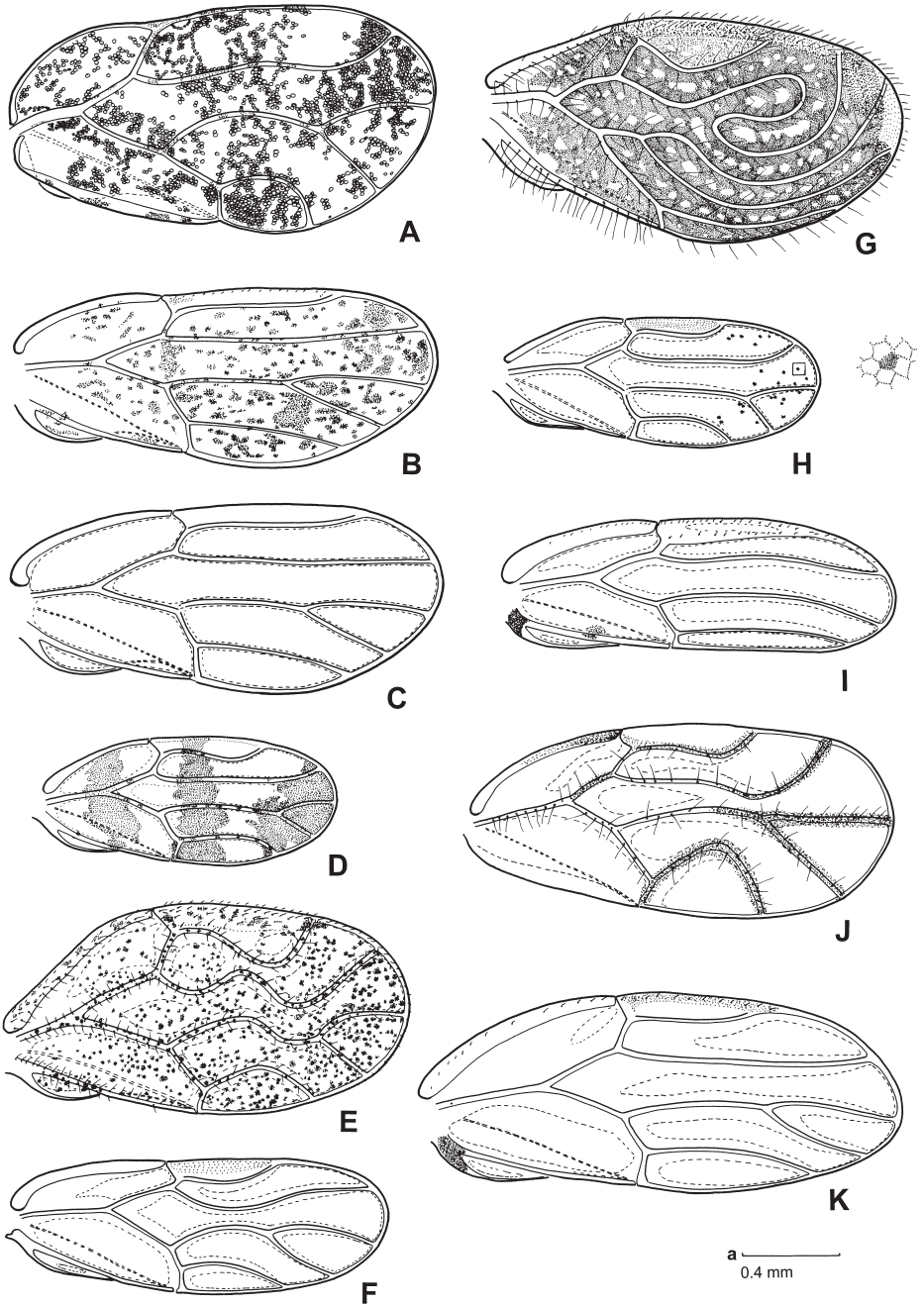

Fig. 1. Forewing. A, *Aphorma lichenoides*; B, *Camarotoscena personata*; C, *C. subrubescens*; D, *Diclidophlebia dahli*; E, *D. excetridendri*; F, *D. lanceomedia*; G, *D. oceanica*; H, *D. paucipunctata*; I. *D. paucivena*; J, *D. setinervis*; K, *D. xuani*. Scale bar a: A–K.

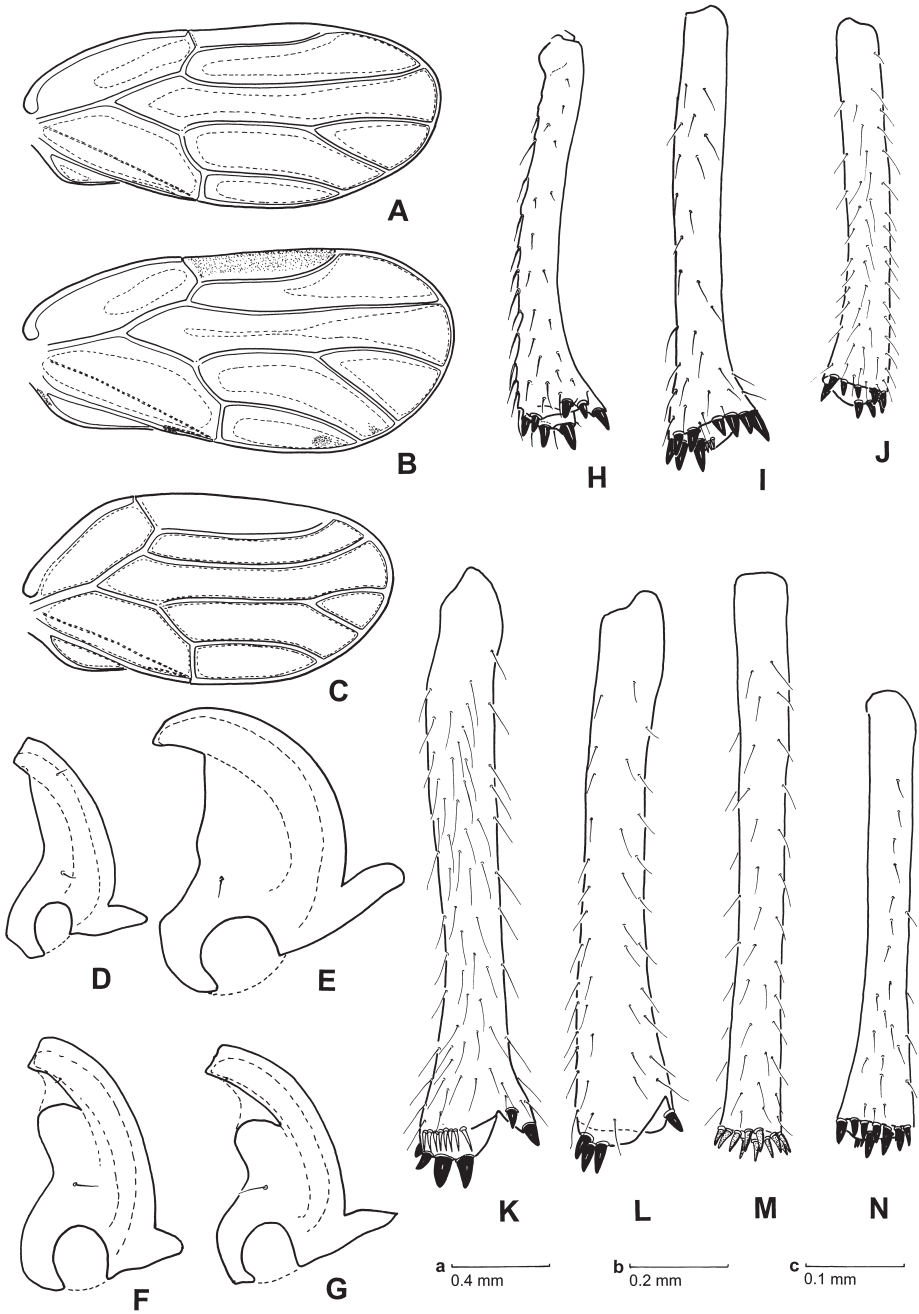

Fig. 2. A–C, Forewing; D–G, metacoxa; H–N, metatibia. A, G, N, *Syntomoza africana*; B, *S. hsenpiniensis*; C, F, *S. scolopiae*; D, I, *Camarotoscena personata*; E, *Diclidophlebia xuani*; H, *Aphorma lichenoides*; J, *Diclidophlebia dahli*; K, *D. oceanica*; L, *D. fremontiae*; M, *D. setinervis*. Scale bar a: A–C; b: D–G; c: H–N.

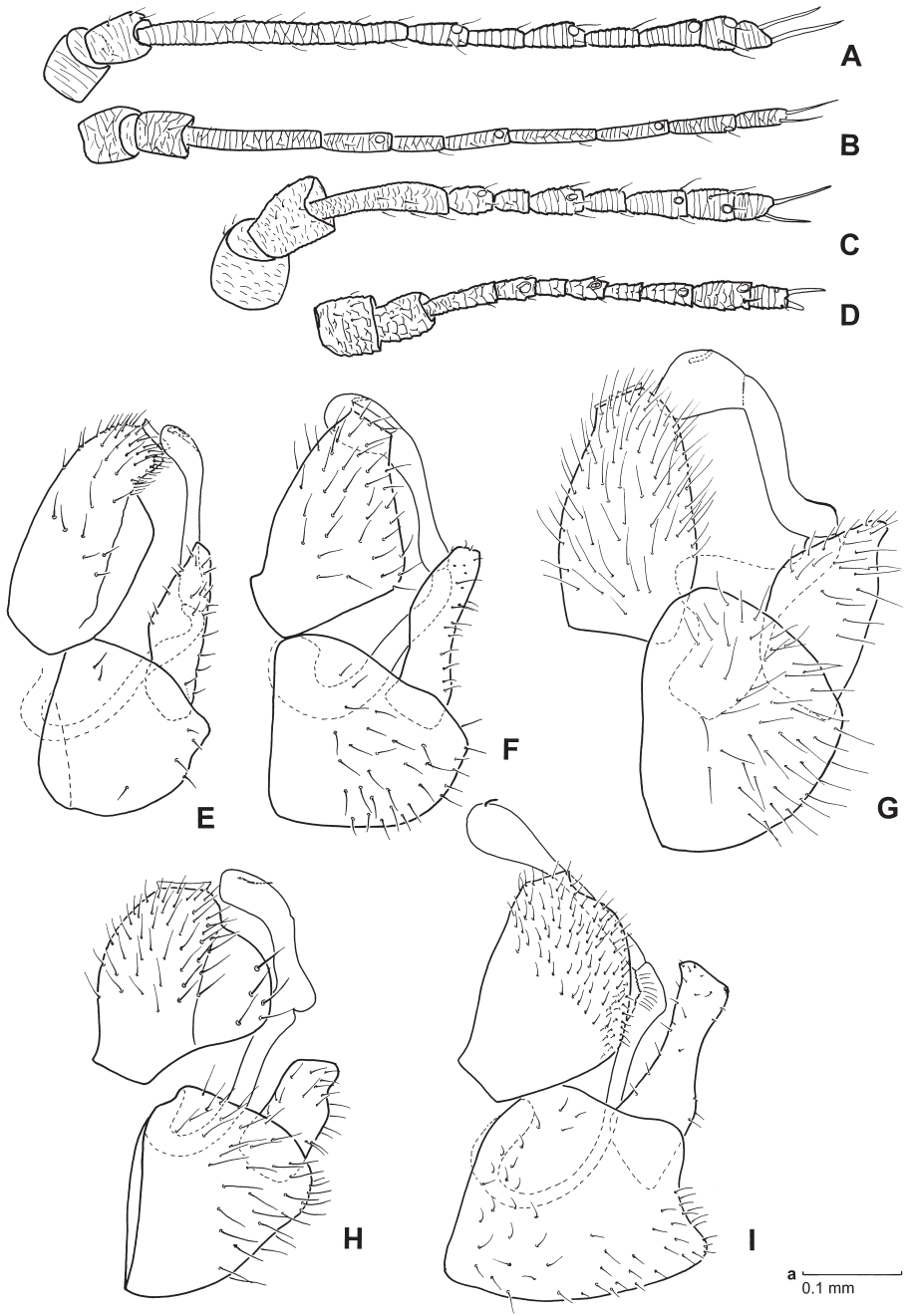

Fig. 3. A–D, Antenna; E–I, male genitalia, lateral view. A, I, *Syntomoza africana*; B, *Diclidophlebia dahli*; C, *Camarotoscena speciosa*; D, E, *Aphorma lichenoides*; F, *Camarotoscena personata*; G, *Diclidophlebia oceanica*; H, *D. xuani*. Scale bar a: A–C; b: D–G; c: H–N.

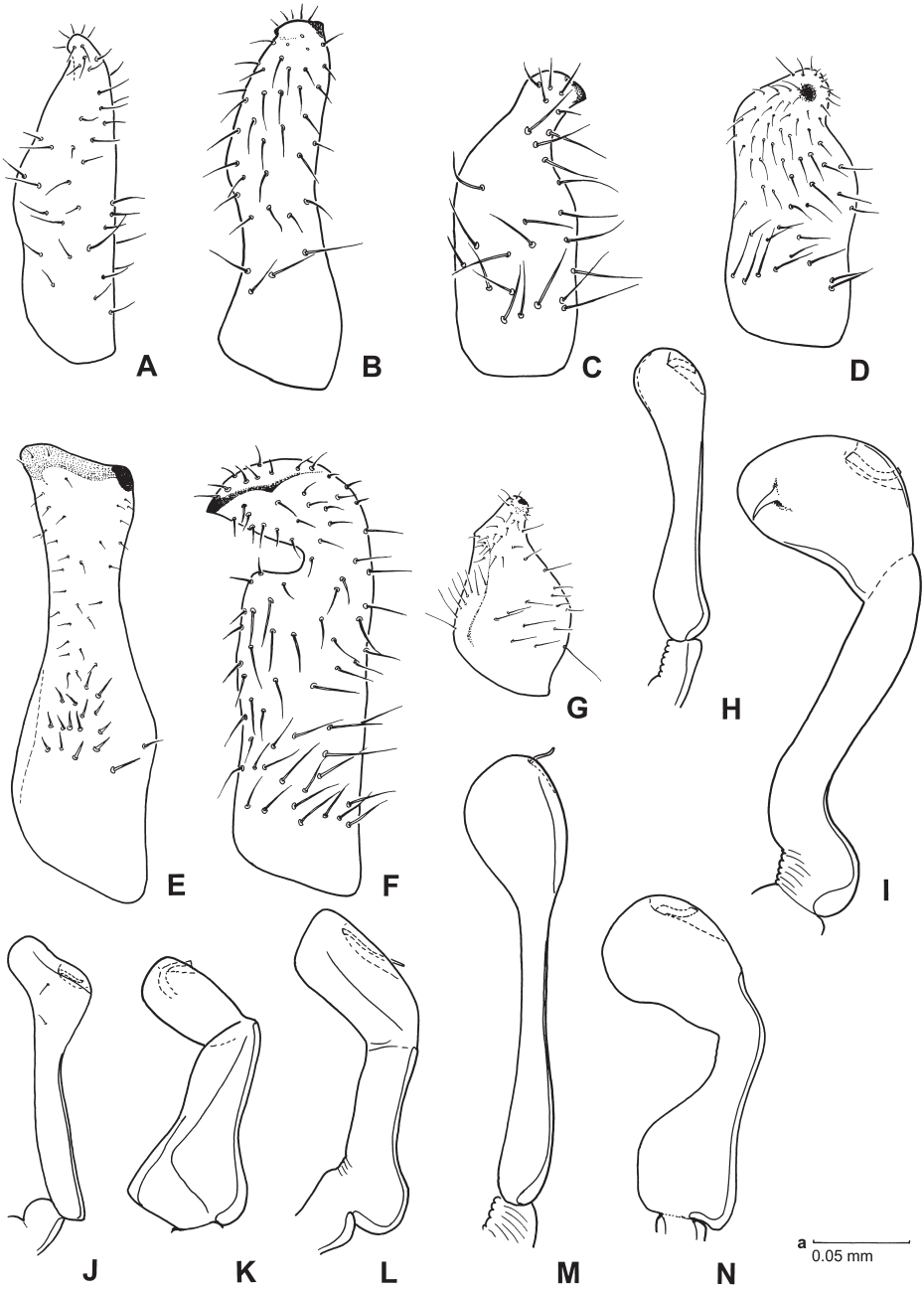

Fig. 4. A–G, paramere, inner surface; H–N, distal portion of aedeagus. A, *Aphorma lichenoides*; B, H, *Camarotoscena personata*; C, K, *Diclidophlebia setinervis*; D, L, *D. xuani*; E, M, *Syntomoza africana*; F, N, *S. hsenpiniensis*; G, J, *Diclidophlebia dahli*; I, *D. oceanica*. Scale bar a: A–N.

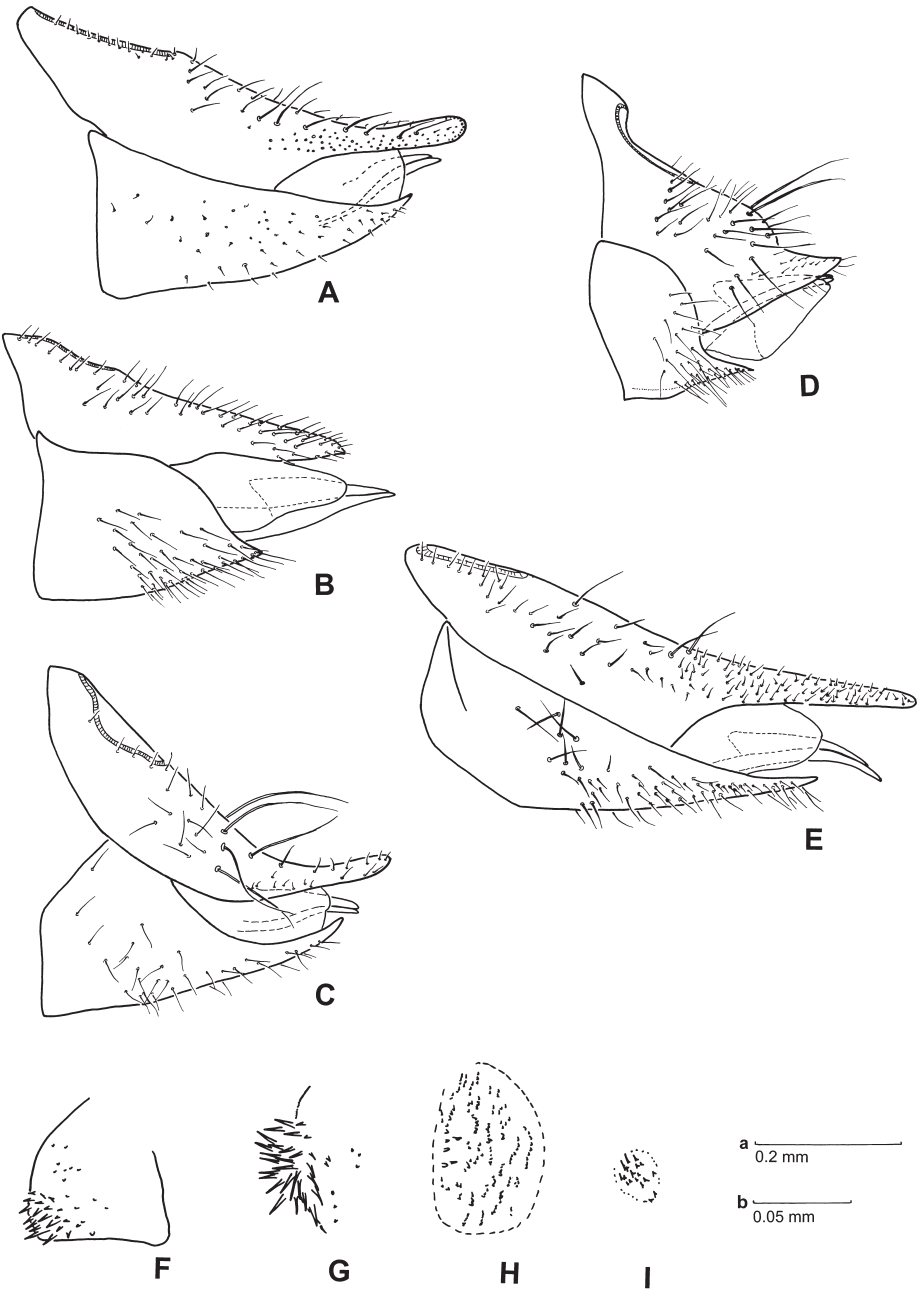

Fig. 5. A–E, Female genitalia, lateral view; F–I, lateral sclerotised patch of spinules on first visible abdominal tergite. A, F, *Aphorma lichenoides*; B, *Camarotoscena speciosa*; C, *Diclidophlebia setinervis*; D, *Diclidophlebia dahli*; E, I, *Syntomoza unicolor*; G, *Camarotoscena subrubescens*; H, *Diclidophlebia excetridendri*. Scale bar a: A–E; b: F–I.

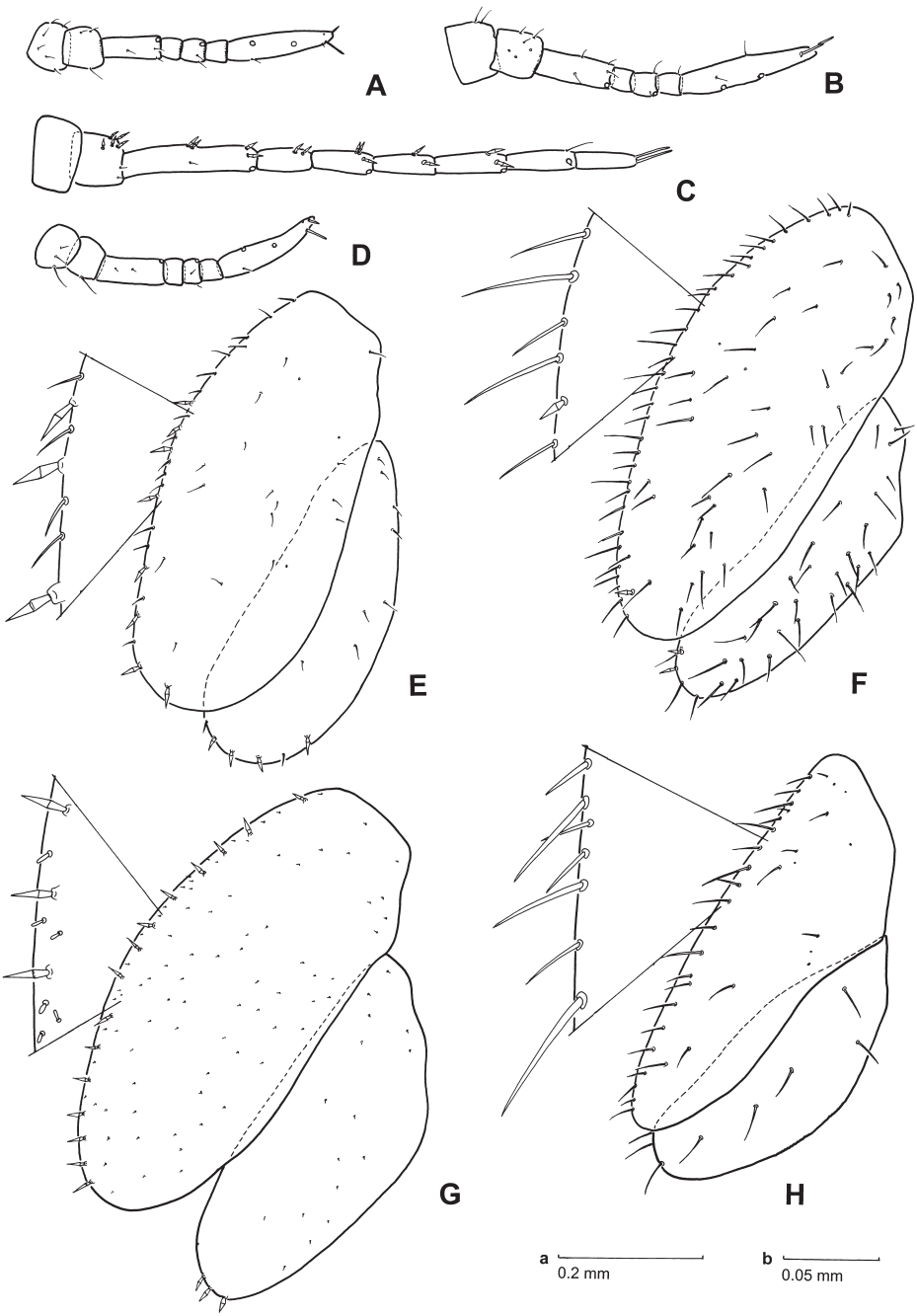

Fig. 6. Fifth instar larva: A–D, antenna; E–H, wing pads. A, E, *Aphorma lichenoides*; B, F, *Camarotoscena fulgidipennis*; C, G, *Diclidophlebia fremontiae*; D, H, *Syntomoza unicolor*. Scale bar a: A–H, b: details of E–H.

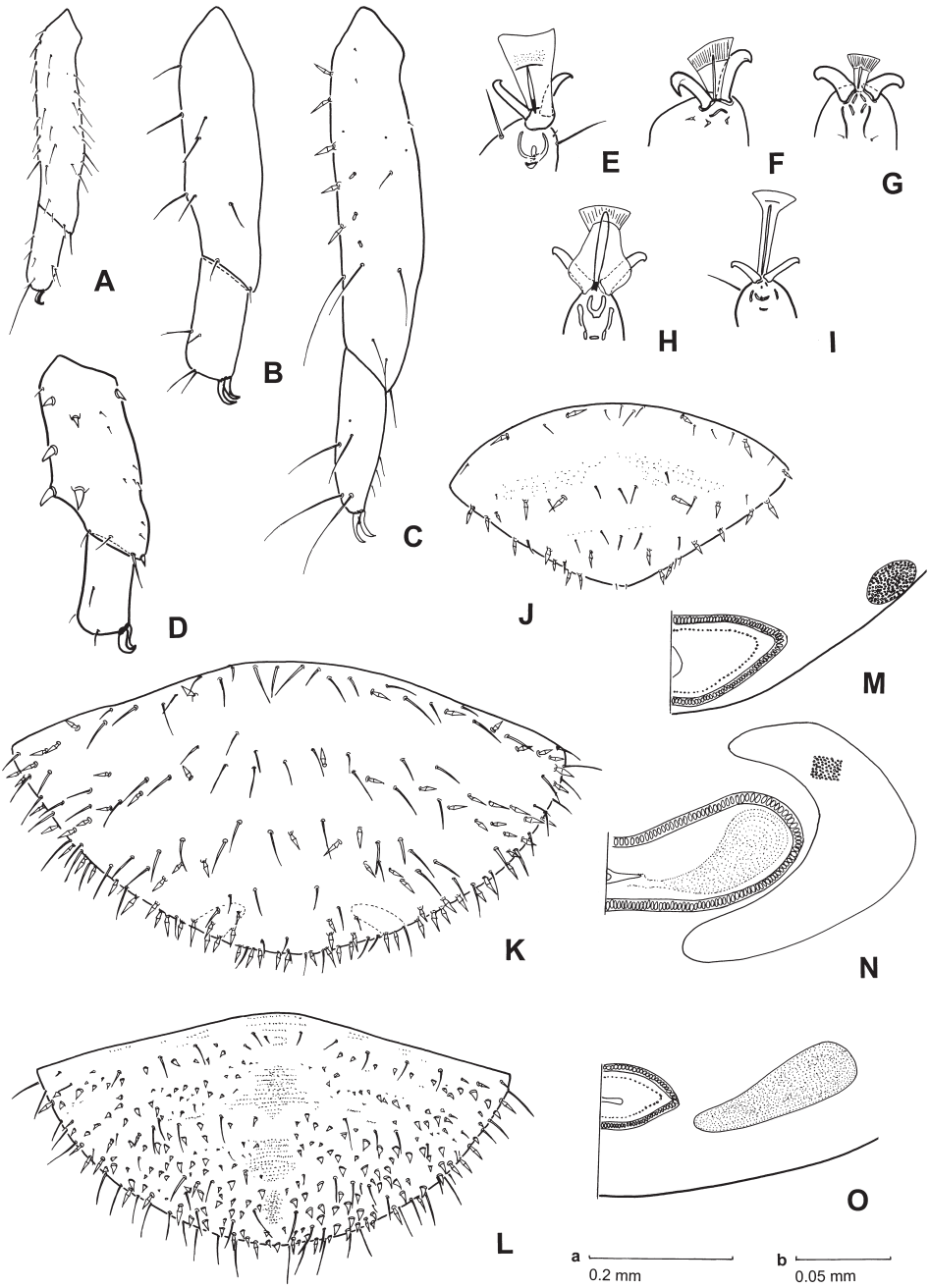

Fig. 7. Fifth instar larva: A–D, tibiotarsus and apical tarsus of hind leg; E–I, apex of tarsus with arolium; J–L, caudal plate, dorsal view; M–O, circumanal ring with additional pore fields, ventral view. A, E, J, M, *Aphorma lichenoides*; B, F, K, N, *Camarotoscena fulgidipennis*; C, H, *Diclidophlebia fremontiae*; D, G, L, *Syntomoza unicolor*; I, *D. dahli*. Scale bar a: A–D, J–L; b: M–O.

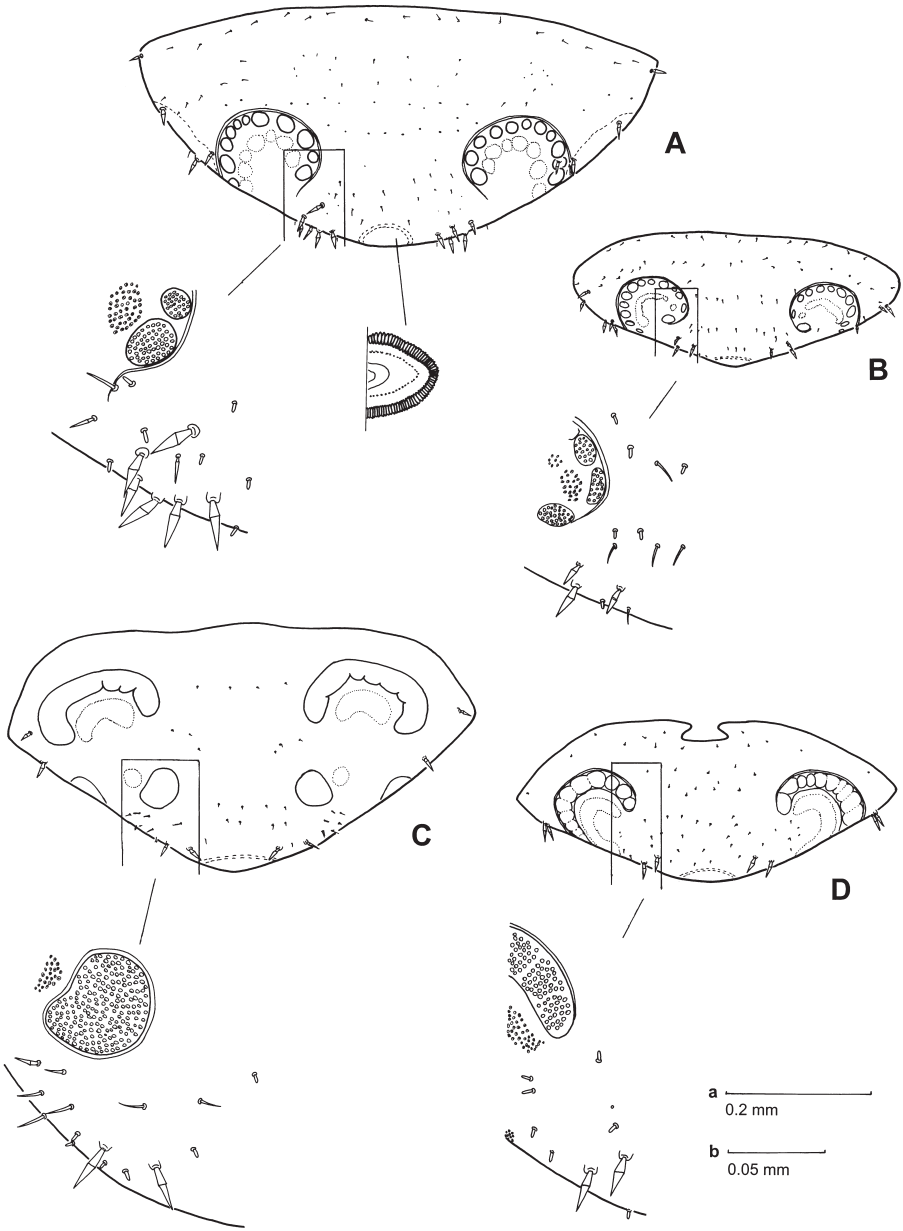

Fig. 8. Fifth instar larva, caudal plate, dorsal view, with details. A, *Diclidophlebia fremontiae*; B, *D. fava*; C, *D. xuani*; D, *D. dahli*. Scale bar a: A–D; b: details.

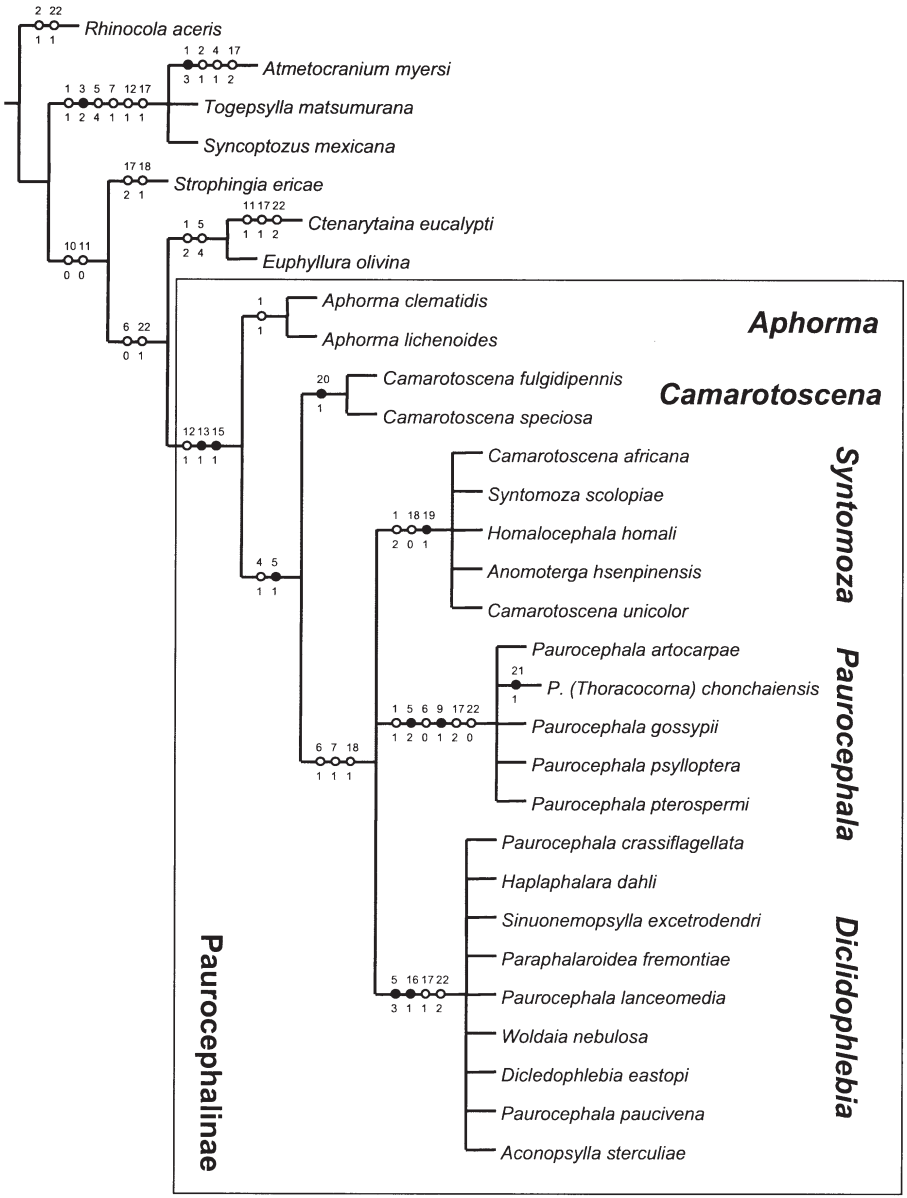

Fig. 9. Cladogram of Paurocephalinae. Nelsen consensus of 18 most parsimonious trees (weighted characters: length 218, consistency index 72, retention index 91; unweighted characters: length 46, consistency index 58, retention index 85). Fast character transformation: full circles = synapomorphies or autapomorphies; open circles homoplasies; numbers above circles = character numbers; numbers below circles = character states. Note that the clade supported by characters 10 and 11 is an artefact of the choice of the out-groups; characters 10 and 11 are, therefore, not genuine synapomorphies.

Wenig beachtete Problemkreise in der phylogenetischen Analyse: Invariante Positionen und die Wahl von Substitutionsmodellen.

Martin Haase und Bernhard Misof

Kurzfassung

Contrib. Nat. Hist. 2: 35–40.

Die Basenzusammensetzung eines Datensatzes hat oft entscheidende Auswirkungen auf die phylogenetische Rekonstruktion. Invariante Positionen können dabei einen grossen Einfluss haben. Das ist der Fall, wenn sie Heterogenität der Basenzusammensetzung der phylogenetisch informativen Positionen überdecken, also Homogenität vortäuschen. Die Basenzusammensetzung eines Datensatzes muss daher vor einer phylogenetischen Analyse ausschliesslich an den variablen Positionen untersucht werden. Die Wahl des einer Maximum-Likelihood-Analyse zugrundeliegenden Substitutionsmodells ist ebenfalls kritisch für die Stammbaumrekonstruktion und sollte nicht willkürlich erfolgen, da es die Topologie entscheidend mitbestimmt. Likelihood-Ratio-Tests ermöglichen die Bestimmung des auf einen Datensatz am besten passenden Modells.

Einleitung

Die Erfindung und Automatisierung der Polymerasekettenreaktion (PCR) hat auch die phylogenetische Forschung nachhaltig beeinflusst: molekulare Daten, insbesondere Sequenzdaten, sind zu einer wichtigen Grundlage in der Erforschung der Verwandtschaftsverhältnisse der Organismen und der Evolution von Merkmalen (im weitesten Sinne) geworden. Der Umfang dieser neuen Datenquelle zusammen mit dem rasanten Fortschritt, den die Computertechnologie vorlegt, hat auch zu einem enormen Aufschwung in der Entwicklung von teilweise sehr komplexen Analysemethoden geführt. Jede Methode, jedes Modell, das einer Methode zugrunde liegt, hat freilich seine Voraussetzungen und Limiten. Diese zu kennen und zu erkennen ist essentiell, die Möglichkeiten dazu sind aber oftmals nicht trivial. Die Gründe dafür liegen u.a. in der „Natur der Sache", also in unserer oft ungenügenden Kenntnis von Eigenschaften der DNS, ihrer Evolution und den Einschränkungen, der letztere unterliegt. Ander-

erseits sind Testverfahren, die die Voraussetzungen von phylogenetischen Analysemethoden hinterfragen, zumeist ähnlich komplex und rechentechnisch aufwändig wie die Methoden selber. In ihrer Entwicklung hinken derartige Tests den Rekonstruktionsmethoden naturgemäss meist hinterher. Zudem sind auch sie nicht frei von Voraussetzungen und Limiten, die ihrerseits exploriert werden müssen.

In der vorliegenden Arbeit wollen wir zwei Probleme und Fragen diskutieren, die erst in jüngerer Zeit erkannt worden sind bzw. für die erst seit kurzem Lösungsmöglichkeiten, auch in Form von Computerprogrammen, vorliegen. 1) Wie beeinflussen invariante Positionen der DNS, also Positionen, die aus funktionellen Gründen keine Veränderung erfahren können, meine Analyse? 2) Wie finde ich das meinen Daten zugrunde liegende Substitutionsmodell für eine Maximum-Likelihood-Analyse? Beiden Problemen sollte man sich grundsätzlich vor jeder phylogenetischen Analyse stellen, die auf molekularen Daten beruht, da sie entscheidend die Wahl der Rekonstruktionsmethoden beeinflussen.

Invariante Positionen

Primär scheint das Auftauchen von invarianten Positionen in molekularen Datensätzen kein grosses Problem zu sein. Offensichtlich haben invariante Merkmale keinen Einfluss auf Stammbaumrekonstruktionen und können geflissentlich ignoriert werden. Dies ist auch als Standard-Option in fast allen frei zugängigen Programmpaketen enthalten.

Konzentrieren wir uns auf die simple Parsimonie-Rekonstruktion, so stimmt es in der Tat, dass invariante Positionen keinen Einfluss auf das Rekonstruktionsverfahren besitzen. Wird aber versucht, mittels Resampling-Methoden (z.B. Bootstrapping) die Robustheit einer Rekonstruktion abzuschätzen, so stossen wir auf ein ernsthaftes Problem. Uninformative, also invariante und autapomorphe Merkmale terminaler Taxa beeinflussen zwar nicht das Resultat der Parsimonie-Rekonstruktion, also die Topologie des Baumes, aber erniedrigen die Trefferwahrscheinlichkeit für jede Position im Resampling-Verfahren. Diese ist abhängig von der Gesamtzahl der Merkmale und nicht von der Gesamtzahl der informativen Merkmale. Konsequenterweise ist ein Resampling-Verfahren also nur mit den parsimonie-informativen Merkmalen durchzuführen, uninformative Merkmale sind aus den Daten zuvor zu entfernen. Ein leicht zu behebendes Problem, das aber gerne übersehen wird (siehe z.B. Zharkikh & Li 1992).

Invariante Positionen halten allerdings auch weniger triviale Überraschungen bereit, die nicht allgemeinen Niederschlag in der speziellen Literatur ge-

funden haben. Wie erinnerlich, setzt sich die DNS aus den vier Grundbausteinen Adenin, Guanin, Cytosin und Thymidin zusammen. Es ist schon lange bekannt, dass die prozentuale Zusammensetzung aus diesen vier Grundbausteinen nicht ausgeglichen, etwa 25% Adenin, 25% Guanin, 25% Cytosin und 25% Thymidin, sein muss, sondern dass sehr wohl Abweichungen von dieser Verteilung in vielen DNS-Abschnitten bzw. spezifischen Genomen zu finden sind (vergleiche Simon & al. 1994) . Besonders die Zusammensetzung der mitochondrialen DNS ist mit ihrem hohen A- und T-Gehalt auffällig. Dieser AT-Gehalt kann in manchen Taxa, ein Beispiel wären etwa die Hymenopteren, bis zu rund 80% betragen (Simon & al. 1994).

Welchen Effekt hat dies auf phylogenetische Analysen? Die Einschränkung der DNS-Varianz auf vier Merkmalszustände hat zur Folge, dass DNS-Sequenzen auch zufällige Übereinstimmungen zeigen können. Je geringer die Anzahl der beobachtbaren Merkmalszustände ist, desto höher ist diese zufällig mögliche Übereinstimmung. Demzufolge werden Sequenzen mit z.B. unabhängig erworbenem hohem AT-Gehalt rein zufällig einen grösseren Ähnlichkeitsgrad aufweisen als Sequenzen mit balancierter Basenkomposition. Ist in verschiedenen evolutiven Linien eine Verschiebung der Basenkomposition konvergent erfolgt, so kann die dadurch erhöhte, zufällige Ähnlichkeit phylogenetisches Signal überdecken (z.B. Lockhart & al. 1994). Es gilt daher, solche möglichen Verschiebungen der Basenkomposition vor, bzw. unabhängig von einer phylogenetischen Analyse zu identifizieren, um mögliche Ursachen für widersprüchliche Signale im Datensatz auszumachen.

Konventionellerweise wird die mögliche Heterogenität der Basenkomposition eines Datensatzes mit einem χ^2-Test getestet. Dieser Test kann allerdings nicht phylogenetische Abhängigkeiten dokumentieren. Er kann nur helfen, ein generelles Problem im Datensatz zu identifizieren. Üblicherweise wird der χ^2-Test über den gesamten Datensatz ausgeführt, also über informative und uninformative Merkmale. Es ist offensichtlich, dass invariante Merkmale, also Merkmale, die aus funktionellen Zwängen keine Variabilität zeigen können, keine Heterogenität der Basenkomposition im Datensatz stützen können. Ganz im Gegenteil, ein χ^2-Test, der invariante Merkmale einschliesst, wird uns meist ein klares Signal für eine homogene Basenkomposition liefern. Häufig überwiegen invariante Merkmale in molekularen Datensätzen. Es ist daher kaum verwunderlich, dass Homogenität der Basenkomposition fast überall dokumentiert wurde. Man bedenke nun allerdings, dass einzig die informativen Merkmale die Topologie eines Stammbaumes bestimmen. Betrachtet man nur informative Merkmale, so kann eine Heterogenität der Basenkomposition durchaus vorkommen, etwa ausgelöst durch nicht zufällige Substitutionsereignisse in einzelnen Artengruppen, und diese Heterogenität kann entscheidenden Einfluss

auf die Rekonstruktion haben. Mit einem simplen χ^2-Test über alle Merkmale wäre das Problem nicht zu identifizieren. Informative und invariante Merkmale müssen in Tests auf Heterogenität der Basenkomposition getrennt behandelt werden (vergleiche Lockhart & al. 1996; Misof & al. 2001).

Wahl des geeigneten Substitutionsmodells in Maximum-Likelihood-Analysen

Die kurze Skizze über invariante Positionen und Heterogenität in der Basenkomposition führt uns unmittelbar zum Problem der Wahl eines geeigneten Substitutionsmodells in Maximum-Likelihood-Analysen. Im Gegensatz zur Parsimonie-Analyse eines molekularen Datensatzes basiert die Maximum-Likelihood-Analyse auf expliziten Substitutionsmodellannahmen. Bei gegebenem Substitutionsmodell wird die Topologie gesucht, die mit grösster kumulativer Wahrscheinlichkeit über alle Merkmale das gefundene Muster der Nukleotidvariationen darstellt. Es ist somit klar, dass die Rekonstruktion eines Stammbaumes vom angenommenen Substitutionsmodell abhängt. Ad hoc-Annahmen zu Substitutionsparametern des Substitutionsmodells waren noch bis vor kurzem üblich. Es war folglich zu erwarten, dass unrealistische Annahmen zu Verzerrungen bzw. Verfälschungen der Ergebnisse führten, eine in der Tat sehr unbefriedigende Situation. Mit der Etablierung des Likelihood-Ratio-Tests (Navidi & al. 1991; Goldman 1993a, 1993b) in der Phylogenetik konnte diesem Problem der Maximum Likelihood Analyse abgeholfen werden. Der Likelihood-Ratio-Test vergleicht bei konstanter Topologie die kumulativen Wahrscheinlichkeitswerte dieser Topologie unter unterschiedlich komplexen Substitutionsmodellen. Im Likelihood-Ratio-Test wird stufenweise ermittelt, ob ein komplexeres Substitutionsmodell einen signifikant besseren Wahrscheinlichkeitswert für die Topologie liefert als ein weniger komplexes. Dieser Test ist mittlerweile gut etabliert, auch wenn teilweise kontroverse Ansichten in der Literatur zu finden sind. Eine sehr übersichtliche Testverfahrensroutine ist im Programm Modeltest (Posada & Crandall 1999) implementiert. Zusammen mit dem Programmpacket PAUP (Swofford 1998) ist die Ermittlung eines relativ besten Substitutionsmodells für einen gegebenen Datensatz möglich.

Aber auch hier gibt es nicht so offensichtliche und vielfach ignorierte Probleme. Substitutionsparameter werden ausgehend vom aktuellen Datensatz unter der Annahme der Gültigkeit für den gesamten Datensatz geschätzt. Sollte sich etwa die Substitutionswahrscheinlichkeit von A nach G innerhalb des Datensatzes ändern, so kann dies durch herkömmliche Modelle nicht beschrieben werden und wird somit zu einer weiteren Ursache für unrealistische Annahmen.

Hier gelangen wir wieder zum Kapitel über invariante Positionen zurück. Eine signifikante Heterogenität der Basenkomposition im Datensatz, ermittelt mit einem χ^2-Test, zeigt uns, dass es im vorliegenden Merkmalssatz zu mindestens einer Veränderung der Substitutionswahrscheinlichkeiten gekommen ist. Die im Maximum-Likelihood-Modell angenommen Substitutionsparameter sind für den Datensatz nicht mehr allgemein gültig. Die Verletzung einer wichtigen Voraussetzung für die Anwendung von Maximum-Likelihood-Methoden liegt vor. In solchen Fällen werden wir auf Methoden der Stammbaumrekonstruktion zurückgreifen, die sich als insensitiv gegenüber Veränderungen der Modellparameter erweisen, etwa das LogDet Verfahren (Lockhart & al. 1994). Die Entwicklung solch robuster Verfahren steckt allerdings leider noch in den Kinderschuhen (siehe auch Galtier & Guoy 1998).

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Autorenadressen:

Martin Haase
Institut für Natur-, Landschafts- und Umweltschutz
Universität Basel
St. Johanns-Vorstadt 10
CH-4056 Basel
Schweiz

Aktuelle Adresse:
National Institute of Water and Atmospheric Research
PO Box 11-115 Hamilton
New Zealand

Bernhard Misof
Zoologisches Institut und Museum Alexander Koenig
Abteilung Entomologie
Adenauerallee 160
D-53113 Bonn
Deutschland

Combining morphological, molecular, and biological characters to sort out taxonomical problems in parasitic Hymenoptera. The case of *Eubazus* spp. (Hymenoptera: Braconidae)

Marc Kenis

ABSTRACT

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A study was carried out to separate four closely related species of *Eubazus* (Hymenoptera: Braconidae), parasitoids of *Pissodes* spp. (Coleoptera: Curculionidae) in conifer trunks and cones. A combination of several methods was needed to provide diagnostic characters. Variations were found in developmental biology, morphometrics, isoenzyme patterns, fecundity, and host preference in the laboratory and in the field. Crosses were made between *Eubazus* species and populations to ascertain their behavioural and genetic compatibility or incompatibility. This study exemplifies the need for an integrated approach in parasitoid taxonomy, including the use of morphological, molecular and biological characters.

Introduction

Parasitoids are insects whose larvae feed exclusively on the body of a single arthropod. Although parasitoids are found in several insect orders, most species are Hymenoptera. Because of their ability to kill and control pests, parasitoids are beneficial insects and are often used in biological control and integrated pest management programmes. Parasitic Hymenoptera form a very large group, with about 50–60'000 species described, which accounts for 7% of all insect species and 3% of all metazoans. However, compared to other insects groups, parasitic wasps are rather poorly known. Estimates suggest that there could be up to 1 or 2 million species, which would represent up to 20% of all insect species (Gaston 1991, 1993; Godfray 1993). The poor knowledge in parasitoid systematics is partly due to a complex of taxonomic problems that are not specific to, but particularly critical in this group, such as high intraspecific variation, large numbers of sibling species, paucity of informative morphological characters of use to the taxonomist, frequent occurrence of convergent evo-

lution, parallel evolution and character reversal, etc. (Godfray 1993). This has led to much confusion in the taxonomic literature.

Morphological studies are often not sufficient to sort out taxonomic problems in parasitic wasps. An approach combining several methods is usually more desirable. Here I present a summary of a long-term study on the biosystematics of sister species of the genus *Eubazus* (Hymenoptera: Braconidae: Helconinae), subgenus *Allodorus*, parasitoids of wood- and cone-boring weevils of the genus *Pissodes* (Coleoptera: Curculionidae). This work was carried out in Europe as part of a biological control programme against the white pine weevil, *Pissodes strobi* (Peck, 1817) in Canada.

Larvae of *Pissodes* spp. live under conifer bark or in pine cones. Pupation occurs in a pupal chamber in the wood or in the cone. Adults live externally and lay their eggs in the bark or in the cone, in a feeding hole covered with frass. Eight species occur in Europe. *P. castaneus* (De Geer, 1775), *P. pini* (Linnaeus, 1758), and *P. piniphilus* (Herbst, 1795) attack pine trunks, *P. piceae* (Illiger, 1807) is a frequent pest of fir trunk, *P. harcyniae* (Herbst, 1795), *P. scabricollis* Miller, 1859 and *P. gyllenhali* (Sahlberg, 1834) feed in spruce trunk and *P. validirostris* (Sahlberg, 1834) is the only species of the genus living in pine cones. Other species occur in Asia and North America, including the Nearctic pine and spruce pest *P. strobi*. In Europe, the main parasitoids of *Pissodes* spp. are braconids of the genus *Eubazus* (Kenis & Mills 1994). All species lay their eggs in *Pissodes* eggs and kill their host when the latter is in its last larval instar. Then they build a cocoon under the bark or in the cone, in which they pupate.

At the beginning of the study, the taxonomy of the genus *Eubazus* was confusing. Several species had been described in the past, in several genera, but the most recent studies on *Pissodes* parasitoids had suggested that a single species attacks all European *Pissodes* spp. (Haeselbarth 1962; Annila 1975; Roques 1975; Alauzet 1982; Mills & Fisher 1986). Our first biological observations, however, suggested the possible occurrence of several sibling species, leading to a larger research programme on the taxonomy of this group. Finally, our studies revealed the existence of at least three European species, each of them being largely specialised in different hosts and microhabitats (Table 1) (Kenis & al. 1996; Kenis & Mills 1998). In addition to these European species, a single North American species was included in the study, *E. strigitergum* (Cushman, 1930) (referred to as *E. crassigaster* [Provancher, 1886] in Kenis & al. [1996] and Kenis & Mills [1998]) since this latter is a parasitoid of *P. strobi* in North America. The taxonomy of the group was revised in van Achterberg & Kenis (2000). *E. semirugosus* (Nees, 1816) is a parasitoid of *Pissodes* spp. which develop in pine and spruce trunks, *E. robustus* (Ratzeburg, 1844) attacks

essentially *P. validirostris* in pine cones and is very occasionally found attacking *Pissodes* spp. in pine trunks, and *E. abieticola* van Achterberg & Kenis, 2000 attacks only *P. piceae* in fir trunks. *E. strigitergum* parasitises *P. strobi* in spruce and pine leaders in North America, and several other closely related species occur in North America and Asia (van Achterberg & Kenis 2000).

A combination of several methods was needed to ascertain the co-existence of three *Eubazus* spp. on *Pissodes* spp. in Europe and to provide a diagnostic separation with the North American *E. strigitergum*. Variations were found in the following traits: developmental biology, morphometrics, isoenzyme patterns, fecundity and host preference. Crosses were made between *Eubazus* spp. populations to assess the general and behavioural compatibility of these populations.

	Hosts	Microhabitats
Europe		
E. semirugosus	*Pissodes pini*	Pine trunks
	P. castaneus	Pine trunks
	P. piniphilus	Pine trunks
	P. harcyniae	Spruce trunks
E. robustus	*P. validirostris*	Pine cones
	(*P. castaneus*)	(Pine trunks)
	(*P. piniphilus*)	(Pine trunks)
E. abieticola	*P. piceae*	Fir trunks
North America		
E. strigitergum	*P. strobi* and others (?)	Spruce and pine leaders

Table 1. *Eubazus* spp. investigated during our studies, with their respective *Pissodes* hosts and microhabitats (from Kenis and Mills 1994, 1998; Kenis & al. 1996). Hosts and microhabitats in brackets are occasional records.

Developmental biology

Observations on variation in developmental responses among *Eubazus* populations were the first signs suggesting that several species exist in Europe, with specialised hosts and habitats (Kenis 1994; Kenis & al. 1996). *Eubazus* spp. strongly differ in their development time when reared on a standard host species, both in a laboratory and under natural conditions, *E. semirugosus* being the quickest developing species, and *E. robustus* the slowest (Kenis & al.

1996). Intraspecific variations were found in *E. semirugosus* and *E. robustus*. Populations of both species collected at high altitudes in the Alps and reared on a non-diapausing *Pissodes* host developed an obligatory diapause in the early larval stage in the host larva. The diapause was broken by a cold period of at least three months. In contrast, populations collected in the lowland developed without diapause when reared in the laboratory. Variations in development time and diapause characteristics were maintained in the offspring generation, suggesting a genetic basis. These variations were regarded as adaptations to the phenology of their respective hosts in their respective environments (Kenis & al. 1996).

Morphometrics

Since no simple morphological character was sufficient to separate *Eubazus* spp., mophometric measurements of over 40 characters were performed on 25 populations of the four investigated species as well as on their offspring emerged from a standard host species (Kenis & Mills 1998). Univariate, bivariate and multivariate analyses were made and morphometric measurements were compounded into canonical discriminant analyses. The ratio of the length of the ovipositor sheath to the fore wing length provided a diagnostic character between *E. robustus* and *E. abieticola*, but there were overlaps with the other species. Canonical discriminant functions including 15 measurements were needed to separate females of the three European species, whereas there were slight overlaps between males of *E. semirugosus* and of the two other species. The North American *E. crassigaster* could be separated from *E. semirugosus* in males only, whereas females overlapped. Canonical discriminant functions were used to assess the identity of doubtful populations. This method showed that *E. semirugosus* also attacks the spruce species *P. harcyniae*. It also revealed that *E. robustus* occasionally emerges from pine *Pissodes* spp. We failed to separate the mountain, diapausing biotypes of *E. semirugosus* and *E. robustus* from their lowland, non-diapausing counterparts, suggesting that the geographic biotypes belong to the same species.

Isoenzyme analyses

Several populations of the four *Eubazus* spp. were compared using isoenzyme starch gel electrophoresis (Kenis and Mills 1998). The banding patterns of two enzymes, Hexokinase and Esterase, provided a diagnostic separation between

E. robustus and *E. abieticola*, but *E. semirugosus* shared common bands with both species. No significant difference was found between the mountain and lowland populations of *E. semirugosus*. The isoenzyme analysis was particularly useful in separating the North American *E. strigitergum* from the European species. The banding pattern of Phosphogluconate Dehydrogenase provided the only diagnostic character found during the study to separate both sexes of *E. strigitergum* from its most closely related species, *E. semirugosus*.

Fecundity

The potential fecundity was compared by counting the number of ovarioles per female. *E. abieticola* females had almost twice as many ovarioles as females of the three other species. These variations were explained by the distribution of their respective hosts, *P. piceae* being more gregarious than the other species (Kenis & Mills 1998).

Host preference

Preference for host species was tested with *E. semirugosus* and *E. abieticola* only. Naive females were given the choice between ovipositing in *P. castaneus* eggs in pine logs and *P. piceae* eggs in fir logs. Both species showed a strong preference for their original host. When reared on *P. castaneus* in pine logs for one generation, the offspring of both species still showed a significant difference in host preference, but the acceptability of *E. abieticola* for pine had significantly increased. This suggested that host preference is partly genetically based and partly influenced by the host or host habitat experienced during the pre-emergence period.

Crosses

Crosses were made between different populations of the three European *Eubazus* species (Kenis & Mills 1998). When a crossing was successful, two offspring generations were reared to monitor the fertility of the progeny. In intraspecific crosses, mating was very frequent and fertile offspring generations were easily produced. The mountain, diapausing biotype and the lowland, non-diapausing biotype of *E. semirugosus* interbred as well as specimens from the same biotype, suggesting again that they belong to the same species. Howev-

	E. semirugosus	*E. robustus*	*E. abieticola*	*E. strigitergum*
E. semirugosus	—			
E. robustus	**DEV; MOR^{f};** ISO; CRO; HOS	—		
E. abieticola	DEV; **MOR^{f}**; ISO; **FEC**; PRE; CRO; **HOS**	DEV; **MOR**; **ISO**; **FEC**; **CRO**; **HOS**	—	
E. strigitergum	DEV; **MOR^{m}**; **ISO**;	DEV; **MOR**; **ISO**;	**MOR**; **ISO**; **FEC**	—

Table 2. Traits in which variations were found among *Eubazus* spp.: DEV = Development time; MOR = Morphometrics; ISO = Isoenzyme patterns; FEC = Fecundity; PRE = host preference in the laboratory; CRO = crosses; HOS = Natural host. Traits in bold provided diagnostic characters. Crosses were not performed with *E. strigitergum*. Host preference was assessed in *E. semirugosus* and *E. abieticola* only. Variations in natural hosts are relevant for European species only. Source: Kenis & al. (1996); Kenis & Mills (1998). MOR^{m}: Morphometrics provide diagnostic characters in males only. MOR^{f}: Morphometrics provide diagnostic characters in females only.

er, the diapause characteristic is genetically based because it is transmitted from father to offspring (Kenis & Mills 1998).

Very few matings were observed in inter-specific crosses, but two out of 10 crosses between *E. semirugosus* and *E. abieticola*, and one out of seven crosses between *E. semirugosus* and *E. robustus* resulted in a fertile offspring. *E. abieticola* and *E. robustus* appeared to be totally reproductively isolated (Kenis & Mills, 1998).

Conclusions

This study established the existence of three sibling *Eubazus* species in Europe, each of them being largely specialised in a different microhabitat. Although no cladistic analysis was performed, observations in morphometrics, isoenzyme analyses and cross-mating experiments suggest that *E. robustus* and *E. abieticola* are most different, whereas *E. semirugosus* occupies an intermediate position in the evolution of the group. Speciation is probably not complete because *E. semirugosus* is still genetically compatible with the two other European species. Discussions on the implications of this study on ecological,

evolutionary and pest management issues are found in Kenis & al. (1996) and Kenis & Mills (1998).

These investigations also exemplify the need for an integrated approach in parasitoid taxonomy. Indeed, none of the methods provided sufficient diagnostic characters for both sexes of all *Eubazus* species (Table 2). The systematic research programme was initiated because observations on developmental biology suggested the existence of sibling species. Morphometrics separated – with difficulty – females of the European species and males of *E. strigitergum* from the European species but failed to separate males of European species and females of *E. strigitergum* and *E. semirugosus*. Isoenzyme analysis was the only method providing a clear separation between *E. strigitergum* and the European species, but separation among the European species was less satisfactory. Morphometrics, isoenzyme analyses and crosses revealed a clear separation and reproductive isolation between *E. robustus* and *E. abieticola*, and an intermediate position of *E. semirugosus*. Crosses, morphometrics and isoenzyme analyses showed that the mountain and lowlands biotypes of *E. semirugosus* and *E. robustus*, albeit showing very different and genetically based developmental responses, belonged to the same species. Finally, observations on fecundity and host preference confirmed the other data.

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Author's address:

CABI Bioscience Switzerland Centre
1 Rue des Grillons
2800 Delémont
Switzerland

Biogeographie und Cospeziation: Erläuterung von Methoden am Beispiel von Psylliden und Peloridiiden (Hemiptera)

Daniel Burckhardt, Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001 Basel. E-Mail: daniel.burckhardt@unibas.ch

Die Verbreitung von Organismen kann vor einem ökologischen oder einem historischen Hintergrund untersucht werden. In der historischen Biogeographie können drei Betrachtungsweisen unterschieden werden: beschreibend, narrativ und analytisch. Im letzten Fall eignen sich kladistische Methoden, die Verwandtschaftshypothesen der untersuchten Organismengruppen voraussetzen. Dabei wird ein Taxonkladogramm (TC) in ein Taxon/Gebiets-Kladogramm (TAC) übersetzt, indem im TC die Endtaxa durch die jeweiligen Gebiete ersetzt werden, in denen sie vorkommen. Falls jedes Endtaxon nur in einem Gebiet vorkommt, und jedes Gebiet nur ein Taxon enthält, stellt das gefundene TAC gleichzeitig auch ein (gelöstes) Gebiets-Kladogramm (RAC) dar. Eine allgemeine biogeographische Hypothese wird dann durch den Vergleich der RACs von verschiedenen Organismengruppen gewonnen.

TACs können aber auch Taxa enthalten, die in mehreren Gebieten vorkommen, oder ein Gebiet kann mehrere Taxa enthalten. In diesem Falle müssen biogeographische Annahmen getroffen werden (assumptions 0, 1, 2), die diese Phänomene verschieden deuten. Zur Auflösung von TACs in RACs können je nach biogeographischer Annahme z. B. folgende Methoden (und Programme) gebraucht werden: Brooks Parsimony Analysis (BPA), Three Area Statements (TAS) oder Komponenten-Analyse (COMPONENT, CAFCA). Die gleichen Methoden können auch gebraucht werden um unterschiedliche RACs zu einer allgemeinen biogeographischen Hypothese zusammenzufassen. Die Grundlagen, Techniken und Eigenheiten dieser Methoden sollen kurz erläutert und anhand von Beispielen aus den Blattflöhen (Psylloidea) und Mooswanzen (Peloridiidae) verdeutlicht werden.

Cospeziation einer wirtsspezifischen Parasitengruppe mit deren Wirten zeigt gewisse Ähnlichkeiten zu Prozessen der historischen Biogeographie (dort Vergleich der Kladogramme von Gebieten und Organismen). Deswegen können zu deren Untersuchung auch ähnliche Methoden verwendet werden. Dies soll wiederum anhand von Beispielen aus den Blattflöhen (Psylloidea) gezeigt werden.

www.araneae.unibe.ch — Ein Bestimmungsschlüssel der Spinnen Mitteleuropas im Internet

Wolfgang Nentwig, Universität Bern, Zoologisches Institut, Baltzerstrasse 6, CH-3012 Bern.
Ambros Hänggi, Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001 Basel.
Christian Kropf, Naturhistorisches Museum Bern, Bernastr. 15, CH-3005 Bern.
Theo Blick, Heidloh 8, D-95503 Hummelthal.

Neben einem dichotomen Textschlüssel müssen Bestimmungsbücher vor allem viele und gute Illustrationen anbieten, damit eine eindeutige Identifikation möglich ist. Da die Nomenklatur einiger Taxa noch nicht gefestigt ist, da ferner auch bei Arthropoden in Mitteleuropa Neubeschreibungen und regionale und nationale Erstnachweise immer noch regelmässig vorkommen, sind gedruckte Werke schnell veraltert. Abhilfe kann hier nur ein flexibles Medium wie das Internet schaffen, welches es erlaubt, Korrekturen und Ergänzungen kontinuierlich vorzunehmen. Für die Spinnen Mitteleuropas wird hier ein Internet-Bestimmungsschlüssel vorgestellt, welcher beim derzeitigen Ausbaustand die Bestimmung von über 1300 Arten aus 43 Familien ermöglicht. Rund 8000 Abbildungen aus vielen Bestimmungsbüchern und aus über 100 Einzelpublikationen stellen jede Art mit Erlaubnis der jeweiligen Copyright-Eigentümer optimal dar.

Die Erfahrung mit Abbildungen hat gezeigt, dass einerseits künstlerische und zeichentechnische Unterschiede oft sehr gross sein können, andererseits gibt es aber auch eine individuelle und geographische Variation der Merkmale. Daher ist unser Konzept, mit einer Reihe von Abbildungen die Breite der Variabilität zu präsentieren, anstatt für jede Art eine einzige jeweils beste oder klarste Abbildung (wie immer definiert) darzustellen. Im Unterschied zu den traditionellen Bestimmungsbüchern haben wir nicht angestrebt, Abbildungen zu allen Arten von einer Hand darzustellen, denn solch ein Unterfangen wäre zunehmend redundant und heute kaum noch zu finanzieren. Um in unserem Internet-Bestimmungsschlüssel jede Art zufriedenstellend abzubilden, greifen wir vielmehr auf die in der Literatur existierenden Abbildungen zurück und reproduzieren sie mit Erlaubnis des Urhebers. Nur soweit nicht verfügbar, bemühen wir uns um Neuzeichnungen.

Im Rahmen des zukünftigen Ausbaues dieser übrigens für jeden frei zugänglichen Bestimmungsmöglichkeit werden zusätzliche Informationen eingefügt, beispielsweise Verbreitungskarten (bisher erst ansatzweise erfolgt) und Angaben zur Vergesellschaftung von Spinnenarten oder zur Habitatbindung (separates Projekt). Ein Teil der zukünftigen Bemühungen wird sich darauf konzentrieren, den behandelten geographischen Bereich in Europa zu erweitern, also immer mehr Arten einzubeziehen. Während West-, Nord und Osteuropa (bis Polen) derzeit bereits recht gut dokumentiert sind, und wir hier auch Vollständigkeit anstreben, ist die Ausweitung auf Südeuropa schwierig. Die grosse Zahl zusätzlicher Arten, die einbezogen werden müsste, und der vergleichsweise schlechte Dokumentationsstand vieler Gruppen erfordern eine grosse zusätzliche Anstrengung, die erst in einigen Jahren erfolgen kann. Desgleichen ist eine englische Fassung, die es derzeit erst für den Familienschlüssel gibt, ein Ziel, das erst in einigen Jahren erreicht sein wird. Dieses Projekt lebt daher von der Rückkopplung durch die Benutzer und Mitarbeiter, um die gebeten wird.

Klassifikation von Fossilien mit hoher morphologischer Variabilität unter Berücksichtigung der lithologischen und allometrischen Abhängigkeiten der taxonomischen Merkmale am Beispiel von Daonellen (Bivalvia, Trias)

Wolfgang Schatz, Paläontologisches Institut und Museum der Universität Zürich, Karl Schmid-Str. 4, 8006 Zürich. E-mail: wowo@pim.unizh.ch

Die biostratigraphische Gliederung des unteren und mittleren Ladinian (242–238 Ma) der Südalpen ist schwierig, da viele lithologische Einheiten nur selten biostratigraphisch relevante Fossilien wie Ammonoideen oder Conodonten aufweisen. Muscheln der Gattung *Daonella* kommen jedoch relativ häufig in diesen Gesteinen vor. Deshalb wurde mehrfach versucht, sie für die Biostratigraphie einzusetzen. Viele dieser Versuche scheiterten jedoch an der inkonsistenten systematischen Einteilung der Daonellen. Einige Daonellenarten sind unzureichend beschrieben oder basieren auf schlecht erhaltenem Material und juvenilen Exemplaren. Des Weiteren wurden viele Arten aufgestellt, welche nur eine lokale Verbreitung aufwiesen.

Damit diese Muscheln als biostratigraphische Leitfossilien verwendet werden konnten, musste ihre systematische Einteilung umfassend überprüft werden. Es galt, einen neuen klassifikatorischen Ansatz zu finden. Viele Faktoren erschweren die Daonellentaxonomie: die Klappen weisen eine hohe morphologische Plastizität sowie nur wenige diskrete Merkmale auf. Ausserdem konnte aufgezeigt werden, dass lithologische und allometrische Faktoren die Klappenmorphologie stark beeinflussen.

Der neue klassifikatorische Ansatz gliedert sich wie folgt: Als Erstes wurden morphometrische Merkmale mit Hilfe von Landmarks und Pseudolandmarks exakt definiert. Diese Merkmale wurden auf ihre taxonomische Signifikanz überprüft. Als Testprobe wählte ich eine Population aus einer Fundschicht aus und überprüfte diese zuerst auf ihre Homogenität mit Hilfe der Normalverteilung. An dieser als homogen angesehenen Testprobe wurde die taxonomische Signifikanz der morphologischen Merkmale untersucht.

Der Test auf Interkorrelation zwischen den Merkmalen: Stark interkorrelierende Merkmale bewirken eine unerwünschte Gewichtung einzelner Merkmalskomplexe. Test auf allometrische und lithologische Abhängigkeit: Merkmale, welche sich während der Ontogenese stark verändern oder deren Überlieferung im Fossilbeleg signifikant von der Lithologie abhängt, wurden als nicht taxonomisch signifikant angesehen und nicht für die Klassifikation der Daonellen berücksichtigt.

Die Holomorphen mussten mit Hilfe von multivariaten Methoden miteinander verglichen werden, da sich auf Grund der hohen Merkmalsvariabilität uni- und bivariate Methoden als nicht ausreichend erwiesen. Die Hauptkomponentenanalyse (PCA) wurde angewandt, um die Verteilung der Holomorphen im multidimensionalen Raum zu erkennen. Auf Grund dieser Verteilung wurden Morphospezies interpretiert. Die Qualität dieser Interpretation wurde mit Hilfe der kanonischen Diskriminanzfunktionsanalyse überprüft.

Der neue klassifikatorische Ansatz (Verwendung von modifikatorisch unabhängigen Merkmalen sowie die Anwendung multivariater Techniken) ermöglichte eine jederzeit nachvollziehbare systematische Gliederung der Gattung *Daonella*. Die derart durchgeführten Untersuchungen konnten aufzeigen, dass viele bis anhin vergebene Namen Sy-

nonyme sind. Vielfach wurden verschiedene Grössenstadien zu unterschiedlichen Arten gestellt. Am Beispiel von *Daonella pichleri* konnte folgende, von der Ontogenie abhängige Klassifikation festgestellt werden: Als *D. obliqua* wurden juvenile, als *D. pichleri* und *D. reticulata* subadulte und als *D. pauli* und *D. nodigulera* adulte Exemplare bezeichnet. Die Zusammenfassung der lokalen Formen ermöglichte eine überregionale Korrelation daonellenführender Gesteinsschichten. So konnten Fundstellen der Buchensteinerschichten aus der Lombardei und den Dolomiten miteinander korreliert und in eine zeitliche Abfolge gebracht werden.

Es konnten neun Daonellenzonen für das obere Anisian und das untere sowie mittlere Ladinian ausgeschieden werden: Die *sturi*-Zone, die *angulata*-Zone, die *caudata*-Zone, die *pseudomoussoni*-Zone, die *fascicostata*- Zone, die *moussoni*-Zone, die *taramelli*-Zone, die *pichleri*-Zone und die *lommeli*-Zone.

Der Biostratigraphie der Mitteltrias steht mit den Daonellenzonen ein neues, zuverlässiges Werkzeug zur Verfügung.

Eignung mitochondrialer Gene zur Klärung der Verwandtschaftsverhältnisse von Kletternattern (*Elaphe*) (Serpentes)

Urs Utiger, Zoologisches Museum der Universität Zürich, Winterthurerstrasse 190, 8057 Zürich. (utiger@zoolmus.unizh.ch)

Die Kletternattern bilden mit über vierzig Vertretern eine grosse Artengruppe, die über weite Teile der Paläarktis und der Orientalis bis hin zu den nördlichsten Inseln der Australis vorkommt. In der Neuen Welt beschränkt sich ihre Verbreitung auf Nord- und Mittelamerika. Die Gattung unterscheidet sich durch eine Kombination von morphologischen Merkmalen von anderen Colubrinen, wobei keines davon exklusiv ist. Im Rahmen einer umfassenden Verwandtschaftsanalyse sollen die Eigenschaften verschiedener mitochondrialer Gene untersucht und deren Tauglichkeit für die Erstellung einer molekularen Phylogenie diskutiert werden. Dafür wurden Teile des Cytochrom Oxidase I - Gens (COI-Sequenz), des Cytochrom Oxidase II - Gens (COII-Sequenz) und des 12S ribosomalen RNA-Gens (12S rRNA-Sequenz) sequenziert und zwischen den Taxa verglichen.

Die beiden codierenden Gene, COI und COII, zeigen an der ersten Position des Aminosäurecodons kaum und an der zweiten Position überhaupt keine Variabilität. An der dritten Position dagegen scheinen bereits starke Sättigungstendenzen aufzutreten, so dass die resultierenden Stammbäume interspezifisch tiefe Bootstrap-Werte erhalten und kaum aussagekräftig sind. Im Gegensatz dazu vermag die Phylogenie aus der 12S rRNA-Sequenz die Arten in gut abgesicherte Gruppen mit hohen Bootstrapwerten aufzulösen. Statistische Tests zeigen weiter, dass sich die Information aus der COII-Sequenz als einzige signifikant von der Gesamtinformation aus der zusammengesetzten Sequenz aller drei Gene unterscheiden. Die zu einem Datenset vereinigten Sequenzen von COI und 12S rDNA dienten der Berechnung einer Phylogenie, deren Bootstrapwerte bei den meisten Verzweigungen höher waren als bei den Phylogenien aus Genkombinationen mit COII.

Diese „optimierte" Phylogenie aus COI und 12S rDNA fasst die endemisch auf Japan vorkommenden *E. climacophora* und *E. quadrivirgata* mit den ostasiatischen *E. bimaculata* und *E. dione* zu einer gut abgesicherten monophyletischen Artengruppe zusammen. Die beiden nearktischen Vertreter, *E. guttata* und *E. vulpina*, sind ebenfalls miteinander verwandt, wogegen die lecithotrophe und semiaquatische *E. rufodorsata* keinen nahen Verwandten hat. Die Indo-Malayische Art *E. flavolineata* hat sich als erste abgespalten und hat genetisch (und morphologisch) nur noch wenige Gemeinsamkeiten mit den untersuchten Kletternattern.