

**PHYLOGENY OF *DICERCA ESCH.* AND *POECILONOTA ESCH.* REVISITED**

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***Introduction***

Ten years ago, as a part of my doctor's dissertation (Holyński 1999), I presented the first, preliminary outline of the taxonomical, zoogeographical and phylogenetical review of the genera *Dicerca Esch.* and *Poecilonota Esch.* Very incomplete (especially as regards Nearctic species) taxon sampling, as well as the “embrional” stage of the development of the applied phylogenetic program (MICSEQ) did not allow to avoid numerous simplifications, poorly substantiated assumptions, and even [now] evident errors. Some of them have been corrected in the paper published six years later (Holyński 2005b) which, however, was mainly intended as a revision of Indo-Pacific taxa and, as such, included but few Nearctic representatives of the genera; moreover, MICSEQ (“version 3.1”) was still very imperfect and hard to “operate”, leaving ample room for both inadvertent and systematic errors in phylogenetic reconstructions. Since that time, thanks to the kindness of several colleagues and museum curators, I had the opportunity to examine (and include in the “character-matrix”) almost all the [sub-]species of *Dicerca Esch.* and *Poecilonota Esch.* hitherto described, and also the very significantly improved (“5.2”) version of my phylogenetic program has become available, enabling me to present a new, comprehensive (including the majority of both Eurasian and American taxa) reconstruction of the evolutionary history of these genera.

The material on which this analysis has been based came from the following collections:

- EONMP** – Entomologické Oddelení Národního Musea, Praha
- FSCA** – Florida State Collection of Arthropods, Gainesville
- JG** – Jerzy GUTOWSKI, Białowieża
- KBIN** – Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels
- MG** – Maurizio GIGLI, Rome
- MN** – Manfred NIEHUIS, Landau
- MNCN** – Museo Nacional de Ciencias Naturales, Madrid
- MNHN** – Muséum National d'Histoire Naturelle, Paris
- NHMG** – Naturhistoriska Museet, Göteborg

<b>NNHM</b>	– Nationaal Natuurhistorisch Museum, Leiden
<b>RBH</b>	– Roman B. HOŁYŃSKI, Milanówek
<b>SB</b>	– Svatopluk BÍLÝ, Praha
<b>TL</b>	– Tiéri LANDER, Genève
<b>TNS</b>	– Thierry Neef de SAINVAL, Brussel
<b>ZIRAN</b>	– Zoologiczeskij Institut Russkoj Akademii Nauk, Petersburg

Following abbreviations are used in the descriptions:

- dfp = “dense-and-fine punctulation” or “densely-and-finely punctulate”; refers to the type of sculpture, especially characteristic of representatives of some subtribes (**Chrysochroina** CAST., **Chalcophorina** LAC., **Lampropeplina** HOŁ., **Hypoprasina** HOŁ., **Dicercina** GISTL &c.) of the **Buprestini** LEACH, occurring mainly in depressed areas (foveae, sulci), and consisting of fine, dense, regular punctulation on usually distinctly microsculptured background, covered with dense pubescence and frequently pulverulent.
- L = length  
W = width  
BW = basal width  
AW = apical width  
MW = maximum width  
H = width of head with eyes  
V = width of vertex between eyes  
F = width of front at upper margin of antennal grooves  
∅ = specimen of unknown sex  
*i.l.* = *in litteris* – used generally for **any** unpublished name (most frequently means name in collection)  
issp. = infrasubspecific, nomenclaturally unavailable name  
I. = (in geographical names) [single] Island  
Is. = [group of] Islands  
→ = transformed into, leading to, resulting in  
**SQ** = “support quotient”;  $SQ=x/y$  [where **x** is the “corrected distance” (at the relevant stage of analysis, *i.e.* when the particular pairing is being performed) between the paired taxa, and **y** – the shortest distance between any of them and any of those remaining “in game”; of course the interpretation of the “quotient” should not be “overmathematized”:  $SQ=1/2$  is evidently **not** equivalent to  $15/30!$ ]  
pu. = phenun (“phenetic unit”): unit of distance shown in distance-matrix; 1 pu. = distance between two neighbour traits [“character states”] in transformation chain, if the weight is settled as 1

### Taxonomic remarks

Taxonomy and distribution of the Indo-Pacific and Far Eastern representatives of *Dicercia* ESCH. and *Poecilonota* ESCH. have been reviewed and discussed in my earlier papers (Hołyński 1999, 2005), those of Nearctic taxa by – respectively – Nelson 1975 and Evans 1957, while western Palaearctic species are well known from numerous publications (*e.g.* Richter 1952; Bílý 1977; Mühle et al. 2000; Curletti 2007; Schaefer 1949; Théry

1930, 1942; Cobos 1986), so now I restrict myself – besides phylogenetic reconstruction – to clarification of the taxonomic status of few hitherto enigmatic nominate taxa.

***Dicerca (s.str.) latouchei* FRM. [= *D. tibialis* LEW.]**

**Material examined:**

**Holotype:** “Amoy” ”*Dicerca Delatouchii* Fair [? – illegible!] – China”  
“TYPE” [red letters] “MUSEUM PARIS, COLL. CH. KERREMANS,  
1923” [♀ (MNHN)]

12.5×5 mm. An ant clings with mandibles to the left mesotarsus, and head of another ant to left metatarsus.

In my earlier paper (Hołyński 2005b), having known only the original description of *D. latouchei* FRM. I mentioned its synonymy to *D. tibialis* LEW. as one of possibilities; now I received the holotype for study, and indeed I am unable to find any taxonomically significant difference between this specimen [labelled as *D. “Delatouchii”*, but described as *D. Latouchei*] and the individuals from Honshu I have for direct comparison (dorsal dfp areas are predominantly green but such colouration does also occur in some Japanese specimens). Whether the locality (Amoy [=Hiamun, =Xiamen] – 24°26’N-108°04’E) is a case of mislabelling, artificial introduction, or *D. tibialis* LEW. does indeed occur in mainland Asia, is not clear to me (Akiyama and Ohmomo 1997 include “China” among the areas of distribution, but I have never seen any specimen from anywhere outside Japan)

***Dicerca (s.str.) pervillosa* HOL. i.l. [= *D. corrugata* FRM.]**

**Material examined:**

**Holotype:** “[label in Chinese; possibly (but not sure!) with date 81.6.25]”  
“cum typo comparavit Sv. Bílý 1993” “*Dicerca corrugata* Fairm., Sv. Bílý  
det. 1993” [♂ (SB)]

16.5×6.5 mm.

**Additional material:** Yunnan: Yulongshan: Baishui, 27°08’N-100°14’E,  
2900-3500 m., 7-12 VII 1990, [ex *Pinus* – KUBÁŇ i.l. 2007] [1 ♀ (VK)]

ca. 14.5×6 mm. Head missing. Initially intended as PT of *pervillosa* HOL. i.l. Pubescence on elytral dfp very short but conspicuous (ca. as in *vitalisi*), that on ventral side long, erect, still more abundant (less worn?) than in the intended HT.

Yunnan: Weibaoshan: W-slope, 25°11’N-100°24’E, 2000-2800 m., 25-28 VI 1992, [on *Pinus* trunk – KUBÁŇ i.l. 2007] [1 ♂ (VK)]

16.5×6.5 mm. Shape and colouration of body somewhat like *vitalisi*, but pronotum wider, elytral basal truncation not sinuate (straightly oblique), sides in apical half conspicuously (as in average *corrugata s.str.*) sinuate (“caudate”).

Yunnan: Yipinglang, 25°03’N-101°55’E, 2000 m., 8-10 VI 1993, [on *Pinus* trunk – KUBÁŇ i.l. 2007] [1 ♀ (VK)]

17.5×6.5 mm. Shape like typical *corrugata s.str.*, but colouration (esp. ventral) somewhat paler. Weibaoshan and Yipinglang specimens with abundant frontal and ventral pilosity as in *vitalisi* [but elytral not apparent]

In the material sent to me few years ago by S. BÍLÝ I found a specimen evidently belonging to the *D. [corrugata FRM.]*-superspecies, but strikingly unusual in long and dense pilosity (comparable only to that in evidently unrelated American *D. horni* CROTCH). Although other apparent differences [lack of median carinula on front and of paired reliefs on vertex, somewhat coarser sculpture with more elevated and less widely interrupted elytral costae, less extensive finely punctured spaces between them, more obliquely truncated elytral apices, lack of distinct smooth reliefs at middle of basal margins of sternites, less conspicuous crenulation of inner edge of distal (behind spur) part of mesotibiae, and some minor details] did not seem to exceed the limits of individual variability of FAIRMAIRE'S species, I was convinced of its taxonomic (at least subspecific) distinctness, labelled the specimen as a holotype and prepared the description for publication. However, somewhat later V. KUBÁŇ sent me some recently collected specimens (all those earlier in my disposition were old examples) from Yunnan, apparently belonging to *D. corrugata FRM.*, but showing head, pronotum and ventral side more or less similarly pilose to the intended holotype. Both the geographical boundaries between, and extent of variability within, races of *D. corrugata FRM.* are still very poorly known so the subspecific distinctness cannot be fully excluded, but the most likely interpretation seems to be the presence of pilosity in most or all fresh specimens of *D. corrugata FRM.*, its apparent lack in old examples being simply the effect of wear.

***Dicerca (s. str.) corrugata vitalisi D.V.***

*Dicerca vitalisi* DESCARPENTRIES et VILLIERS 1963

**Material examined:**

3 ♂, 2 ♀

Thanks to the kindness of some colleagues I have the opportunity to examine three specimens of this species from Laos, I had also studied one in the MNCN collection, so I am now able to provide the detailed, complying to my usual standard, description of this taxon:

**Characters:**

Males [3] 15×5.5 – 17×6.5; female [1] 16×6 mm. Dorsal side dark cupreous-bronzed with brownish-black reliefs; pubescence white, on head and (esp. in male) prosternal process long and erect, otherwise on ventral side short and semirecumbent, pronotum glabrous, elytra lateroapically with very short and inconspicuous (somewhat more distinct at apices) hairs. Head: V:H≈0.56-0.57 (♂), 0.58 (♀); frontal sculpture consists of dense, irregular, small, partly confluent, lustrous asperities (with more or less distinct narrow median carinula in upper part, ending in somewhat larger tubercle at middle), leaving irregular, depressed dfp spaces in between; pair of longitudinal reliefs on vertex usually discernible but poorly developed. Pronotum: BW:MW:AW:L≈1.28-1.40:1.28-1.40:1.04-1.09:1 (♂), 1.41:1.44:1.12:1 (♀); pronotal sides indistinctly sinuately subparallel from acute basal angles to anterior <sup>2</sup>/<sub>5</sub> (where pronotum is slightly wider than at base) and roundedly convergent anterad; basal and apical margins bisinuate with narrowly (base) or broadly (apex) rounded median lobe; lateral margins (esp. in anterior half) coarsely crenulated. Disk with pair of conspicuous oblique depressions before base, five (very narrow but usually entire and almost regular median, pair of broad but less regular perimedial,

and somewhat shortened and still less regular midlateral) elevated lustrous longitudinal carinae, and some very irregular small asperities on sides; depressed parts between them finely, very densely punctured; prescutellar pits variable, placed in broader foveae making proximal end of perimedial sulci; lateral carina entire, sharp in basal half, rather blunt apically, very irregular, coarsely and densely granulated. Elytra: L:W $\approx$ 1.89-1.91 ( $\sigma$ ), 1.98 ( $\omega$ ); more or less distinctly “caudate”, apices deeply emarginated between pair of sharp and rather long denticles (lateral equal to or slightly longer than sutural); lateral margins moderately crenulate throughout. Transverse depression behind base (“elytral collar”) usually very conspicuous; sutural costa sharp, regular, entire; disk with 4 others (less distinct and lower in  $\omega$ ), 1. (perisutural) almost regular, 2.-4. increasingly broken, intervals with rows of coarse foveolate punctures (hardly appreciable towards sides); finely punctured depressed areas relatively small and irregular medially in males, definitely more extensive on sides and generally in female. Anterior margin of prosternum almost straight or very shallowly emarginate; median part of prosternal process 4-5 $\times$  wider than lateral rim, covered with irregular network of fine ( $\sigma$ ) to rather coarse ( $\omega$ ) elevated ridges; proepisterna coarsely irregularly reticulate; broad and rather deep longitudinal depression runs along median line of prosternum, metasternum and 1. sternite; no metacoxal dent; smooth basal reliefs on 2. and 3. sternites distinct, pair of longitudinal carinae on 5. segment often inconspicuous); otherwise ventral side covered with dense jumble of small callosities and coarse ocellate punctures; apex of anal sternite in  $\omega$  rounded, with pair of deep (much deeper than wide) notches; in  $\sigma$  very broadly, shallowly trapezoidally emarginate between two denticles. Mesotibiae above middle with long spur strongly flattened frontocaudally, directed inwards and somewhat upwards.

**Geographical distribution:** Known from several localities in Laos; one specimen has been collected apparently in China but exact locality remains unknown (label in Chinese, unintelligible to me).

**Remarks:**

Looks slenderer and brighter coloured than *D. corrugata* FRM. s.str.; frontal, elytral and ventral pubescence more conspicuous; pronotal sides in basal half subparallel, not or but slightly sinuate; elytra with transverse basal depression (“collar”) more conspicuous, oblique basal truncation between humeral angles and humeral protuberances distinctly sinuate, sides almost parallel in basal half, not or very slightly caudate apically; sides of parameres more regularly arcuate – all these differences (except perhaps proportions and colouration) are rather vague. Subspecific distinction of the Laotian population seems uncontested; on the other hand, specific rank given to it by Descarpentries and Villiers (1963) cannot be accepted in view of the occurrence of some apparently intermediate specimens in Yunnan.

**“*Lamprodila* MOTSCHULSKY 1860”**

When some months ago I had found this name in an [at least then] unpublished faunistic paper by one of Polish coleopterists (as far as I know, not specializing in **Buprestidae**), I thought it was an erroneous misspelling or misinterpretation and quickly forgot it. However, just when the present paper was ready for submission, I received the publication of Bílý et al. (2009), where this name has been consistently applied as valid, so that any suspicion of inadvertent mistake must have been excluded. Unfortunately, the Authors do not specify which of MOTSCHULSKY’S several publications dated for 1860 contains the original introduction of *Lamprodila* (nor do they include

the respective title in the References); I have checked the two available in the library of the Zoological Institute PAS in Warsaw, but failed to find the name in any of them – indeed, MOTSCHULSKY refers there to the genus “traditionally” as “*Poecilonota (Lampra)*”. I suspected that it has been “reintroduced” in the recent (2006) catalogue of Palaearctic Coleoptera edited by Löbl and Smetana, and there are some indications in Bílý et al.’s (2009) paper suggesting that it was used in the buprestid world catalogue by Bellamy (2008), but both these publications remain inaccessible to me... [Bellamy’s earlier (2003) catalogue does not mention this name]; I am not able now to check the last volumes of *Bulletin of Zoological Nomenclature*, but do not remember to have ever seen a Commission’s decision to revalidate MOTSCHULSKY’S name after 150 years of oblivion. So I do not know whether *Lamprodila* had been validly introduced, nor what exactly it refers to (what is its type-species); nor why this rather than *Dendrochariessa GISTL 1848* should be resurrected; nor (last not least...) why BÍLÝ, KUBÁŇ and VOLKOVITSH, known as **opponents** of “nomenclatural archaeologists” trying to validate the oldest available names, just in this case themselves “unearthed” (or at least readily accepted) a long forgotten (in fact, apparently never used since its introduction one and half a century ago...) name (and, at that, such which meets all the usually adduced characteristics of those especially deserving suppression “*in the interest of stability of nomenclature*”: referring to a very well known, speciose, widely distributed, economically important taxon which was already known under 5 different names but now has a well established and widely accepted one...). With so many uncertainties, I must have decided – contrary, in turn, to **my** general attitude... – to retain tentatively the younger, well known name *Ovalisia KERREMANS 1900* for the genus and *Palmar SCHAEFER 1949* and *Scintillatrix OBENBERGER 1952* for subgenera [this paradoxical situation, by the way, seems one more nice example of the chaos resulting from the Principle of Posteriority (“current usage”) introduced in the last editions of the Code but not felt worth to be consistently observed even by ardent supporters!].

## Phylogenetic reconstruction

### *Taxon sampling and procedures*

Phylogenetic reconstructions have been done by the currently available (provisionally “labelled” as 5.2) version of MICSEQ (general idea of the program, and procedure used at the earliest stage of its development, was outlined by Holyński 2001). The study includes all the hitherto described valid recent [sub-]species of *Dicerca* ESCH. and *Poecilonota* ESCH. with the following exceptions: *D. nishidai* TMA., *D. shimoni* HRI. [fortunately the descriptions of these two very important species are sufficiently detailed to allow the tentative scoring of their characters for the character-matrix, but of course the possibility of even serious misinterpretations cannot be excluded...], *D. pectorosa* LEC., *D. horni nelsoni* BEER and *D. obtusa* KR. remained unavailable for me, while the phylogenetically informative (in the context of the present analysis) characters of *D. aenea validiuscula* SEM., *D. a. bella* AB., *P. variolosa dicercoides* RTT. and *P. v. populialbae* RCHD. are identical to those of their closest relatives [Evans (1957) writes that “one species (of *Poecilonota* ESCH.) is found only in Mexico”, but this information is apparently based on Obenberger’s (1930) misclassification of *Dicerca inconspicua* WATH.]. Altogether 79 taxa were included in the preliminary analysis, of which 9 more remote outgroups (*Ptosima* DEJ., *Haplotrinchus* KERR., *Hippomelas* C.G., *Apateum* SPIN.,

*Dicercomorpha* DEYR., *Zoolrecordia* HOL., *Eurythyrea* DEJ., *Phaenops* DEJ. and *Anilara* SND.) were thereafter disregarded, leaving two proximal outgroups (*Spinthoptera* CSY. and *Philanthaxia* DEYR.), *Touzalinia* THY., *Latipalpis* SPIN., all (8) subgenera of *Ovalisia* KERR., and 58 species-level taxa of *Dicerca* ESCH. (46) and *Poecilonota* ESCH. (12) to be considered in the final discussion; thus the completeness of taxon sampling (at the species level) reached 95% in case of *Dicerca* ESCH. and 100% in that of *Poecilonota* ESCH. I have not considered any fossil species, unfortunately invariably too poorly preserved and/or described not only to reliably score their characters for the data-matrix, but even to be certain as to their generic placement – although e.g. Prokop and Bílý (1999) seem fully convinced that “*there is easily possible to put*” their Miocene *D. bilinica* P.B. “*to the recent genus Dicerca and to the subgenus Dicerca s.str.*”, I do not find anything in the description or pictures to exclude e.g. *Poecilonota* ESCH. or *Latipalpis* SPIN., to say nothing of some unknown extinct taxa...

Supraspecific terminal taxa (subgenera and genera) have been represented by their supposed “Groundplan” (presumably plesiomorphous character-states), while in cases of intra[sub-]specific variability the most common trait was chosen. The first, preliminary analysis (1), including all 79 taxa, served as the basis of general orientation, detection of weak points and planning of more specifically focused study. In the next one (2) remote outgroups were omitted and clades well supported in 1 and intuitively acceptable were represented by their “reconstructed ancestors”. For the following step (3) the number of terminal taxa was further reduced (by replacement of clades well supported in 2 by their “reconstructed ancestors”), and some ambiguous character-states of few terminal taxa [see **Appendix**] replaced by their neighbour traits. At last, the results were evaluated according to the external (e.g. biogeographical) evidence and degree of support (SQ) for incongruent (between analyses) branchings, and summarized as the final tree (figs. 1-2) commented below. The scale on the left of each figure shows the phenetic distance in phenuns (**pu** – see **Abbreviations** above); please note that these distances can be considered as “additive” **only** for estimation of the “amount of evolution” but are definitely **not additive** for direct comparison between taxa (either terminal or “reconstructed ancestors”) not being immediate neighbours: due to homoplasies (reversals, parallelisms, convergences) the actual phenetic distance between any pair of non-neighbours will be usually (sometimes considerably) shorter than those counted along branches of the tree.

### ***Cladistic relationships between genera***

Already the first (1) reconstruction had (not unexpectedly) shown, and later (2, 3) analyses confirmed, that *Dicerca* ESCH. and *Poecilonota* ESCH. were not sister taxa: the latter formed a common clade with *Ovalisia* KERR., the situation of the former was more complicated (see later), while *Philanthaxia* DEYR., *Anilara* SND., *Phaenops* DEJ., *Eurythyrea* DEJ., *Haplotrinchus* KERR. and *Ptosima* DEJ. remained evidently outside and only *Philanthaxia* DEYR. has been left to represent them in further considerations. Although not the primary target of this study, it seems worth mentioning that the relations within (between subgenera of) *Ovalisia* KERR. proved similar to those resulting from my previous analyses (Hołyński 1999, 2000): only *Palmar* SCHAEF. changed the position from the sister of the [(*Cinyrissia* HOL. - *Mabomisia* HOL.) *Erialata* ZYK.] clade to that of (*Zykovissia* HOL. - *Ovalisia* KERR. s.str.), and *Scintillatrix* OBB. “jumped up” to form the basalmost branch of the latter complex rather than that of the entire genus. As regards *Dicerca* ESCH., it consistently appeared as paraphyletic in relation to *Touzalinia* THY. (coupled to the Mexican group *D. aeneovaria* WATH. - *D. inconspicua*

*WATH.* - *D. propinqua* *WATH.*) and *Latipalpis* *SPIN.* [basal either to the latter complex plus *D. nishidai* *TMA.* - *D. shimonoi* *HRI.*, or (separately or together with *D. mutica* *LEC.*) to all the remaining *Dicercia* *ESCH.*]; their sister-group seemed to be *Spinthoptera* *CSY.*, while *Zoolrecordia* *HOL.*, *Dicercomorpha* *DEYR.*, *Apateum* *SPIN.* and *Hippomelas* *C.G.* turned out as more remotely related and have been excluded from further considerations. However, while the placement of *Touzalinia* *THY.* and *Latipalpis* *SPIN.* within (or at least very close to) *Dicercia* *ESCH.* (though not their exact position within the clade), as well as “sister” relations between *Poecilonota* *ESCH.* and *Ovalisia* *KERR.*, seem rather firmly established, the relationships between these complexes and outgroups should be treated merely as a kind of “working hypothesis”: the (anyway weakly supported) affinity of the *Dicercia* *ESCH.* - *Touzalinia* *THY.* - *Latipalpis* *SPIN.* clade to *Spinthoptera* *CSY.* rather than to *Poecilonota* *ESCH.* - *Ovalisia* *KERR.* (or perhaps to *Zoolrecordia* *HOL.*, *Dicercomorpha* *DEYR.*, or any other genus of the subtribe **Dicercina** **Gistl**) may be merely the effect of suboptimal selection of outgroups or (aimed at the clarification of patterns *within* the target genera) characters.

### *Dicercia* *ESCH.*

According to the analysis **1** the basalmost (rather well supported: SQ=26/33 for the node **1:PPP**) split within the *Dicercia* *ESCH.* (incl. *Touzalinia* *THY.* and *Latipalpis* *SPIN.*)-clade was between **1:A** (*D. nishidai* *TMA.* + *D. shimonoi* *HRI.*) and **1:OOO** (all the rest), basalmost branch (**3:W** – SQ=21/22) of the reconstruction **3** contained this pair (**1:A**) plus the Mexican group and *Touzalinia* *THY.* – **1:EEE**), while to their equivalent in **2** (**2:OO**) additionally *Latipalpis* *SPIN.* is joined; as the support for pairing **1:EEE** with the bulk of *Dicercia* *ESCH.* rather than with **1:A** was very weakly supported (SQ=27/28), as alternative arrangement results in “shorter” tree, as generally (on theoretical grounds) the reconstruction **3** should be considered more reliable than the earlier two, and as also intuitively it looks most plausible, I selected the clade **3:W** for the final tree. The node joining it and its sister-clade [**3:V**] is **3:X**, the common ancestor of all *Dicercia* *ESCH.* (and, indirectly, *Touzalinia* *THY.* and *Latipalpis* *SPIN.*). This – if my reconstruction is correct – was a rather big (*ca.* 20 mm.), moderately robust (L:W<3.0), bronzed, inconspicuously pubescent beetle with small smooth “mirror”-spots in elytral intervals, labrum quadrangular without transverse carina, normal short supraantennal carinae, no transverse frontal ridge, vertex wide (V:H≈0.5-0.6); sides of pronotum straightly subparallel in basal half, no distinct depressions or reliefs except poorly developed paramedian ridges, lateral carina sharp only at base, scutellum small; elytra slightly caudate (lateroapical margins shallowly sinuate), apex bidentate, striae continuously depressed, punctures in them moderately coarse, interstriae flat, rugoso-punctate with slightly elevated, rather sparse “mirrors”, elytral dfp patches extensive but poorly delimited, no densely pubescent spots, epipleura narrow but reaching to near apex; anterior margin of prosternum straight, prosternal process bordered with sublateral (running parallel to, but not just at, lateral margin) stria, sparsely punctured at middle; metasternum deeply sulcate medially, metacoxal denticle broadly obliterated; 1. sternite deeply depressed along midline, no lateral abdominal furrow, lateral reliefs inconspicuous; mandible rounded laterally, antennal joints not expanded, 3. subaequal to 4.; 1. metatarsomere robust, not much longer than 2.; male mesotibia simple, anal sternite with inconspicuous perimedial ridges, apex bidenticulate in male, roundedly truncated in female. It lived most probably in early Tertiary eastern Palaearctis, though wider – even “Panholartic” – distribution also cannot be excluded.

As described above, the first split of **3:X** occurred (probably still in E-Palaeartcis) between **3:W** and **3:V≈1:III** (here and further, the “near-equation” mark “≈” means only that the respective clades contain the same terminal taxa, but the branching patterns and, consequently, the characters of the “reconstructed ancestor”, need not be identical – the latter as discussed in the text are based on the optimization according to the “summary tree” presented on fig. 1). As regards the analyzed characters, **3:W** differed from **3:X** only in conspicuous dorsal pubescence, narrow but distinct median pronotal relief, and no lateral reliefs on sternites. It divided into Japanese **1:A** (black, with deeply caudate elytral apices, very coarse puncturation in striae, subcareniform interstriae, no “mirrors”, small and sharply defined dfp spots, regularly convex 1. sternite and long spiniform spur on male mesotibiae) and continental **3:M** (body L:W≈2.5, conspicuous oblique depressions on pronotal disk, prominently bituberculate anterior margin of prosternum, obtuse but distinctly angular metacoxal denticle, apex of anal sternite emarginate without lateral denticles). **1:A** (sg. *Tokaranodicerca* HRI.) evolved into two species known to me only from descriptions: *D. nishidai* TMA. (differing in inconspicuously depressed midline of 1. sternite) and *D. shimonoi* HRI. (notched apex of female anal sternite). **3:M** spread across Beringia to N-America where it gave rise to **1:O** (narrower – V:H<0.5 – vertex, sides of pronotum shallowly sinuate in basal half, no median pronotal relief, flat interstriae and “mirrors”), while the remaining Palaeartic population evolved (large – >25 mm. – body, green colouration, smooth reliefs on lateral parts of pronotum, elytral dfp reduced to interstitial foveae, distinct though poorly developed lateral reliefs on sternites, conspicuous perimedial ridges on anal sternite) into the genus *Touzalinia* THY.; with the ongoing late Tertiary deterioration of climate, both withdrew southwards: American branch to the present Mexico, Palaeartic one to S-China [Hörschemeyer and Wedmann 1994 identified some fossils from the Eocene of Germany as possible *Touzalinia* THY., what would mean that the genus evolved in northern Palaeartcis, but from their descriptions and pictures (Wedmann and Hörschemeyer 1994) all specimens assigned by them to “Psilopterini/Dicercini” seem to belong rather to *Psiloptera* DEJ. s.l. (most probably to sg. *Sphintoptera* CSY., likely the “mother” taxon of the entire genus)]. In Mexico **1:O** has differentiated into *D. aeneovaria* WATH. (male mesotibia with angular protrusion) and **1:N** (black colouration, small and sharply defined dfp patches on elytra, bidentulate apex of male anal sternite) which, in turn, gave rise to *D. inconspicua* WATH. (supraantennal carinae prolonged upwards, lateral carina of pronotum sharp to ca. midlength) and *D. propinqua* WATH. [body somewhat more elongated (L:W>2.7), vertex wider (V:H>0.5), apex of female anal sternite binotched).

The position of *Latipalpis* SPIN. is ambiguous: according to the reconstruction **1** it is (SQ=25/27) a basal branch of the **1:III** clade, in **3** it makes (SQ=22/23) the equivalent basal branch together with *D. mutica* LEC., whereas in **2** it appears (with only “symbolic” – SQ=23/23 – support restricted to the accepted heuristic conventions) as the “sister” to **2:NN** (≈**3:W**); as two, somewhat better (though still poorly) supported, analyses point to its placement in the “main” clade of *Dicercia* ESCH., I prefer this option, but the “sister” relationship between eastern N-American *D. mutica* LEC. and western Palaeartic *Latipalpis* SPIN. – even if not *a priori* impossible – seems to me rather unlikely, therefore I accept the arrangement **1** in the “final” tree and discussion. So, **1:III** (pronotum with poorly developed but distinct midlateral ridges, lateral carina entire, puncture rows on elytra fine, stria bordering prosternal process runs very close to lateral margins) spread to the west to evolve into (now Mediterranean) *Latipalpis* SPIN. (labrum deeply emarginate, pronotum widest at midlength, sinuately narrowed basalwards, smooth median stripe

narrow, surface otherwise uniformly punctured, elytral mirrors flat and sparse, metacoxal denticle sharply right-angled, female anal sternite uninotched at apex) and to the east to gave rise to N-American **1:HHH** (differing from **1:III** only in binotched apex of female anal sternite). The split at **1:HHH** was again extremely asymmetric: one descendant branch (lateral carina of pronotum sharp only at base, sides cuneately – lateroapical margins straight – tapering to apices, these tridentate, metasternum broadly depressed) represented by a single eastern N-American species, *D. mutica* LEC., its (also American) “sister” [**3:R**: body broader (L:W $\approx$ 2.5), dorsal side black, pronotal sides deeply sinuate basally, oblique depressions on disk conspicuous, paramedian ridges prominent, one pair additional ridges on sides, lateral carina sharp to before midlength but not entire, elytral “mirrors” subcareiform, prosternal process densely punctured at middle, bordered with smooth lateral rim without stria] was the ancestor of all the remaining species of *Dicerca* ESCH. One of the descendants of **3:R** re-invaded E-Asia to evolve into **1:DD** (median pronotal relief narrow but regular, elytral striae coarsely punctured, inner intercostate interstriae slightly convex, metasternum broadly depressed, no metacoxal denticle, perimedial ridges on anal sternite inconspicuous), the other (**3:Q**: dorsal pubescence inconspicuous, male anal sternite emarginate) remained in America, as did both its “daughters”: **3:N** (no reliefs between midlateral pair and sides of pronotum, elytral apices narrowly rounded/truncated, interstitial “mirrors” slightly convex, epipleura broad, metacoxal denticle obtuse but well developed, 1. sternite flat, 1. metatarsomere subequal to 2. and 3. together, female anal sternite rounded) and **3:P** (no lateral reliefs on sternites). Western populations of **3:P** again spread to E-Asia, undergoing a minor transformation (lateral carina shortened, reaching to but  $\frac{2}{3}$ - $\frac{3}{4}$  of pronotal length, male mesotibia with long spur) into **3:L**, while in the remainder (**3:O**) body became slenderer (L:W slightly below 3.0), dorsal side bronzed, apex of male anal sternite bidenticulate.

Further change of dorsal colouration into cupreous, development of irregular transverse frontal ridge, narrower (V:H<0.5) vertex, straight basal part of pronotal sides, not entire but broad and regular median and reduction of paramedian carinulae on pronotum, and somewhat coarser punctures in elytral striae, transformed the southeastern population of **3:O** into *D. spreata* (Gy.), whereas in the remainder (**3:G**) metacoxal denticle became more conspicuous (though still obtuse), 1. sternite nearly flat, 3. joint of antennae short (subequal to 2.), perimedial ridges on anal sternite weak but discernible. The dispersal to E-Asia led to **1:JJ** (no paramedian or more lateral ridges on pronotum, lateral carina abbreviated (ending distinctly before apical margin), elytral puncture rows depressed into striae, “mirrors” sparse and but slightly convex, metacoxal denticle sharply right-angled, apex of male anal sternite emarginate without lateral denticles), while almost (except disappearance of angular protrusion on male mesotibiae) unchanged American populations (**3:D**) divided into western **3:C** (black colouration, weak frontal transverse ridge) and eastern **2:Q** (V:H < 0.5, basal part of pronotal sides straight, lateral carina reaching only to *ca.* midlength, elytra strongly caudate, 1. sternite sulcate along midline), whose one descendant evolved (length of body < 15 mm., elytra strongly caudate, elytral “mirrors” flat) into *D. pugnata* (GRM.), the other (pronotal sides convergent from base, no oblique depressions on disk, paramedian ridges inconspicuous) became **2:P**, the ancestor of *D. obscura* (F.) (black, labrum deeply emarginate, frontal transverse ridge inconspicuous but discernible, lateral carina of pronotum entire, punctures in striae somewhat coarser, lateral reliefs on sternites appreciable) on the one hand, and **2:B** [body very slender (L:W>3.0), no additional reliefs laterally of midlateral ridges] on the other. **2:B**, in turn, gave rise to *D. juncea* KN. (body length < 15 mm., 3. antennomere subequal

to 4., no perimedial ridges on anal sternite) and *D. lurida* (*F.*), differing in pronotal sides subparallel in basal half, no paramedian ridges, metacoxal denticle broadly obliterated, and conspicuous perimedial ridges on anal sternite. Meanwhile, **3:C** gave rise to an eastern (**2:O** – no appreciable changes) and western [**2:T** – body more robust (L:W $\approx$ 2.5), frontal transverse ridge prominent, sides of pronotum markedly sinuately divergent from base to midlength, 3. antennomere subequal to 4., 1. metatarsomere to joint 2.+3., emargination of male anal sternite without bordering denticles) lineages; the former's descendants are *D. lepida* *LEC.* (conspicuous frontal pubescence, V:H<0.5, midlateral pronotal ridges prominent, lateral carina ending distinctly behind anterior margin, elytral striae very finely punctulated, median part of prosternal process sparsely punctured, 1. sternite deeply depressed, no perimedial ridges on anal sternite) and *D. asperata* (*C.G.*) (body length <15 mm., frontal transverse ridge prominent, elytral “mirrors” dense, metacoxal denticle obliterated), those of the latter **1:J** (prominent transverse ridge on front) and **2:N** (metasternum broadly depressed, metacoxal denticle obliterated, male mesotibia with angular protrusion). **1:J** gave rise to *D. crassicollis* *LEC.* (bronzed colouration, coarser punctures in elytral striae) and *D. sexualis* (*Cr.*) (conspicuous frontal pubescence, prominent pronotal midlateral ridges, broad epipleura, 1. sternite sulcate, apex of female anal sternite rounded), while **2:N** expanded to Palaearctis to become there *D. herbsti* (*KSW.*) (dorsal colouration bronzed, V:H<0.5, lateral carina of pronotum not entire, elytra not caudate, anal sternite with conspicuous perimedial ridges, apex in male bidentate, and the American populations evolved into **2:M** (body L:W >2.7, elytral apex narrowly roundedly truncated, punctures in striae somewhat stronger, no perimedial ridges on anal sternite). Western populations of **2:M**, after very little modifications (no transverse ridge on front, no additional reliefs at pronotal sides) developed into *D. tenebrosa* (*KBY.*), whereas on the East pronotum became less expanded at midlength (MW:BW $\approx$ 1), elytral “mirrors” dense, male mesotibiae unarmed and female anal sternite simply rounded to become **2:L**. The series of asymmetric splits continues: one of the descendants of **2:L** is *D. tuberculata* (*C.G.*) (bronzed colouration, pronotal sides shallowly sinuate before base, paramedian ridges inconspicuous, elytral apices bidentate, striae finely punctulate, elytral “mirrors” but slightly convex), the other a three-species clade **2:F** (body length <15 mm., otherwise as **2:L**); then, **2:F** branched into *D. lugubris* *LEC.* (inconspicuous perimedial ridges on anal sternite, its apex in male bidentate) on the one hand and **2:E** (V:H<0.5, pronotum strikingly expanded at midlength, elytral striae coarsely punctured, metacoxal denticle obtuse but well developed) on the other; at last, one [*D. dumolini* (*C.G.*) – bronzed, elytral “mirrors” dense, 1. sternite deeply depressed] of the “daughters” of **2:E** remained in eastern N-America, while the other [*D. moesta* (*F.*) – no additional reliefs on sides of pronotum, elytral “mirrors” sparse and but slightly convex, metacoxal denticle sharply right-angled, no reliefs on sides of sternites, 1. metatarsomere subequal to 2.] colonized Palaearctis [this situation is somewhat unusual, because *D. moesta* (*F.*) is known for sure from **western** Palaearctis (from western Siberia eastwards); the only report from E-China (KUROSAWA 1954) badly needs confirmation], while its all three – *D. dumolini* (*C.G.*), *D. lugubris* *LEC.* and *D. tuberculata* (*C.G.*) – consecutive “sister”-species inhabit **eastern** N-America: such E-Nearctic – W-Palaearctic disjunctions are characteristic rather of old, basal, early Tertiary nodes, not of terminal (and thence probably relatively recent) ones; however, support for the pairing of *D. dumolini* (*C.G.*) with *D. moesta* (*F.*) rather than with *D. lugubris* *LEC.* is restricted to heuristic convention (SQ=10/10), and the next-closest relative of the Palaearctic species is widely distributed (in **northwestern** N-America up

to Alaska) *D. tenebrosa* (KBY.), so the biogeographically more plausible phylogenetic relationships within the **2:M** clade seem very likely].

**1:JJ** spread to western Palaearctic without appreciable change (**1:AA=1:JJ**), while members of the populations remaining in eastern Siberia [**1:C** = *D. aenea* (L.)] after having become more robust (L:W $\approx$ 2.5), developed more conspicuous frontal pubescence, pronotum without midlateral ridges, elytral “mirrors” flat and sparse, epipleura ending far before elytral apex and metasternum broadly depressed, invaded northern China (*D. a. chinensis* OBB. – pronotum widest at middle, poorly developed relief along midline, lateral carina reaching only to *ca.* midlength), while the remainder (without changes detectable in this analysis) extended over all Palaearctis from Pacific to Atlantic Ocean as *D. aenea* (L.) *s.str.* and closely related subspecies differing merely in some trifling details]. Westernmost (European?) populations of **1:AA** evolved (sides of pronotum more deeply sinuate before base, no paramedian ridges, lateral carina entire, elytral striae represented by rows of very fine punctures) into *D. berolinensis* (HBST.), while in those inhabiting Siberia elytral “mirrors” became somewhat denser, 1. sternite deeply depressed along midline, and apex of anal sternite bidenticulate to become **1:Z**. This gave rise to two branches: one (**1:G** – no midlateral ridges, 1. metatarsomere nearly as long as 2.+3. together) remained in Siberia, the other (**1:X** – lateral carina of pronotum reaching only to *ca.* midlength, elytra strongly caudate with apical portions strikingly narrow and elongate, apices roundedly truncate, punctures in striae somewhat coarser, metacoxal denticle broadly obliterated, perimedial ridges on anal sternite prominent) re-invaded N-America. **1:G** (= *D. [alni* (F.-W.)]-superspecies) spread to the west (Europe, NW-Africa) and evolved there into *D. [alni* (F.-W.)] *s.str.* (differing only in darker dorsal colouration), whereas Siberian populations changed somewhat more (conspicuous frontal pubescence, discernible lateral reliefs on sternites, conspicuous perimedial ridge on anal sternite, its apex in male simply emarginated) to become **1:F**. This, in turn, evolved into *D. [a.] chlorostigma* MNNH. (no paramedian ridges on pronotal disk, 1. metatarsomere subaequal to 2.) in Caucasus and *D. [a.] scabida* MARS. (broad epipleura) in Persia [and – not included in the reconstruction – *D. [a.] obtusa* KR. in Transcaspia]. American branch split into **1:B** (pronotum strongly expanded at midlength, elytral striae represented by rows of punctures, male mesotibiae simple, apex of male anal sternite rounded) and **1:T** (re-developed irregular lateral reliefs on sternites); the former (= *D. callosa* CSY.) is recently represented by two subspecies: somewhat smaller Canadian nominotypical *D. callosa* CSY. *s.str.* and *D. c. frosti* NELS. (differing, as far as the characters included in analysis show, only in longer – reaching to *ca.* midlength – pronotal lateral carina) inhabiting western third of USA. Of the two “daughters” of **1:T** one (**1:M**) remained almost (except more distinct frontal pubescence) unchanged, in the other (**1:S**) median depression of 1. sternite and perimedial ridges on anal segment almost disappeared. Eastern populations of **1:M** evolved (V:H<0.5, 1 pair of additional ridges on sides of pronotum, lateral carina sharp only at base, metasternum broadly but not deeply depressed, metacoxal denticle obtuse but well developed) into *D. hesperoborealis* H.B., the rest became slenderer (L;W>3.0) and lateral reliefs on sternites disappeared to become **1:D** and then split into unchanged *D. tenebrica* (KBY.) and somewhat further modified (no paramedian or midlateral ridges on pronotum, elytral striae represented by rows of fine punctures) *D. divaricata* (SAY). At last, **1:S** again re-invaded Palaearctis to evolve there (black body, 1 pair of additional reliefs on pronotal sides, lateral carina short, metacoxal denticle conspicuous though obtuse, male mesotibiae with prominent “spurs”) into *D. furcata* (THB.), while only disruption of elytral striae into rows of very fine punctures marked the appearance of *D. caudata* LEC.

The **3:L** is a somewhat “exotic-looking” clade, grouping quite dissimilar taxa – perhaps some artificial effect of a kind of “long branch attraction” may be involved [in the **1.** and **2.** reconstructions, and in my earlier (Hołyński 2005b) analysis, positions of these species (especially of *D. tibialis* LEW.) vary disappointingly as well in relation to other groups, as to one another...]. [?Sino-]Japanese *D. tibialis* LEW. [smaller (<15 mm.), with conspicuously pubescent front and pronotum, broad epipleura, medial part of prosternal process sparsely punctured] makes the basal outshoot of **3:L**, its “sister” clade, **3:H** (paramedian ridges on pronotum reduced, no additional lateral reliefs, elytral striae continuous, inner intercostate elytral interstriae flat, elytral “mirrors” slightly convex, perimedial ridges on anal sternite conspicuous) gave rise to Formosan *D. unokichii* HRI. [slender (L:W close to 3.0), paramedian ridges on pronotum totally absent, elytral striae coarsely punctured, metacoxal denticle sharply right-angled, 1. sternite flat or almost so, sides of sternites with irregular reliefs, male mesotibiae with angular protrusion instead of “spur”] and Transcaspian *D. fritillum* MĚN. [conspicuous frontal pubescence, V:H<0.5, elytra not or but very slightly caudate (lateroapical margins nearly straight), apex of anal sternite bidenticulate in male, simply rounded in female]. In America, **3:N** split into eastern *D. punctulata* (SCHH.) [slender (L:W close to 3), bronzed, frontal transverse ridge prominent, elytral “mirrors” sparse] and western **3:F** (frontal pubescence conspicuous, pronotal sides in basal half straight) which, in turn, spread to Palaearctis to evolve there into *D. amphibia* MARS. [additional pair of reliefs on pronotal sides, elytral striae continuous, coarsely punctured), while the populations remaining on the eastern side of the Pacific became **1:EE** (characterized by long pilosity on dorsal side, narrower (V:H<0.5) vertex, reduced paramedian ridges on pronotum, very fine elytral striae, narrow epipleura, broadly obliterated metacoxal denticle, regularly convex 1. sternite, no lateral reliefs on abdominal sides, and inconspicuous perimedial ridges on anal segment). The “daughters” of **1:EE** are widely distributed northern *D. horni* CR. (L:W almost 3, no pronotal midlateral ridges, male mesotibiae with “spur”) and restricted to southern California *D. querci* KN. s.l. (**1:K** – 1 pair of additional reliefs on pronotal sides, elytral “mirrors” sparse, anterior margin of prosternum emarginated, apex of anal sternite bidenticulate in male, binotched in female), which then diverged into two subspecies: *D. q. cajonensis* KN. (V:H>0.5, median and paramedian ridges of pronotum narrow but regular) and *D. querci* KN. s.str. (pronotal sides divergent in basal half, metacoxal denticle sharply right-angled)

The last “pure-*Dicerca* ESCH.” clade, **1:DD**, is exclusively E-Asian. It is represented by Formosan *D. kurosawai* H.A. [characterized by smaller size (length <15 mm.), dense elytral “mirrors” and lack of lateral reliefs on sternites] and continental *D. corrugata* FRM. s.l. (**1:H** – distinct pronotal pilosity, narrow but regular median pronotal carinula, no additional lateral reliefs, male mesotibia with “spur”, perimedial ridges on anal sternite conspicuous). Northernmost (Thibetan) subspecies of the latter is *D. c. thibetana* HOL (paramedian pronotal ridges reduced, perimedial ridges on anal sternite prominent), while its “sister”-clade (**1:E** – median pronotal ridge entire) consists of S-Chinese (Yunnan, Szechuan) *D. corrugata* FRM. s.str. (differing in inconspicuous pronotal pilosity) and somewhat more differentiated [more elongated (L:W almost 3), bronzed, sides of pronotum in basal half straight, elytra cuneately narrowed to apices (not caudate)], Indochinese (Laos) *D. c. vitalisi* D.V.

#### ***Ovalisia* KERR.**

*Ovalisia* KERR. was not a primary target of the present study, and – having been treated only at the subgeneric level – its reconstruction is anyway not comparable to those of

*Dicerca* ESCH. and *Poecilonota* ESCH.; however, as in all successive analyses (Hołyński 1999, 2000, 2005) it has been consistently shown (in full accordance with the traditional views of almost all earlier authors) to occupy the “sister” position to *Poecilonota* ESCH., the consideration of its (even if “coarse-grained”) phylogenetic structure and clarification of the plesiomorphic condition of its characters (“reconstructed ancestor”) seems warranted to make the analysis of the target genus more exact and reliable.

According to my reconstruction, the common ancestor of the *Ovalisia* KERR. + *Poecilonota* ESCH. complex (**2:RR**) was a small (L≈10-15 mm.), rather robust (L:W≈2.5), dorsally bronzed beetle with elytral ornamentation in form of small dark interstitial “mirrors”, inconspicuous dorsal pubescence, quadrangular labrum without transverse carina, short supraantennal ridges, poorly developed transverse frontal edge, relatively narrow (V:H<0.5) vertex, basal half of pronotal sides subparallel, straight, no oblique depressions on disk, median relief regular but narrow and not entire, no paramedian ridges, midlaterals reduced, no additional reliefs on sides, lateral carina reaching to beyond midlength, scutellum large and strongly transverse, elytra slightly caudate, apex narrowly rounded, striae continuous, very finely punctulated, interstriae simply punctured, flat (including moderately dense “mirrors”), elytral dfp patches large, no densely pubescent dfp spots, epipleura ending far before apices, anterior margin of prosternum nearly straight, prosternal process densely punctured, bordered with marginal stria, metasternum flat, no metacoxal denticle, 1. sternite regularly convex, no lateral abdominal furrow nor reliefs, mandible rounded laterally, antennae of normal width, 3. joint subequal to 4., 1. metatarsomere robust, nearly as long as 2.+3., male mesotibia simple, no perimedial ridges on anal sternite, its apex simply emarginate in both sexes. As far as can be judged from the present reconstruction, this ancestral form lived in SE-Asia.

The ancestral *Ovalisia* KERR. – **2:KK** – seems to have evolved from southern (Indochinese) populations of **2:RR** by becoming slenderer (L:W>2.7), dorsally cupreous, elytral “mirrors” transformed into broader patches, vertex still narrower (V:H<0.4), lateral carina of pronotum shorter (reaching only to *ca.* midlength), elytra not caudate (lateroapical margin straight), apex tridenticulate, no elytral dfp areas, lateral abdominal furrow well developed, apex of anal sternite in male bidenticulate. One of its descendants, **2:JJ** (dorsal colouration green, conspicuous oblique depressions on pronotum, pair of additional dark spots on sides of disk, lateroapical margins of elytra roundedly converging to apices, prosternal process sparsely punctured), remained in Indochina, while the other, **2:GG** (sides of pronotum shallowly sinuate in basal half, no or but traces of median dark stripe, anterior margin of prosternum straight), took the opportunity offered by one of the early Pleistocene sea regressions to invade what is now Malay Archipelago. Northernmost populations of **2:JJ** expanded further north, re-gained dense elytral “mirrors”, lost transverse frontal ridge and additional dark spots on sides of pronotal disk, as well as abdominal lateral furrow, developed entire median relief on pronotum and long (subaequal to 2.+3. together) slender 1. metatarsomere, to evolve into *sg. Scintillatrix* OBB. [reversals of two otherwise rather stable characters (elytral “mirrors”, lateral abdominal furrow) may represent Sæther’s (1979) “underlying synapomorphies”, but it is also possible that the true position of *Scintillatrix* OBB. is (like in my earlier – Hołyński 2000 – reconstruction) “two steps lower”: as the basalmost branch of *Ovalisia* KERR. *s.l.*, or even (like in Hołyński 1999) as “sister” to the *Dicerca* ESCH. + *Poecilonota* ESCH. clade]. In the beetles inhabiting southern part of **2:JJ** distribution median midlateral pronotal ridges became broad and prominent, elytral apex multidenticulate, punctures in striae somewhat coarser – **1:PP** was born, whose one, almost unchanged (with the

exception of the stria bordering prosternal process, which “moved” inwards leaving more space for marginal “rim”) “daughter” remained in continental SE-Asia as sg. *Palmar SCHAEF.*, while the other [**1:W** – smaller ( $L < 10$  mm.), cupreous, labrum semicircular and transversely ridged, supraantennal carinae prolonged upwards, posterior part of elytra cuneate (lateroapical margins straight), apices simply rounded, elytral sculpture granulate, prosternal process not bordered by either stria or distinct rim, mandible with blade-like lateral expansion, 3. antennomere subequal to 2., male anal sternite bispinose at apex] invaded the Malayan Archipelago and gave rise to *Zykovisia HOL.* (pronotal sides rounded in basal half, scutellum but slightly transverse) on Sundaland and *Ovalisia KERR. s.str.* [body more robust ( $L:W \approx 2.5$ ), no oblique depressions on pronotal disk, midlateral ridges reduced, no additional reliefs on sides, lateral carina extends beyond midlength, elytra slightly caudate, elytral surface extensively dark, anterior margin of prosternum distinctly emarginate] on New Guinea.

The second main clade of *Ovalisia KERR.* (**2:GG**) is entirely Sundan: all subgenera are sympatric on Borneo: *Mabomisia HOL.* is endemic to that island, *Poecilisia HOL.* and *Erialata ZYK.* occur also on southern part of the Malay Peninsula, and the distribution area of *Cinyrisia HOL.* extends to Sumatra (see maps in Holyński 2000). The basalmost offshoot is *Poecilisia HOL.* [body very slender ( $L:W > 3.0$ ), dorsal side bronzed, elytral spots irregular, vertex somewhat wider ( $V:H \approx 0.4-0.5$ ), elytra slightly caudate, anterior margin of prosternum bituberculate, metacoxal denticle broadly obliterated, 1. sternite nearly flat, lateral reliefs on abdomen inconspicuous but discernible]; its “sister”, **1:YY**, was characterized by short and very dense recumbent dorsal pubescence, lack of transverse ridge on front, no or very narrow dark median pronotal stripe, lateral carina reaching beyond midlength, scutellum but slightly ( $W:L < 2$ ) transverse, sparse elytral dark spots, and prosternal process not bordered laterally. It evolved into *Erialata ZYK.* [vertex very narrow ( $V:H < 0.3$ ), midlateral pronotal spots prominent, one pair of additional ones on sides of disk, antennal joints strikingly widened] on the one hand, and **1:OO** (length of body above 15 mm., supraantennal carinae prolonged upwards, no midlateral spots on pronotum, elytral striae finely, prosternal process sparsely punctured, 3. antennomere subequal to 2.) on the other. At last, **1:OO** is the “mother” taxon for *Mabomisia HOL.* [elytra slightly caudate, prosternal process bordered with sublateral (running at some distance from lateral margin) stria] and *Cinyrisia HOL.* (dorsally bronzed, elytral spots small and irregular, no distinct dorsal pubescence, frontal transverse ridge poorly developed but present, pronotal sides straight in basal half, anterior margin of prosternum bituberculate, apex of male anal sternite carinately bispinose).

### *Poecilonota* ESCH.

The ancestral *Poecilonota* ESCH. (**2:QQ**) differed from **2:RR** (see above under *Ovalisia KERR.*) in black colouration, long frontal pilosity, entire lateral carina of pronotum, slightly convex interstriae and dense “mirrors”, nearly flat 1. sternite, and uninotched apex of female anal sternite; it apparently have lived in the early or middle Tertiary somewhere to the north of the “proto- *Ovalisia KERR.* (**2:KK**), in the present China or even E-Siberia, from there spread to N-America, and then the late-Cenozoic deterioration of climate pushed both the Nearctic and Palaeartic populations back to the south where they evolved into, respectively, *P. bridwelli* VD. [body slenderer ( $L:W$  approaching 3), dorsal pilosity extends to elytra, pronotal sides shallowly sinuate in basal half, punctulation of prosternal process sparse, metasternum broadly depressed, 1. sternite sulcate along midline] and **2:MM** (pronotum widest at middle, median pronotal relief broad and

regular, elytral apex bidenticulate, punctures in striae somewhat coarser, metacoxal denticle broadly obliterated but distinct, 1. metatarsomere subequal in length to 2. and 3. together). Disspeciation (see HOLYŃSKI 2005a, 2009 for the terminology) in **2:MM** produced *P. semenovi* OBB. [vertex wide (V:H>0.5), pronotal midlateral ridges prominent, pair of additional reliefs on sides, elytra very deeply caudate (just before apices sides parallel), elytral intercostal interstriae and “mirrors” subcareiform, anterior margin of prosternum bituberculate] in S-China and **3:K** (length of body above 15 mm., pronotal lateral carina definitely not reaching apex, elytral intercostate interstriae flat, apex of female anal sternite shallowly emarginated) further north. This latter again invaded America to evolve [body wider (L:W>2.7), bronzed, sides of pronotum subparallel in basal half, metasternum deeply sulcate medially) into **3:E**, whereas the E-Asian remainder became **3:J** [*P. variolosa* (PK.) s.l.: no frontal transverse ridge, no midlateral ridges on pronotum, no metacoxal denticle]. Northern populations of the latter spread throughout Palaeartcis as *P. variolosa* (PK.) s.str. and closely related races (basal half of pronotal sides rounded, elytra not caudate); those remaining south of Amur evolved into **3:I** (size below 15 mm., scutellum less transverse, inner intercostate interstriae on elytra convex, indistinct lateral reliefs on abdomen) and then split into continental *P. v. chinensis* THY. (punctures in elytral striae very fine, inner intercostate interstriae and moderately dense “mirrors” subcareiform, metasternum broadly depressed, metacoxal denticle broadly obliterated but appreciable, 1. sternite regularly convex, 3. antennal joint subequal to 2.) and Japanese *P. v. yanoi* KUR. (transverse frontal ridge poorly developed but present, basal half of pronotal sides subparallel, medial relief very broad, paramedian and midlateral ridges discernible).

Meanwhile, division (by uplift of Rocky Mts.?) of American populations (**3:E**) resulted in their diversification into western *P. salicis* CHAMB. (median pronotal relief very broad, stria bordering prosternal process inconspicuous, 1. metatarsomere subequal to 2.) and eastern **3:B** (elytral “mirrors” moderately dense, prosternal process sparsely punctured). The latter, in turn, differentiated to become *P. thureura* (SAY) (frontal pubescence inconspicuous, pair of additional reliefs on pronotal sides, punctures in elytral striae moderately coarse, elytral “mirrors” flat, distinct obtuse metacoxal denticle, lateral reliefs on abdomen discernible) in SE of what is now USA and **3:A** (length of body <15 mm., colouration black, metasternum broadly depressed) along the Canadian border. Western populations of **3:A** re-invaded the Pacific side of the Rockies to evolve (pronotum widest at middle, intercostal interstriae of elytra convex, “mirrors” dense) into **2:A**, while those remaining on the east changed but slightly (1. sternite sulcate) as **1:L**. and then into widely distributed *P. cyanipes* (SAY) (no transverse ridge on front) and restricted to mid-eastern areas *P. ferrea* (MELSH.) [body larger (>15 mm.) and more robust (L:W≈2.5), sides of pronotum shallowly sinuate before base, 1 pair of additional reliefs discernible, lateral carina reaching beyond midlength, irregular lateral reliefs on sternites present, apex of anal sternite in female notched]. The geographical pattern of disspeciatiions in the western (**2:A**) clade is not quite clear: apparently its southernmost populations evolved into *P. fraseri* CHAMB. (L:W≈2.5, lateral carina of pronotum reaching distinctly beyond midlength, elytra markedly caudate, metasternum deeply sulcate), while its “sister”, **1:I** (no frontal transverse ridge, elytral apices simply narrowly rounded) diversified into *P. californica* CHAMB. (median parts of prosternal process smooth, 1. sternite deeply sulcate, indistinct but discernible lateral reliefs on sternites) and northernmost *P. montana* CHAMB. (median pronotal ridge narrow, midlaterals lacking). Thus, the basal position of *P. bridwelli* VD. and the relative holophyly of the remaining Nearctic taxa have been confirmed, but the

latter group appeared as “daughter” rather than – as in the previous reconstruction – “sister” of the Eurasian *Variolosa*-circle.

### **General phylogenetic patterns**

The relationships between genera, as recovered by the present reconstruction, do not agree exactly with any of the earlier classifications or phylogenetical analyses, although some features were already suggested. So, *e.g.* Russian authors (Alexeev and Bebka 1970, Volkovitsh 2001, followed by Bellamy 2003) denied the close relationship between *Dicerca* *ESCH.* and *Poecilonota* *ESCH.*, placing (Volkovitsh 2001, Bellamy 2003) the **Poecilonotini** *JAK.* in the “**Chalcophorioid** lineage” (including also the **Chrysochroina** *CAST.*, **Chalcophorina** *LAC.*, **Euchromatina** *HOL.*, **Pristipterina** *HOL.*, *Nanularia* *CSY. &c.*) and **Psilopterini** *LAC.* (= **Dicercini** *GISTL*) in “**Psilopteroideid** (= **Dicercioideid**) lineage” (together with *e.g.* **Sphenopterini** *LAC.*, **Hippomelanina** *HOL.*, **Pseudoperotina** *TMA.*, *Psiloptera* *DEJ.* and **Haplotrinchina** *HOL.* – even though both “lineages” as wholes seem rather unnatural, the separation between *Dicerca* *ESCH.* and *Poecilonota* *ESCH.*, and the affinity of the former to *Psiloptera* *DEJ.*, receive some (albeit weak) support in my reconstruction – if confirmed by further studies, this would be a remarkable example of (probably mimetic) convergence. Nor the paraphyly of *Dicerca* *ESCH.* in relation to *Touzalinia* *THY.* is a total novelty: it was already discussed in my previous paper (Hołyński 2005), where *Touzalinia* *THY.* appeared as “sister” to *Dicerca nishidai* *TMA.*; now, with much more exhaustive taxon sampling, it turned out most closely related to the Mexican *D. aeneovaria* *WATH.* group, and together with them form one branch of the clade whose another branch is (*D. nishidai* *TMA.* + *D. shimonoi* *HRI.*). As neither of the latter two species has been known to me in nature, and also the Mexican taxa are now not available to me (the *D. aeneovaria* *WATH.* group is currently being studied by R. WESTCOTT), the naturalness of this clade demands confirmation, but even if paraphyly of *Dicerca* *ESCH.* is established beyond doubt, *Touzalinia* *THY.* is too distinctive to be included in it, and *D. nishidai* *TMA.* and *D. aeneovaria* *WATH.* groups not distinctive enough to be excluded [though closer examination may prove warranted to accept their **subgeneric** status, in which case the name *Tokaranodicerca* *HRI.* (Hattori 2004) is available for the former].

The holophyly of most traditionally recognized and/or intuitively obvious subgroups of *Dicerca* *ESCH.* [*D. shimonoi* (*HRI.*) – *D. nishidai* *TMA.* (**1:A** – *Tokaranodicerca* *HRI.*), *D. aeneovaria* *WATH.* through *D. propinqua* *WATH.* (**1:O** – Mexican group), *D. furcata* (*THB.*) through *D. callosa* *CSY.* (**1:X** – *Furcata*-circle), *D. obscura* (*F.*) through *D. lurida* (*F.*) (**2:P**), *D. lepida* *LEC.* – *D. asperata* (*C.G.*) (**2:O**), *D. tuberculata* (*C.G.*) through *D. sexualis* *CR.* (**2:T** – *Argante* *GISTL*), *D. cajonensis* *KN.* – *D. horni* *CR.* (**1:EE**), *D. kurosawai* *H.A.* – *D. corrugata* *FRM.* (**1:DD** – *Corrugata*-circle)] has been confirmed; some others – most notably the *Alni*-circle [*D. alni* *F.-W.* – *D. berolinensis* (*HBST.*), paraphyletic in relation to the *Furcata*-circle] – proved indeed natural in the traditional “evolutionary” but not in dogmatically cladistic sense (mono- but not holophyletic). On the other hand, much more exhaustive taxon sampling must have introduced modifications or even substantial changes in relations between circles and isolated species in comparison with previous (Hołyński 1999, 2005) reconstructions. Noteworthy is the basal (in the “strict ingroup” *Dicerca* *ESCH.*) position of *D. mutica* *LEC.*, and rather unexpected (but not too strongly supported : SQ=18/20 for **3:L** and 16/18 for **3:H**) association of *D. tibialis* *LEW.* + (*D. unokichii* *HRI.* + *D. fritillum* *MÉN.*), though the latter two appeared rather close already in my earlier (Hołyński 2005) analysis, as did also *D. horni* *CR.* and *D. amphibia* *MARS.*

### *General zoogeographic patterns*

The recent geographical distributions, mapped onto the cladograms resulting from the present reconstruction, might suggest that both analysed groupings (*Ovalisia* KERR. – *Poecilonota* ESCH. and *Touzalinia* THY. – *Latipalpis* SOL. – *Dicerca* ESCH.) originated in SE-Asia; however, taking into consideration the climatic past of what is now Holarctic area, much warmer during the early and even middle Tertiary than now [in the “latest Paleocene-early Eocene ...Tropical Rain forest had its greatest latitudinal extent (up to latitude 50°), except for mountainous areas. Paratropical Rain forest extended to latitude 60°-65°, except for a 70° limit in coastal areas. In the continental areas, Notophyllous Broad-leaved Evergreen forest extended from 60°-65° to 70° (Wolfe 1985)”; then after “a sharp drop in mean annual temperature ... in the early Oligocene” (Wolfe 1978, see also e.g. Zanazzi et al. 2007, Liu et al. 2009) the late Oligocene to middle Miocene climate was again somewhat milder (Mosbrugger et al. 2005) to finally “turn down” thereafter], we cannot exclude the possibility that the arena of their early history lay further north, and only later dramatic deterioration of climate pushed the involved taxa to where they live today. Such latitudinal shifts are evidenced by disjunct Oriental-Mediterranean distributions of many taxa (e.g. *Ovalisia* KERR. sg. *Scintillatrix* OBB. and especially sg. *Palmar* SCHAEF. among those considered here) and have apparently occurred also in later evolution of *Dicerca* ESCH. (see below). Moreover, the Palaeartic outset of presently SE-Asian taxa have been established e.g. by [palaeo-]botanists (Martinetto 2000, Martinetto and Tiffney 2000), and even the Middle Eocene buprestid fauna of Messel (Germany) is dominated by the **Dicercina** GISTL belonging or at least related to now definitely [sub-]tropical *Psiloptera* DEJ. or *Touzalinia* THY. (Hörschemeyer and Wedmann 1994, Wedmann & Hörschemeyer 1994). Whether or not these groups originated in SE-Asia and spread to Siberia and Europe in early Tertiary to withdraw southwards again in the newer times, or they first evolved in Palaeartica and their present distribution is the result of secondary dispersal, is impossible to decide without relevant palaeontological findings in the Indo-Pacific region, but in discussing the biogeographical history of not-very-young taxa we should be aware of the latter possibility.

The patterns of further evolution of both major clades are quite different. The primary scene of the “*Ovalisia* KERR. – *Poecilonota* ESCH. story” remained (keeping in mind the reservations discussed above) within SE-Asia, with only three (*Scintillatrix* OBB., *Palmar* SCHAEF., and *Poecilonota variolosa* (PK.) s.str. “megasubspecies”) “excursions” to the Eurosiberian area and two (*P. bridwelli* VD. and **3:E**) to N-America – all unidirectional: none of the northern “emigrants” has descendants south of Yang-tse-kiang. The most notable difference between the present reconstruction and the previous one (Holyński 2005) is the “reversal of geographical polarity”: while then the American assemblage of *Poecilonota* ESCH. appeared as paraphyletic in relation to Eurasian taxa (suggesting Nearctic origin of the genus), now almost (with the exception of *P. bridwelli* VD.) the opposite seems true, pointing to the SE-Asia as the “motherland”. The source of the difference was alluded to already in the 2005 paper: if (what, “as traditionally believed and reflected in most classifications”, was then tentatively assumed) *Dicerca* ESCH. and *Poecilonota* ESCH. are “sister”-groups, the Nearctic origin of one or both of them seem plausible, but if (as suggested by present analysis) they are not immediately related, the former being closer to *Psiloptera* DEJ. and the latter – together with *Ovalisia* KERR. – to *Philanthaxia* DEYR., then the Indo-Pacific provenience is evident.

The pattern of distributional history of *Dicerca* ESCH. is quite different. As mentioned above, the initial development of the *Touzalinia* THY. – *Latipalpis* SOL. – *Dicerca* ESCH.

complex seems to have taken place in SE-Asia [or at least there are now living as well the closest outgroup (Oriental *Sphintoptera* *CSY.*) as the basal offshoots (*Tokaranodicerca* *HRI.* and *Touzalinia* *THY.*) of the target clade], but then the “leitmotiv” of further evolution was recurrent sequence of dispersals from Asia to America and back – Bering Strait has apparently been independently crossed three times [**1:O**, **1:HHH** and **1:X**] from west to east and seven times [**1:DD**, *D. amphibia* *MARS.*, **3:L**, *D. herbsti* *KSW.*, *D. moesta* (*F.*), **1:JJ** and *D. furcata* (*THB.*)] in the opposite direction – with several separate episodes of radiation on each side of Pacific (but mainly in the Nearctic). Similar – though, due to the very poor taxon sampling (especially as regards America), naturally different in details – pattern had emerged from my earlier (Hołyński 2005) analysis.

### Acknowledgements

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### Appendix

#### *Definitions of traits and costs of transformation*

Upper line – codes of character-states; *italics* – terminal automorphies

Lower line – weights (costs of transformation) [0↔1↔2=2: additively equidistant (distance between 0 and 1 the same (=2) as between 1 to 2, that between 0 and 2 = 2+2 = 4; (abc)↔(de)=1: equidistant between groups (a↔d=a↔e=b↔d=b↔e=c↔d=c↔e=1); (bcd) = 1: equidistant within group (b↔c = c↔d = b↔d = 1)]

1. Body length (average) – [**0**] <10; [1] 10-15; [2] 15-25; [3] >25  
0↔1↔2↔3=1
2. Body proportions (L:W) – [**0**] <2.4; [1] 2.4-2.7; [2] 2.7-3.0; [3] >3.0  
0↔1↔2↔3=1
3. Colour (basic dorsal) – [**0**] black; [1] bronzed; [2] cupreous; [3] green or blue;  
0↔1↔2↔3=1
4. Spots – [**a**] Scintillatrix-type; [**k**] Poecilisia-type; [**m**] Palmar-type; [**h**] none  
a↔k↔m=2; (akm)↔h=3;
5. Pubescence (dorsal) – [**p**] Erialata-type; [**a**] inconspicuous; [**b**] front; [**c**] pronotum;  
[**d**] elytra; [**x**] long pilosity on elytral margins and legs  
p↔a=2; p↔d=3; a↔b↔c↔d=1; (bd)↔x=1
6. Labrum shape – [**0**] deeply emarginate, no transverse carina; [1] quadrangular, no transverse carina; [2] semicircular, transversely carinate  
0↔1=1; 1↔2=3
8. Front: supraantennal carinae – [**0**] normal, short; [**1**] prolonged upwards  
0↔1=3
9. Front: transverse ridge – [**0**] none; [1] weak and/or irregular; [2] prominent  
0↔1↔2=1
11. Vertex width (V:H) – [**0**] <0.3; [1] 0.3-0.4; [2] 0.4-0.5; [3] 0.5-0.6; [4] >0.6  
0↔1↔2↔3↔4=1
12. Pronotum: proportions (MW:BW): [**0**] 0.85-0.95; (1) 0.95-1.05; [2] 1.05-1.15  
0↔1↔2=2

13. Pronotum: sides basally – [**0**] deeply sinuate; [1] shallowly sinuate; [2] straight; [3] rounded  
0↔1↔2↔3=1
14. Pronotum: oblique depressions – [**0**] none or indistinct; [**1**] conspicuous  
0↔1=2
15. Pronotum: median relief or dark stripe – [**0**] undifferentiated or traces; [1] regular reduced; [2] regular entire  
0↔1↔2=2
16. Pronotum: median relief or dark stripe – [**0**] undifferentiated or very narrow; [1] narrow; [2] broad; [3] very broad  
0↔1↔2↔3=1
- A. Pronotum – paramedian ridges: [**0**] none; [1] reduced or inconspicuous; [2] prominent  
0↔1↔2=2
17. Pronotum – midlateral spots/ridges: [**0**] none; [1] reduced; [2] prominent  
0↔1↔2=1
18. Number of [pairs of] pronotal additional dark spots/ridges: [**0**] none; [1] 1; [2] 2  
0↔1↔2=1
19. Pronotum: lateral carina (sharp to) – [**0**] <<midlength; [1] *ca.* midlength; [2] >>midlength; [3] ≈entire  
0↔1↔2↔3=1
22. Scutellum: proportions – [**0**] small; [1] large, slightly (<2×) transverse; [2] large, strongly transverse  
0↔1=3; 1↔2=1
23. Elytra: lateroapical margin (shape) – [**0**] rounded; [1] [almost] straight; [2] shallowly sinuate [sides definitely convergent]; [3] deeply caudate [sides subparallel]; [4] narrowly prolonged  
0↔1↔2↔3↔4=1
25. Elytra: apex – [z] tridentate; [m] multidenticulate; [t] narrowly rounded/truncated; [b] bidentate  
z↔m=2; m↔t=1; t↔b=2
26. Elytra: striae [inner] structure – [**0**] none or puncture rows; [**1**] continuous  
0↔1=1
27. Elytra: punctures in striae – [**0**] none or very fine; [1] fine; [2] moderate; [3] coarse; [4] very coarse  
0↔1↔2↔3↔4=1
28. Elytra: [background-]sculpture – [**0**] [rugoso-]punctate; [**1**] granulate  
0↔1=2
29. Elytral interstriae – elevation: [**0**] equal; [**1**] alternately unequal  
0↔1=3
30. Elytral inner intercostate interstriae – convexity: [**0**] flat/depressed; [1] slightly convex; [2] subcareiform  
0↔1↔2=2
- C. Elytral spots – convexity: [**0**] none or flat; [1] slightly convex; [2] subcareiform  
0↔1↔2=1
- D. Elytral spots – density: [**0**] none or sparse; [1] moderate; [2] dense; [3] entire surface  
0↔1↔2=1; 2↔3=2
31. Elytral dfp – type: [a] none; [b] interstitial foveae; [c] extensive patches  
(abc)=2
- E. Elytral densely pubescent dfp spots: [**0**] none or extensive and poorly delimited; [1] moderate; [2] small and sharply defined  
0↔1=3; 1↔2=1

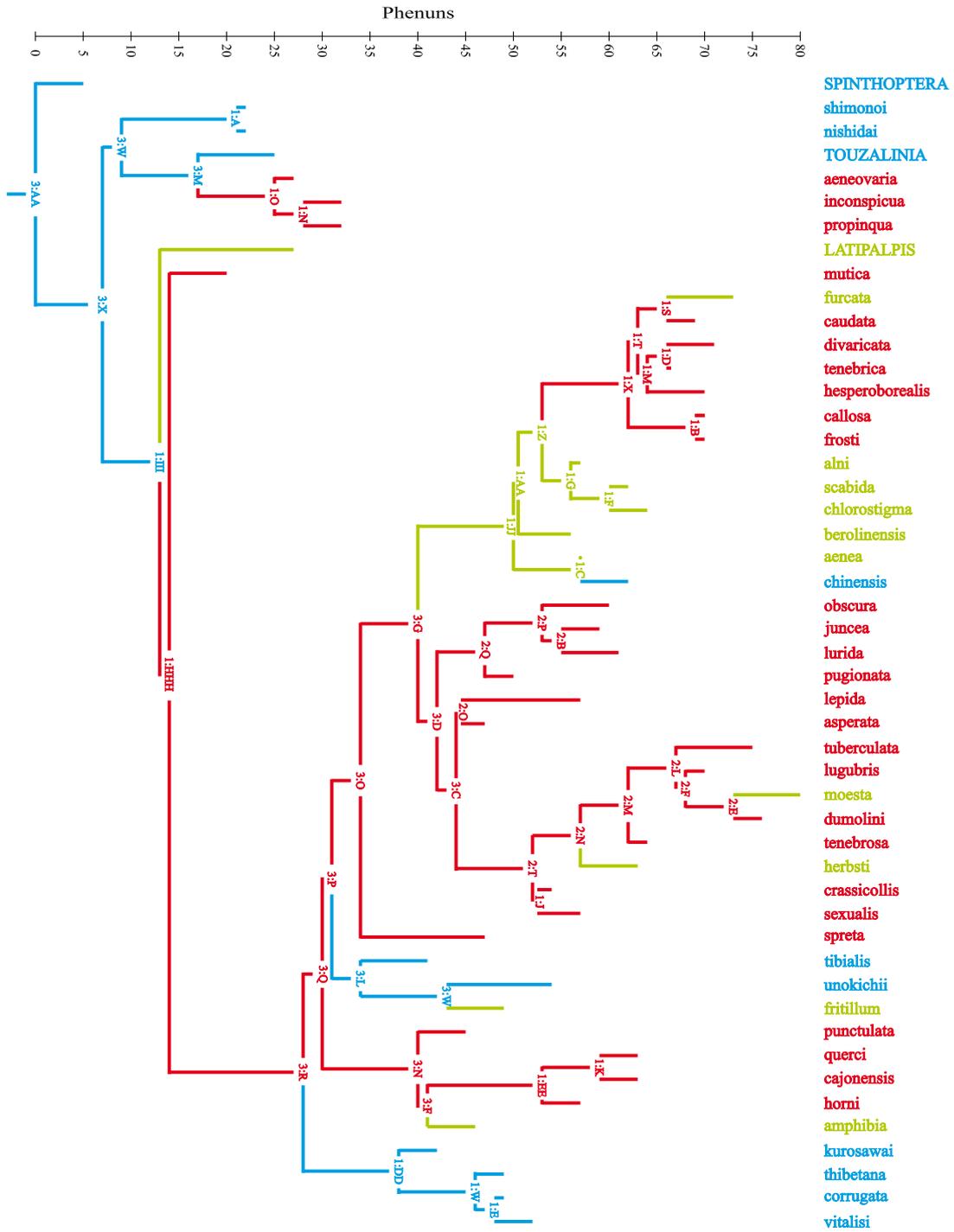
32. Epipleura: length – [**0**] broad to [near] apex; [1] narrow but reaching to [near] apex; [2] ending far before apex  
 $0 \leftrightarrow 1 = 1$ ;  $1 \leftrightarrow 2 = 3$
33. Prosternal apex – [**0**] [almost] straight; [1] definitely emarginate; [2] indistinctly bituberculate; [**3**] prominently bituberculate  
 $0 \leftrightarrow 1 = 1$ ;  $1 \leftrightarrow 2 \leftrightarrow 3 = 2$
34. Prosternal process sculpture medially ( $\varphi$ ) – [**0**] smooth; [1] sparsely punctured; [2] densely punctured  
 $0 \leftrightarrow 1 \leftrightarrow 2 = 2$
35. Prosternal process: border structure – [**0**] none or indistinct; [1] lateral rim; [2] stria  
 $0 \leftrightarrow 1 \leftrightarrow 2 = 2$
36. Prosternal process: border position – [**0**] none or marginal; [**1**] sublateral  
 $0 \leftrightarrow 1 = 1$
38. Metasternum: [**a**] flat; [**b**] broadly depressed; [**c**] deeply sulcate  
 $(abc) = 2$
39. Metacoxal denticle: [**0**] none; [1] broadly obliterated; [2] distinct but obtuse; [**3**] well marked, sharp, right-angled  
 $0 \leftrightarrow 1 \leftrightarrow 2 \leftrightarrow 3 = 1$
40. 1. sternite ( $\varphi$ ) – [**0**] regularly convex; [1] flat/inconspicuously depressed; [2] deeply depressed or sulcate  
 $0 \leftrightarrow 1 \leftrightarrow 2 = 1$
- F. Abdomen: lateral furrow** – [**0**] none or indistinct; [**1**] deep, prominent  
 $0 \leftrightarrow 1 = 3$
41. Abdomen: lateral reliefs – [**0**] none; [1] indistinct and/or irregular; [2] prominent, regular  
 $0 \leftrightarrow 1 \leftrightarrow 2 = 1$
42. Mandible – [**0**] laterally rounded; [**1**] laterally blade-like expanded  
 $0 \leftrightarrow 1 = 3$
43. Antennae: width – [**0**] normal; [**1**] strikingly widened  
 $0 \leftrightarrow 1 = 3$
44. Antennae: 3. joint – [**0**]  $\approx 2.$ ; [**1**]  $\approx 4.$   
 $0 \leftrightarrow 1 = 2$
45. 1. metatarsomere: proportions – [**0**] robust, L:W < 3; [**1**] slender, L:W  $\approx 4$   
 $0 \leftrightarrow 1 = 2$
46. 1. metatarsomere: relative length – [**0**]  $\approx 2.$ ; [**1**]  $\approx 2.+3.$   
 $0 \leftrightarrow 1 = 2$
47. Male mesotibia: [**0**] simple; [1] angular protrusion; [2] long spine  
 $0 \leftrightarrow 1 \leftrightarrow 2 = 2$
48. Anal sternite: perimedial ridges – [**0**] none; [1] inconspicuous; [2] conspicuous; [**3**] prominent  
 $0 \leftrightarrow 1 \leftrightarrow 2 \leftrightarrow 3 = 1$
49. Anal sternite (male): apex – [**0**] rounded; [1] truncate; [2] emarginate; [3] bidenticulate; [4] bispinose; [**5**] carinately bispinose  
 $0 \leftrightarrow 1 \leftrightarrow 2 \leftrightarrow 3 \leftrightarrow 4 \leftrightarrow 5 = 1$
50. Anal sternite (female): apex – [**a**] rounded or truncated; [**e**] like in male; [**n**] notched; [**x**] binotched  
 $n \leftrightarrow a \leftrightarrow x = 1$ ;  $(anx) \leftrightarrow e = 1$

## Final character-matrix

	12345	<u>68912</u>	3456A	78923	56789	<u>0CD1E</u>	<u>23456</u>	890F1	23456	7890
<b>SPT</b> Spinthoptera	223aa	11 <u>221</u>	20000	0000 <u>1</u>	b1 <u>300</u>	110 <u>b2</u>	10021	a1201	00000	011a= 5
<b>Dni</b> D.n.nishidai	220ad	10031	20011	00003	b1400	220c2	10121	c0 <u>100</u>	00100	213a= 1
<b>Dsh</b> D.n.shimonoi	220ad	10031	20011	00003	b1400	220c2	10121	c0200	00100	213n= 1
<b>Dpr</b> D.propinqua	<u>220ad</u>	100 <u>31</u>	11000	00002	b1 <u>300</u>	001c2	13121	c2200	00100	013x= 4
<b>Din</b> D.inconspicua	210ad	<u>11021</u>	11000	00 <u>102</u>	b1200	001c2	13121	c2200	00100	013a= 4
<b>Dav</b> D.aeneovaria	211ad	10021	11000	00002	b1200	001c1	13121	c2200	00100	<u>112a= 2</u>
<b>TZL</b> Touzalinia	<u>313ad</u>	10031	21011	<u>11002</u>	b1200	111 <u>b0</u>	13121	c220 <u>1</u>	00100	022a= 8
<b>LTP</b> Latipalpis	221ab	<u>00032</u>	<u>00010</u>	10302	b0100	<u>000c0</u>	10120	c <u>3201</u>	00100	013n=13
<b>Dmu</b> D.mutica	221ab	10031	20001	100 <u>01</u>	t0100	011c0	10120	b1201	00100	003x= 6
<b>Dfu</b> D.furcata	<u>220aa</u>	10031	11001	<u>11004</u>	t1200	011c0	10210	c <u>2101</u>	00000	<u>213x= 6</u>
<b>Dcd</b> D.caudata	221aa	10031	11001	00104	t <u>0000</u>	011c0	10210	c1101	00000	113x= 3
<b>Ddi</b> D.divaricata	231ab	10031	1100 <u>0</u>	00104	t <u>0100</u>	011c0	10210	c1200	00000	133x= 5
<b>Dtc</b> D.tenebrica	231ab	10031	11001	10104	t1200	011c0	10210	c1200	00000	133x= 0
<b>Dhb</b> D.hesperoborealis	221ab	100 <u>21</u>	11001	<u>11004</u>	t1200	011c0	10210	b <u>2201</u>	00000	133x= 6
<b>Dcl</b> D.c.callosa	<u>121aa</u>	10032	11001	10104	t0200	011c0	10210	c1200	00000	030x= 1
<b>Dfs</b> D.c.frosti	221aa	10032	11001	<u>10204</u>	t0200	011c0	10210	c1200	00000	030x= 1
<b>Dal</b> D.a.alni	<u>220aa</u>	10031	11001	00202	b1100	011c0	10210	c2200	00001	113x= 1
<b>Dsc</b> D.a.scabida	221ab	10031	11001	00202	b1100	011c0	<u>00210</u>	c2201	00001	122x= 1
<b>Dcl</b> D.a.chlorostigma	221ab	10031	1100 <u>0</u>	00202	b1100	011c0	10210	c2201	0000 <u>0</u>	122x= 4
<b>Dbe</b> D.berolinensis	221aa	10031	<u>01000</u>	<u>10302</u>	b <u>0000</u>	010c0	10210	c2100	00000	112x= 6
<b>Dae</b> D.a.aenea	211ab	10031	11000	00202	b1100	000c0	20210	b3100	00000	112x= 0
<b>Dch</b> D.a.chinensis	211ab	100 <u>32</u>	<u>11100</u>	00102	b1100	000c0	20210	b3100	00000	112x= 5
<b>Dob</b> D.obscura	<u>220aa</u>	<u>00120</u>	20001	<u>11302</u>	b <u>0200</u>	011c0	10210	c220 <u>1</u>	00000	013x= 7
<b>Dju</b> D.juncea	<u>131aa</u>	10020	20001	10102	b0100	011c0	10210	c2200	00 <u>100</u>	003x= 4
<b>Dlr</b> D.lurida	231aa	100 <u>21</u>	2000 <u>0</u>	10102	b0100	011c0	10210	c <u>1200</u>	00000	023x= 6
<b>Dpg</b> D.pugionata	<u>121aa</u>	10021	21002	1110 <u>3</u>	b0100	<u>001c0</u>	10210	c2200	00000	013x= 3
<b>Dle</b> D.lepida	<u>220ab</u>	101 <u>21</u>	11002	<u>21202</u>	b <u>0000</u>	021c0	101 <u>10</u>	c <u>2201</u>	00000	003x= 9
<b>Das</b> D.asperata	<u>120aa</u>	<u>10231</u>	11002	11302	b0100	<u>022c0</u>	10210	c <u>1101</u>	00000	013x= 4
<b>Dtu</b> D.tuberculata	<u>221aa</u>	10131	<u>11001</u>	11302	b <u>0100</u>	<u>012c0</u>	10200	b1101	00101	002a= 8
<b>Dlg</b> D.lugubris	120aa	10131	01002	11302	t0200	021c0	10200	b1101	00101	013a= 2
<b>Dmo</b> D.moesta	120aa	10122	01002	<u>10302</u>	t0300	<u>010c0</u>	10200	b <u>3100</u>	00100	002a= 7
<b>Ddu</b> D.dumolini	121aa	10122	01002	11302	t0300	<u>022c0</u>	10200	b <u>2201</u>	00101	002a= 3
<b>Dto</b> D.tenebrosa	220aa	10 <u>032</u>	01002	<u>10302</u>	t0200	021c0	10200	b1101	00100	102x= 2
<b>Dhe</b> D.herbsti	211aa	101 <u>22</u>	01002	<u>11201</u>	b0100	021c0	10200	b1101	00100	123x= 6
<b>Dcr</b> D.crassicollis	211aa	10232	01002	11302	b <u>0200</u>	021c0	10200	c2101	00101	012x= 2
<b>Dse</b> D.sexualis	210ab	10232	01002	<u>21302</u>	b0100	021c0	<u>00200</u>	c <u>2201</u>	00101	012a= 5
<b>Dsp</b> D.spreti	<u>220aa</u>	10 <u>121</u>	<u>21121</u>	11302	b <u>0200</u>	021c0	10210	c1200	00100	103x=12
<b>Dti</b> D.tibialis	<u>110ac</u>	10031	11002	11202	b0100	021c0	<u>00110</u>	c1200	00100	202x= 6
<b>Dun</b> D.unokichii	<u>220aa</u>	10031	11001	10002	b1 <u>300</u>	111c0	10210	c <u>3101</u>	00100	122x=11
<b>Dfr</b> D.fritillum	210ab	100 <u>21</u>	11001	1020 <u>1</u>	b1100	111c0	10210	c1200	00100	223a= 5
<b>Dpc</b> D.punctulata	<u>121aa</u>	10 <u>231</u>	11002	10302	t0100	010c0	00210	c2101	00101	002a= 5
<b>Dqu</b> D.quercei	210ad	100 <u>22</u>	21001	11302	t0000	010c0	11210	c <u>3200</u>	00101	113x= 4
<b>Decj</b> D.cajonensis	210ad	100 <u>31</u>	<u>21111</u>	11302	t0000	010c0	11210	c1200	00101	113x= 4
<b>Dho</b> D.horni	<u>220ad</u>	10021	21001	<u>00302</u>	t0000	011c0	10210	c1200	00101	212a= 4
<b>Dam</b> D.amphibia	210ab	10031	21002	<u>11302</u>	t <u>1300</u>	011c0	00210	c2101	00101	102a= 4
<b>Dku</b> D.kurosawai	<u>110ab</u>	10031	11102	11202	b0300	<u>122c0</u>	10210	b020 <u>0</u>	00100	013x= 3
<b>Dth</b> D.c.thibetana	210ac	10031	1111 <u>1</u>	10202	b0300	121c0	10210	b0201	00100	233x= 3
<b>Dco</b> d.c.corrugata	210ab	10031	11212	10202	b0300	121c0	10210	b0201	00100	223x= 1
<b>Dvi</b> D.c.vitalisi	<u>221ac</u>	10031	<u>21212</u>	1020 <u>1</u>	b0300	121c0	10210	b0201	00100	223x= 4
<b>Pbr</b> P.bridwelli	<u>120ad</u>	10121	<u>10110</u>	10322	t1000	112c0	<u>20120</u>	b <u>0200</u>	00100	002n= 9
<b>Psa</b> P.salicis	221ab	10121	202 <u>30</u>	10122	b1100	012c0	202 <u>00</u>	c1100	00100	002e= 5
<b>Pcy</b> P.cyanipes	120ab	10 <u>021</u>	20220	10122	b1100	011c0	20120	b1200	00101	002e= 1
<b>Pfe</b> P.ferrea	<u>210ab</u>	10121	<u>10220</u>	<u>11222</u>	b1100	011c0	20120	b120 <u>1</u>	00101	002n= 7
<b>Pmo</b> P.c.montana	120ab	10022	202 <u>10</u>	<u>00122</u>	t1100	112c0	20120	b1100	00101	002e= 2
<b>Pca</b> P.c.californica	120ab	10022	20220	10122	t1100	112c0	<u>20020</u>	b1 <u>201</u>	00101	002e= 4
<b>Pfr</b> P.fraseri	<u>110ab</u>	10122	20220	102 <u>23</u>	b1100	112c0	20120	c1100	00101	002e= 5
<b>Pth</b> P.thureura	221aa	10121	20220	<u>11122</u>	b1 <u>200</u>	001c0	20120	c <u>2101</u>	00101	002e= 6
<b>Pva</b> P.v.variolosa	210ab	10022	<u>30220</u>	<u>00221</u>	b1100	012c0	20220	a0100	00101	002e= 2
<b>Pya</b> P.v.yanoi	110ab	10 <u>121</u>	<u>20231</u>	<u>10212</u>	b1100	112c0	20220	a0101	00101	002e= 7
<b>Pch</b> P.v.chinensis	110ab	10022	20220	00212	b1000	<u>221c0</u>	20220	b1001	00001	002e=11
<b>Pse</b> P.semenovi	110ax	101 <u>32</u>	2022 <u>2</u>	<u>11323</u>	b1100	<u>222c0</u>	22220	a1100	00101	002n=10
<b>POE</b> Poecilisia	<u>131ka</u>	10121	10010	10122	z1000	001a0	22220	a <u>1111</u>	00100	003e=14
<b>CIN</b> Cinyrsia	<u>221ka</u>	11 <u>111</u>	<u>20000</u>	00211	z1100	000a0	<u>22100</u>	a0010	00000	005e=11
<b>MAB</b> Mabomisia	222mp	11011	10000	0021 <u>2</u>	z1100	000a0	<u>21121</u>	a0010	00000	003e= 4
<b>ERI</b> Erialata	122mp	100 <u>01</u>	10000	<u>21211</u>	z1000	000a0	21200	a0010	<u>01100</u>	003e= 5

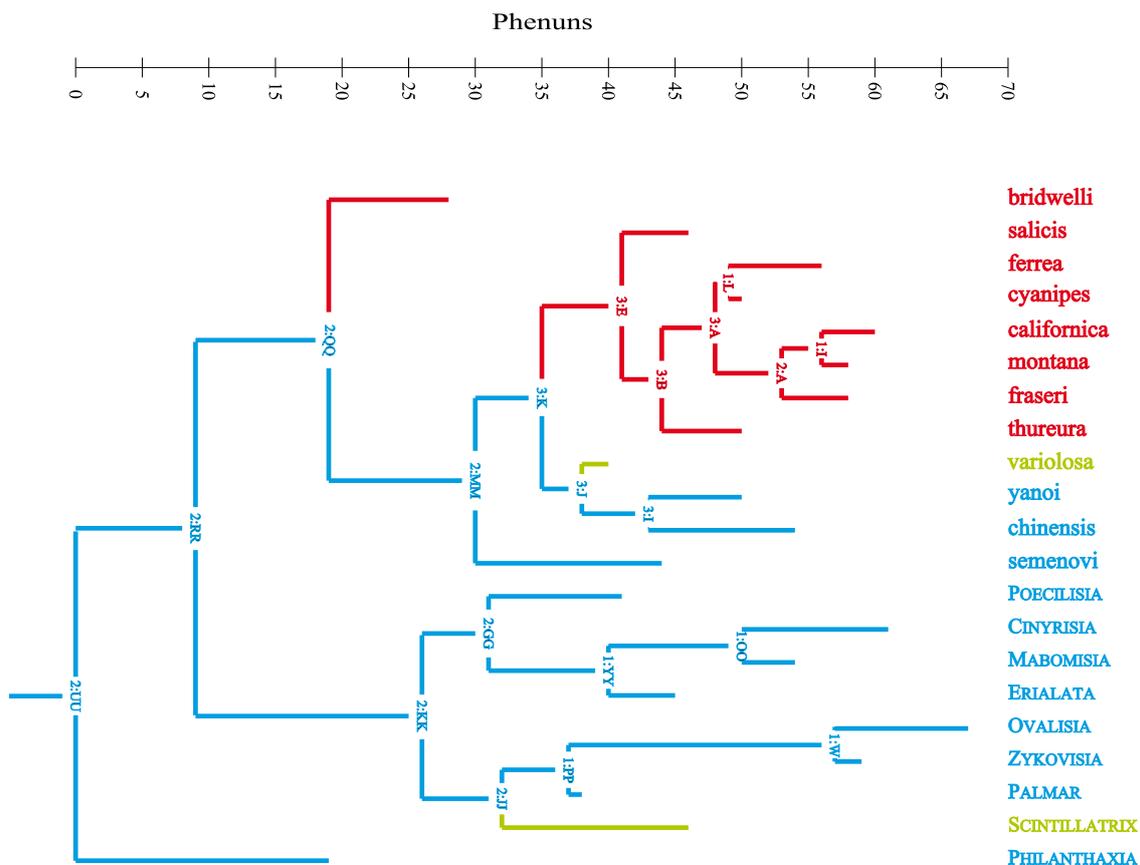
OVA	Ovalisia	012ma	21111	20120	10222	t1110	003a0	21100	a0010	10000	004e=10
ZYK	Zykovisia	022ma	21111	31120	21111	t1110	001a0	20100	a0010	10000	004e= 2
PAL	Palmar	123ma	10111	21120	21120	m1100	001a0	20121	a0010	00100	003e= 1
SCI	Scintillatrix	123aa	10011	21210	10120	z1000	002a0	20120	a0000	00111	003e=13
PHI	Philanthaxia	013ha	11040	30000	00212	t1100	000a0	10200	a0000	00011	000e=19
A:A		220ad	10031	20011	00003	b1400	220c2	10121	c0200	00100	213a=16 ( 2/28)
A:B		221aa	10032	11001	10104	t0200	011c0	10210	c1200	00000	030x= 7 ( 2/11)
A:C		211ab	10031	11000	00202	b1100	000c0	20210	b3100	00000	112x= 7 ( 5/12)
A:D		231ab	10031	11001	10104	t1200	011c0	10210	c1200	00000	133x= 2 ( 5/ 8)
A:E		210ac	10031	11212	10202	b0300	121c0	10210	b0201	00100	223x= 2 ( 5/ 6)
A:F		221ab	10031	11001	00202	b1100	011c0	10210	c2201	00001	122x= 4 ( 6/13)
A:G		221aa	10031	11001	00202	b1100	011c0	10210	c2200	00001	113x= 3 ( 6/13)
A:H		210ac	10031	11112	10202	b0300	121c0	10210	b0201	00100	223x= 8 ( 6/12)
A:I		120ab	10022	20220	10122	t1100	112c0	20120	b1100	00101	002e= 3 ( 6/10)
A:J		210aa	10232	01002	11302	b0100	021c0	10200	c2101	00101	012x= 3 ( 7/13)
A:K		210ad	10021	21001	11302	t0000	010c0	11210	c1200	00101	113x= 6 ( 8/13)
A:L		120ab	10121	20220	10122	b1100	011c0	20120	b1200	00101	002e= 1 ( 8/12)
A:M		221ab	10031	11001	10104	t1200	011c0	10210	c1201	00000	133x= 1 ( 8/10)
A:T		221aa	10031	11001	10104	t1200	011c0	10210	c1201	00000	133x= 1 (10/11)
A:X		221aa	10031	11001	10104	t1200	011c0	10210	c1200	00000	133x= 9 (11/15)
A:N		210ad	10021	11000	00002	b1200	001c2	13121	c2200	00100	013a= 3 ( 8/ 9)
A:O		211ad	10021	11000	00002	b1200	001c1	13121	c2200	00100	012a= 8 ( 9/22)
A:S		221aa	10031	11001	10104	t1200	011c0	10210	c1101	00000	113x= 3 ( 10/10)
A:T		221aa	10031	11001	10104	t1200	011c0	10210	c1201	00000	133x= 1 (10/11)
A:W		022ma	21111	21120	21121	t1110	001a0	20100	a0010	10000	004e=20 (11/25)
A:X		221aa	10031	11001	10104	t1200	011c0	10210	c1200	00000	133x= 9 (11/15)
A:Z		221aa	10031	11001	10202	b1100	011c0	10210	c2200	00000	113x= 3 (12/13)
A:AA		221aa	10031	11001	10202	b1100	010c0	10210	c2100	00000	112x= 0 (12/14)
A:DD		210ab	10031	11102	11202	b0300	121c0	10210	b0201	00100	013x=10 (13/18)
A:EE		210ad	10021	21001	10302	t0000	011c0	10210	c1200	00101	112a=11 (13/17)
A:JJ		221aa	10031	11001	10202	b1100	010c0	10210	c2100	00000	112x= 8 (14/19)
A:OO		222mp	11011	10000	00211	z1100	000a0	21100	a0010	00000	003e=10 (16/19)
A:PP		123ma	10111	21120	21120	m1100	001a0	20120	a0010	00100	003e= 5 (16/22)
A:YY		122mp	10011	10000	10211	z1000	000a0	21200	a0010	00100	003e= 9 (19/25)
A:EEE		211ad	10031	21011	10002	b1200	011c2	13121	c2201	00100	012a= 9 (21/28)
A:HHH		221ab	10031	20001	10302	b0100	011c0	10120	c1201	00100	003x= 1 (23/25)
A:III		221ab	10031	20001	10302	b0100	011c0	10120	c1201	00100	013a= 6 (25/27)
B:A		120ab	10122	20220	10122	b1100	112c0	20120	b1100	00101	002e= 5 ( 8/11)
B:B		231aa	10020	20001	10102	b0100	011c0	10210	c2200	00000	013x= 2 (10/13)
B:E		120aa	10122	01002	11302	t0300	021c0	10200	b2101	00101	002a= 5 (10/10)
B:F		120aa	10131	01002	11302	t0200	021c0	10200	b1101	00101	002a= 1 (10/12)
B:L		220aa	10131	01002	11302	t0200	021c0	10200	b1101	00101	002a= 5 (12/13)
B:M		220aa	10132	01002	11302	t0200	021c0	10200	b1101	00100	102x= 5 (11/13)
B:N		210aa	10132	01002	11302	b0100	021c0	10200	b1101	00100	112x= 5 (13/14)
B:O		220aa	10131	11002	11302	b0100	021c0	10210	c2101	00000	013x= 0 (14/14)
B:P		221aa	10020	20001	11102	b0100	011c0	10210	c2200	00000	013x= 6 (13/14)
B:Q		221aa	10021	21002	11102	b0100	011c0	10210	c2200	00000	013x= 5 (12/14)
B:T		210aa	10132	01002	11302	b0100	021c0	10200	c2101	00100	012x= 8 (13/13)
B:GG		122ma	10111	10010	10121	z1000	001a0	21220	a0010	00100	003e= 5 (19/24)
B:JJ		123ma	10111	21110	11120	z1000	001a0	20120	a0010	00100	003e= 6 (20/24)
B:KK		122ma	10111	20110	10121	z1000	001a0	20220	a0010	00100	003e=17 (21/25)
B:MM		110ab	10122	20220	10322	b1100	112c0	20220	a1100	00101	002n=11 (13/24)
B:QQ		110ab	10121	20110	10322	t1000	112c0	20220	a0100	00100	002n= 8 (19/22)
B:RR		111aa	10121	20110	10222	t1000	001c0	20220	a0000	00100	002e= 9 (20/25)
B:UU		111aa	10031	20000	10212	t1100	000c0	10220	a0000	00100	002e≈10 (11/18)
C:A		120ab	10121	20220	10122	b1100	011c0	20120	b1100	00101	002e= 4 ( 8/11)
C:B		221ab	10121	20220	10122	b1100	011c0	20120	c1100	00101	002e= 3 (11/15)
C:C		220aa	10131	11002	11302	b0100	021c0	10210	c2101	00000	013x= 2 (11/12)
C:D		221aa	10031	11002	11302	b0100	021c0	10210	c2100	00000	013x= 2 ( 9/15)
C:E		221ab	10121	20220	10122	b1100	012c0	20220	c1100	00101	002e= 6 (14/15)
C:F		210ab	10031	21002	10302	t0100	011c0	00210	c2101	00101	102a= 2 (15/17)
C:G		221aa	10031	11002	11302	b0100	021c0	10210	c2100	00000	113x= 6 (19/20)
C:H		210aa	10031	11001	10202	b1100	111c0	10210	c1200	00100	222x= 9 (16/18)
C:I		110ab	10022	20220	00212	b1100	112c0	20220	a0101	00101	002e= 5 (17/17)
C:J		210ab	10022	20220	00222	b1100	012c0	20220	a0100	00101	002e= 3 (17/17)
C:K		210ab	10122	20220	10222	b1100	012c0	20220	a1100	00101	002e= 5 (17/20)
C:L		210aa	10031	11002	11202	b0100	021c0	10210	c1200	00100	202x= 3 (18/20)
C:N		210aa	10031	11002	10302	t0100	011c0	00210	c2101	00101	102a=10 (19/20)
C:O		221aa	10031	11002	11302	b0100	021c0	10210	c1200	00100	103x= 3 (19/20)
C:P		210aa	10031	11002	11302	b0100	021c0	10210	c1200	00100	102x= 1 (18/20)

C-Q	210a	10031	11002	11302	b0100	021c0	10210	c1201	00100	102x=2	(17/18)
C-R	210ab	10031	11002	11302	b0100	021c0	10210	c1201	00100	103x=14	(17/26)
C-W	221ad	10031	20011	00002	b1200	011c0	10121	c1200	00100	013a=4	(21/22)
C-X	221ab	10031	20001	00002	b1200	011c0	10121	c1201	00100	013a=10	(17/24)
Σ	111aa	10031	20000	10002	b1100	010c0	10220	a0200	00100	002e	
	22			0 21	t 2	10 2	1 1	10 1		1 a	



**Fig. 1** – Phylogenetic reconstruction of the genus *Dicerca* Esch. Names of supraspecific taxa (initially considered as outgroups) in CAPITAL LETTERS. Blue: E-Asia north to (including)

Manchuria, Korea and Japan; green: Siberia and Europe; red: N-America.



**Fig. 2** – Phylogenetic reconstruction of the genus *Poecilonota* Esch. Explanations as for **fig. 1**.

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