Dugesiana 20(2): 251-260
Fecha de publicación: 28 de diciembre de 2013

Is the elmid fauna of Colombia strongly marked by Nearctic elements? A remote analysis of genus names provided in 30 recently published benthic macroinvertebrate assessments: (Coleoptera: Byrrhoidea: Elmidae)

¿Está la fauna Colombiana de élmidos fuertemente marcada por elementos neárticos? Análisis a distancia de nombres de géneros provistos en 30 inventarios de macroinvertebrados bentónicos recientemente publicados: (Coleoptera: Byrrhoidea: Elmidae)

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RESUMEN

Se evaluaron reportes de géneros de coleópteros acuáticos de la familia Elmidae encontrados en el estado adulto en aguas corrientes de Colombia, analizando la literatura taxonómica usada para la identificación, y a través de un análisis de plausibilidad zoogeográfica. Se comprobaron como erróneos aproximadamente el 42% de los géneros reportados, y el 15% de los reportes en total, atribuyendo 12 géneros neárticos y un género del Viejo Mundo a la fauna colombiana de élmidos. Se estima que la proporción total de reportes equivocados pueda ser significativamente mayor, básicamente generada por la aplicación de claves taxonómicas no adecuadas para la identificación taxonómica de la fauna neotropical. Por otro lado, una clave existente, apropiada para los géneros suramericanos (Manzo 2005), se encontró como claramente subaprovechada. Se presentan algunas notas complementarias a la misma clave, junto con recomendaciones generales para la identificación taxonómica de élmidos neotropicales y un listado actualizado de los géneros americanos, con datos sobre sus principales áreas de distribución.

Palabras clave: Escarabajos acuáticos, élmidos, taxonomía, zoogeografía, Colombia, neotrópico.

ABSTRACT

The genus records of adult aquatic Coleoptera of the family Elmidae, generated by 30 macroinvertebrate assessments of Colombian running waters, were evaluated against the background of taxonomic literature used for identification and by means of zoogeographical plausibility checks. Around 42% of the reported genera and 15% of the overall genus records turned out to be presumably erroneous, attributing 12 Nearctic genera and one Old World genus to the Colombian elmid fauna. The total of misleading generic identifications is assumed to be much higher and turned out to be generally induced by common appliance of taxonomic identification keys not suitable for taxonomic treatment of the Neotropical fauna. On the other hand, an existing appropriate key to South American genera (Manzo 2005) was found to have rarely been used. Some supplementary notes to this key are given, together with general recommendations for coherent genus determination of Elmidae from the Neotropical realm, and an updated checklist of New World genera and their principal distribution areas.

Key words: Macroinvertebrates, riffle beetles, taxonomy, zoogeography, Colombia, Neotropic.

INTRODUCTION

The beetle family Elmidae (Polyphaga: Byrrhoidea) contains 56 New World genera, 19 of which are restricted to the Nearctic, and 35 to the Neotropics. Only 10 genera are present in both biogeographical regions (nine Elminae and one Larainae) (Table 1). Segura *et al.* (2011) list 39 elmid genera present in South America, 29 belonging to the subfamily Elminae, and 10 belonging to the subfamily Larainae. A 30th Elminae genus has been described recently by Maier (2012). Additional South American genera described from the Guyana Region by Makhan (2007, 2008) and Mahhan & Ezzatpanah (2011), have been excluded from the here presented analysis: the deficient descriptions and poor differential notes make these genus names to "nomina seminuda", and the (first) author is regrettably known to produce aplenty synonyms (Short & Hebauer 2006). The number of described Neotropical elmid species has been estimated to be around 330 (Manzo 2005), but has raised since then continuously and rapidly (Čiampor *et al*. 2013, Fernandes *et al*. 2010a, 2010b, 2011, Fernandes & Hamada 2012, Gómez & Bello 2006, Kodada *et al*. 2012, Lanzellotti-Sampaio *et al*. 2011, 2012, Maier 2012, 2013, Maier & Spangler 2011, Manzo 2006, Manzo & Archangelsky 2012, Manzo & Moya 2010, Miranda *et al.* 2012, Monte & Mascagni 2012, Przewoźny & Fernandes 2012). The list of Neotropical Elmidae recently published by Segura *et al.* (2013) comprises 430 species including several taxa of uncertain identity. Here, the actual number is appraised to 421 (Table 1).

Many species of Elmidae are bottom dwellers in various types of running waters, and thus are collected frequently by common methods of macroinvertebrate inventories, such as surber-sampling and kick-sampling. In Colombia, elmids are mostly collected during the course of water quality assessment studies, and determined to genus level. With respect to water beetles, Colombia is situated in what one might call the "north western South American biodiversity investigation gap", which also includes Venezuela, the Guyana region, Ecuador, Peru, most parts of Brazil, and Bolivia, what means that taxonomic keys adapted to the region are lacking for most families. And it

is here, where serious lack of taxonomic tools meets extremely high biological diversity. Applied limnologists do not collect and compare original genus descriptions, but in 2005 Manzo made this type of efforts dispensable by publishing an excellently illustrated key to the South American genera of Elmidae, thus enabling the identification at this taxonomic level. Since then, the new genera *Elachistelmis* and *Hypsilara* have been described from Venezuela (Maier & Spangler 2011, Maier 2012), and various reports of the genus *Neocylloepus* in South America (Salcedo *et al*. 1999, Arango *et al*. 2008, Arias-Díaz *et al*. 2007, Caupas-Flórez *et al*. 2006, Jaramillo-Londoño 2006, Meza-Salazar *et al*. 2012, Moya *et al.* 2003) have been finally confirmed by Manzo & Moya (2010). The remaining Neotropical genera not included in the key provided by Manzo (2005) are evidently restricted either to Mexico (*Tolriolus*), or the West Indies (*Anommatelmis*, *Hispaniolara*, *Lemalelmis*, and *Xenelmoides*).

The present paper checks the given genus names of Elmidae reported in 30 scientific papers, and determined within the scope of the biological monitoring of running waters, or watersheds, conducted in Colombia. The results were analyzed against the background of the taxonomic sources used for taxonomic identification as well as the known distributional areas of the genera.

MATERIAL AND METHODS

Selection of papers. Papers selected for analysis are: Arango *et al*. 2008, Arias-Díaz *et al*. 2007, Castellanos y Serrato 2008, Caupas-Flórez *et al*. 2006, Chará-Serna *et al.* 2010, Eyes-Escalante *et al*. 2011, García-Alzate *et al.* 2008, 2010a, 2010b, Jaramillo-Londoño 2006, Longo-Sánchez *et al*. 2009, 2010, Manjarres-Pinzón y Manjarres-García 2004, Marín-Villegas *et al*. 2011, Mathuriau & Chauvet 2002 combined with Mathuriau *et al.* 2008, Meza-Salazar *et al*. 2012, Milan-Valoyes *et al*. 2011, Mondragón-Pérez 2006a, 2006b, Montoya-Moreno 2008, Montoya-Moreno *et al*. 2007, 2010, Parra-Trujillo *et al*. 2010, Posada-García *et al*. 2000, 2008, Rivera-Rondón *et al*. 2010, Rico *et al*. 2009, Rodríguez-Barrios 2011, Sarria-Nuñez 2011, and Valverde-Legarda *et al*. 2009. These papers comply with the following requirements: Freely accessible in an electronic format, actual (published not before the year 2000), and published by an academic or administrative corporate body (not self published, no gray literature). The chosen papers deal explicitly with aquatic Coleoptera, or include them in broader benthological studies. They contain at least one name of an elmid genus, determined in the adult stage within the scope of an environmental quality assessment. PhD theses have been included but no other types of theses. All together, the papers have been published by 22 different publishers.

The selected papers deal with assessments conducted in various bioregions of Colombia, reaching from sea level to 3,500 m.a.s.l., or situated in the Colombian 2nd level divisions of Antioquia (8 papers), Cauca (5; one of which from the belonging Gorgona Island), Valle del Cauca (4), Magdalena, Tolima (3 each), Norte de Santander, Quindío (2 each), Caldas, Risaralda, and Vichada (1 each). As frequently happens in running water investigations, lowland sampling stations are clearly underrepresented and none of the papers deal with data generated in the important Amazon and Chocó biogeographical regions.

Extraction of taxonomic sources for genus identification. The methods section of each paper was checked for taxonomic keys, revisions, and other sources consulted for genus level identification. These sources were, in general, categorized by their supposed relevance for the Colombian aquatic macroinvertebrate fauna, and, in particular, for their adequacy to identify the listed genera. They are listed in the below bibliography and marked with asterisks.

Evaluation of reported genus names. Recorded genus names were subjected to plausibility checks. Genus records were generally considered to be erroneous if the reliably known distribution of the recorded genus is essentially limited to the Nearctic inclusive Mexico, to the West Indies, or to the austral parts of South America.

RESULTS

Taxonomic sources of genus identification (scientific papers). Twenty of the 30 examined papers provided, within their methods section, information about the used taxonomic sources (Table 2). The source most often cited (by 22 papers) are the field guides of Roldán-Pérez (1988, 2003). These are, however, rather visual guides, presenting only examples of some genera. The edition most frequently used was the first one, dating from 1988; it contains non-differential genus descriptions of *Cylloepus*, *Disersus*, *Heterelmis*, *Macrelmis* (partly as *Elsianus*), *Microcylloepus*, and *Neoelmis*, and well done illustrations of the adults of the genera *Cylloepus*, *Heterelmis*, and *Macrelmis*. None of these editions provide dichotomous keys. The source second most often quoted (by 20 papers) are the compendia cited as "Merritt & Cummings (1978, 1984, 1996)" (with respect to beetles referring to Doyen & Ulrich 1978, White *et al*. 1984, or White & Brigham 1996), providing dichotomous genus keys, but dealing with the fauna of aquatic insects present in North America, and only eight of the keyed genera are also found in the Neotropic: *Cylloepus*, *Heterelmis*, *Hexacylloepus*, *Macrelmis*, *Microcylloepus*, *Neocylloepus*, *Neoelmis*, and *Phanocerus*. Other taxonomic sources frequently consulted are Archangelsky 2001 (cited by 12 papers as Fernandez & Domínguez (2001), McCaffery & Provonsha (1981, 10 papers), Pennak (1978, 7 papers), and Machado (1989, 7 papers). However, none of these sources provide a dichotomous key enabling diagnoses of elmid genera. Despite Merritt & Cummings (1978, 1984, 1996), publications which provide dichotomous keys to genera have been used only rarely: Archangelsky *et al*. (2009, quoted by 1 paper as Fernández & Domínguez 2008), Manzo (2005, 1 paper), Spangler & Santiago-Fragoso (1987, 1 paper, 1992, 3 papers), and Usinger (1956, 3 papers). The last mentioned work deals once more with aquatic insects from the Nearctic. The mentioned keys provided by Spangler & Santiago-Fragoso (loc. cit.) deal only with the smaller subfamily Larainae. Thus, the only taxonomic sources used and really adequate to identify nearly all genera of Neotropical Elmidae, Archangelsky *et al*. (2009) and Manzo (2005), have been consulted each by only a single paper. Archangelsky *et al*. (2009), however,

was published after several of the papers analysed herein, but Manzo (2005) has been consulted by Arias-Díaz *et al.* as early as 2007.

Other facilities of identification than literature. The authors of one paper declared to have consulted an unstated reference collection. Seemingly, all identifications in all 30 papers have been conducted by the authors themselves, since assistance of external taxonomists was not found to be mentioned.

Reported genera. The papers together provide 127 records of 25 Elminae and 42 records of six Larainae genera (Table 1). Within the New World, and given the current state of knowledge, 12 of the reported genera are most likely found exclusively in the Nearctic: *Ampumixis* (1 record), *Ancyronyx* (3), *Cleptelmis* (1), *Gonielmis* (1), *Narpus* (2), *Optioservus* (2), *Ordobrevia* (1), *Oulimnius* (3), *Promoresia* (3), *Rhizelmis* (1), *Stenelmis* (6), and *Lara* (1). However, *Promoresia*, based on the supposed identification of the larva, has been recently included in a key to elmid genera present in south-eastern Brazil (Passos *et al.* 2007). One genus, *Elmis* (1 record), is not present in the New World. Thus, 13 genera have to be considered as determined in error, this are 42% of the overall reported genera. The number of obviously erroneous records is 26, this are 15.4% of the total of 169 records. The remaining 18 reported genera (58%) are present either as well in the Nearctic as in the Neotropic (9), or restricted to the Neotropical realm (9). In this case, the correspondent genus identifications may be correct, or otherwise erroneous. Two records are marked with a sign of uncertainty by the respective author(s), as like "cf. [genus]" or "[genus]?", and are excluded from analysis. No reported genus has been supposed to be hitherto undescribed. Reflections of the general distribution areas of the reported genera (internal plausibility checks) have generally not been undergone.

Of the 28 overall described exclusively Nearctic genera, 43% (12) have been reported for Colombia, in contrast to 25% (9) of the overall known 36 genera with distribution areas confined to the Neotropic. This would indicate a transitional character of the Colombian elmid fauna consisting of Nearctic elements, which would be clearly prevalent, and a distinctly minor proportion of true Neotropical elements.

Types of publications and corporate bodies. Misleading genus identifications have been found in publications generated by 11 of 22 (50%) publishers as well as in all types of journals and other types of publications.

DISCUSSION

Discussion of methods. Correctness of reported genus identifications has been evaluated by means of a simple zoogeographical analysis, reflecting the actual state of knowledge about the Neotropical fauna. However, future surprises cannot totally be excluded, and it may turn out that some of the here listed genera are much wider distributed than actually known. Examination of the insect material might lead to more precision. In eight papers (27%) information is provided about where the collected material has been deposited (Table 2). However, the relocation of older samples, as tried by the authors of one follow-up investigation, might fail (see Longo-Sánchez *et al*. 2009).

The chosen biogeographical method was merely apt to detect most likely misleading genus records, but was inappropriate, contrariwise, to confirm records positively. Taking advantage of keys which have been worked out for another fauna might have produced many more erroneous but unsuspicious records, and in fact, here it is supposed that the real percentage of such records is much higher than the above asserted 15%. More precisely, it is especially assumed that various unremarkable records of genera that are present in the Neotropics as well as in the Nearctic - and thus, are included in the genus key provided by Merritt & Cummings (1996) - refer to other, in part strictly Neotropical genera.

Nevertheless, it seems that not all papers have listed all used taxonomic working materials. There are papers which list genera that do not appear in any of the referenced taxonomic literature.

Discussion of results. The evaluation of identification tools makes evident that the overall amount of Nearctic elmid genera reported from Colombian running waters is an artefact produced by the use of taxonomic resources not designed for the country.

The non-application of appropriate diagnostic sources, going along with presumably erroneous results, is not a specific Colombian phenomenon. Merritt & Cummings (1996) turned out to be a major identification tool for elmid genera as far from the Nearctic as Bolivia (e.g. Goitia & Bustamante 2009; report of the Nearctic genus *Cleptelmis*), and south-eastern Brazil (e.g. Mugnai *et al*. 2008: report of the Nearctic genera *Gonielmis* and *Promoresia*; Segura *et al*. 2007: report of the Nearctic genera *Macronychus*, *Ordobrevia*, *Promoresia*, *Stenelmis*, and *Zaitzevia*).

CONCLUSIONS

Genus level determination of Neotropical Elmidae. The genus key provided by Manzo (2005) is an excellent base for identification. No major faults have been registered by the present author, nor have been found to be reported otherwise. However, using this key, the examination of the genus *Elachistelmis* Maier, 2012, recently described from Surinam, leads to no logical result. According to the author it is easily recognizable by "its small size (ca. 1.0–1.2 mm), pronotum with sublateral carinae and lacking depressions, and the presence of a narrow band of plastron setae on the lateral edge of each elytron". The inclusion of *Neocylloepus* in the key of Manzo (2005) can be done as follows in three steps (Information about the genus is taken from Brown (1970):

I. Replace couplet 6 as follows:

"6. Elytra with short basal accessory stria between sutural stria and 2nd stria.

USA, Central America and South America: *Macrelmis*

- Elytra without accessory striae, or with accessory stria at the base of the 3rd stria: 7"

II. Insert a new couplet 22a after the second part of couplet 21 (*Heterelmis*) as follows:

"22a. Pronotal median longitudinal impression simple, not forked, incomplete, extending from base up to three-fifths of the distance toward anterior margin, then terminating in a more or less distinct transverse impression (Fig.1). Pronotum with

sublateral carina, elytra with one sublateral carina. Southern USA to Bolivia: *Neocylloepus*

- Pronotal median longitudinal impression either forked and incomplete, extending from base, or simple, not forked, then incomplete, not reaching the base, or complete, extending from base nearly toward anterior margin, pronotum with or without sublateral carina, elytra with one or two sublateral carinae: 22b"

III. Change the numeration of couplet 22 to 22b.

Other six Neotropical genera of Elmidae are not included in existing keys, neither from the Nearctic (Merritt & Cummings 1996) nor from the South American (Manzo 2005) perspective. Two of them (*Hispaniolara*, *Hypsilara*) belong to the Larainae subfamily, and can be identified with the key provided by Maier & Spangler (2011). Due to their small distribution areas within transitional zones between the Nearctic realm and South America, the four genera *Tolriolus*, *Anommatelmis*, *Lemalelmis*, and *Xenelmoides* remain orphaned respective inclusion in wider genus keys. Therefore, interpretations of elmid samplings from Mexico should take account of the original genus description given by Hinton (1940, *Tolriolus*), and from the Great Antilles the genus descriptions given by Darlington (1927, *Xenelmoides*) and Spangler (1981, *Anommatelmis* and *Lemalelmis*). However, even taking into account the above mentioned advices, not all elmid beetles found in the Neotropics will fit existent genus concepts. Certainly, future findings of still undescribed forms will force the reorganization of existing genus delimitations as well as the erection of new genera.

Suggestions. On the whole, it seems that genus records generated in the course of many northern South American water quality assessments should not be used for biogeographical analyses without preceding, concise plausibility checks, and this may be also recommended for the handling of genus records of other macroinvertebrate taxa. Future analyses should clarify to which extent the apparent taxonomic confusion also affects essential objectives of corresponding macroinvertebrate studies, like BMWP scores, or species richness estimations. It is recommended that reviewers take a close look on given taxa records against the background of used taxonomic sources, and that authors of macroinvertebrate assessment studies describe more in detail how they identified each taxa.

Last but not least it should be noted that neither the editors nor authors of Merritt & Cummings (1978, 1984, 1996) and Merritt *et al*. (2008) are responsible of past or future overstretched use of their splendid work.

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* Taxonomic sources used by the evaluated papers

Recibido: 7 de febrero 2013
Aceptado: 18 de junio 2013

Table 1. A. New World genera of Elmidae, B. principal distribution areas, and species numbers, and C. number of genus records in the here checked benthic macroinvertebrate assessments. A and B compiled from Barr (2011), Brown (1981), Fernandes *et al*. (2010a, 2010b, 2011), Fernandes & Hamada (2012), Gómez & Bello (2006), Kodada & Jäch (2005), Kodada *et al.* (2012), Lanzellotti-Sampaio *et al.* (2011, 2012), Maier (2012), Maier & Spangler (2011), Manzo (2006), Manzo & Archangelsky (2012), Manzo & Moya (2010), Miranda *et al*. (2012), Monte & Mascagni (2012), Przewoźny & Fernandes (2012), and Segura *et al*., (2011, 2013). C extracted from the literature mentioned in the methods section.

A. New World genera	B. Principal distribution; species numbers		C. Number of records
	Nearctic	Neotropical	
Subfamily Elminae			
Ampumixis Sanderson, 1954:3	1	-	1
Ancyronyx Erichson, 1847:522	1	-	3
Anommatelmis Spangler, 1981:376	-	1	-
Atractelmis Chandler, 1954:125	1	-	-
Austrelmis Brown, 1984:126	-	21	1
Austrolimnius Carter & Zeck, 1929:61	-	21	1
Bryelmis Barr, 2011:198	3	-	-
Cleptelmis Sanderson, 1954:4	1	-	1
Cylloepus Erichson, 1847:521	2	55	22
Dubiraphia Sanderson, 1954:3	10	-	-
Elachistelmis Maier, 2012	-	2	-
(*Elmis* Latreille, 1802:221)	restricted to the Old World		1
Epodelmis Hinton, 1973:5	-	1	-
Gonielmis Sanderson, 1954:5	1	-	1
Gyrelmis Hinton, 1940	-	13	-
Heterelmis Sharp, 1882:130	4	17	23
Heterlimnius Hinton, 1935:178	2	-	-
Hexacylloepus Hinton, 1940:229	1	24	6
Hintonelmis Spangler in Patrick, 1966:411	-	11	-
Holcelmis Hinton, 1973:1	-	2	-
Huleechius Brown, 1981:230	1	2	1
Jolyelmis Spangler & Faitoute, 1991:322	-	4	-
Lemalelmis Spangler, 1981:380	-	2	-
Luchoelmis Spangler & Staines, 2004:215	-	4	-
Macrelmis Motschulsky, 1860:52	3	44	20
Macronychus Müller, 1806:207	1	-	-
Microcylloepus Hinton, 1935:178	4	23	11
Narpus Casey, 1893:582	3	-	2
Neocylloepus Brown, 1970:6	1	8	5
Neoelmis Musgrave, 1935:34	1	48	6
Neolimnius Hinton, 1939:41	-	1	-
Notelmis Hinton, 1941:65	-	2	2
Onychelmis Hinton, 1941:66	-	3	3
Oolimnius Hinton, 1939:36	-	1	-
Optioservus Sanderson, 1954:8	13	-	2
Ordobrevia Sanderson, 1953:159	1	-	1
Oulimnius Des Gozis, 1886:9	2	-	3
Pagelmis Spangler, 1981:286	-	1	-
Phanoceroides Hinton, 1939:169	-	1	-
Pilielmis Hinton, 1971:161	-	6	-
Portelmis Sanderson, 1953:35	-	5	-
Promoresia Sanderson, 1954:9	2	-	3
Rhizelmis Chandler, 1954:126	1	-	1
Stegoelmis Hinton, 1939:30		13	

Stenelmis Dufour, 1835:158	35		6
Stenhelmoides Grouvelle, 1908:182		15	
Stethelmis Hinton, 1945:73		2	
Tolmerelmis Hinton, 1972:39		1	
Tolriolus Hinton, 1940:254		1	
Tyletelmis Hinton, 1972:37		1	
Xenelmis Hinton, 1936:427	1	13	1
Xenelmoides Hinton, 1936:5		1	
Zaitzevia Champion, 1923:170	2		
Subfamily Larainae			
Disersus Sharp, 1882:127		10	12
Hexanchorus Sharp, 1882:127		19	5
Hispaniolara Brown, 1981:85		1	
Hydora Broun, 1882:409		2	
Hypsilara Maier & Spangler, 2011:27		2	
Lara LeConte, 1852:42	2		1
Neblinagena Spangler, 1985:541		2	
Phanocerus Sharp, 1882:128	1	6	14
Pharceonus Spangler & Santiago-Fragoso, 1992:23		4	1
Potamophilops Grouvelle, 1896:78		3	
Pseudodisersus Brown, 1981:98		1	9
Roraima Kodada & Jäch, 1999:14		1	
Total	101	421	169

Table 2. A. Anonymous number assigned to each analyzed paper; B. Misleading recorded genera; C. Answers the question whether the paper provides information about deposition of insect material; D. Answers the question if an edition of Merritt & Cummings (eds.) (1978, 1984, 1996) is listed as taxonomic tool in the methods section.

A. Publication number	B. Misleading genus records	C. Deposition of material	D. Merritt & Cummings
1	*Promoresia*	yes	no data
2	*Lara* *Gonielmis* *Oulimnius* *Promoresia*	yes	yes
3	*Ancyronyx* *Cleptelmis* *Elmis* *Narpus* *Oulimnius* *Promoresia* *Rhizelmis* *Stenelmis*	yes	yes
4		yes	no
5		no	yes
6		no	yes
7		no	no
8		no	no
9	*Stenelmis*	no	yes
10		yes	yes
11		no	yes
12		yes	yes
13		no	yes
14		no	yes
15		no	no data
16		no	no data
17	*Ancyronyx* *Stenelmis*	no	yes
18	*Optioservus*	no	yes
19	*Stenelmis*	no	no data
20		yes	yes
21	*Ampumixis* *Ordobrevia* *Stenelmis*	yes	yes

22	*Ancyronyx* *Oulimnius*	no	yes
23	*Narpus*	no	yes
24	*Optioservus*	no	no
25	*Stenelmis*	no	yes
26		no	yes
27		no	yes
28		no	no
29		no	yes
30		no	no data
Totals and percentages	26 records (15.4%) 13 genera (42%)	yes: 8 (26.7%) no: 22 (73.3%)	yes: 20 (66.7%) no: 5 (16.7%) no data: 5 (16.7%)

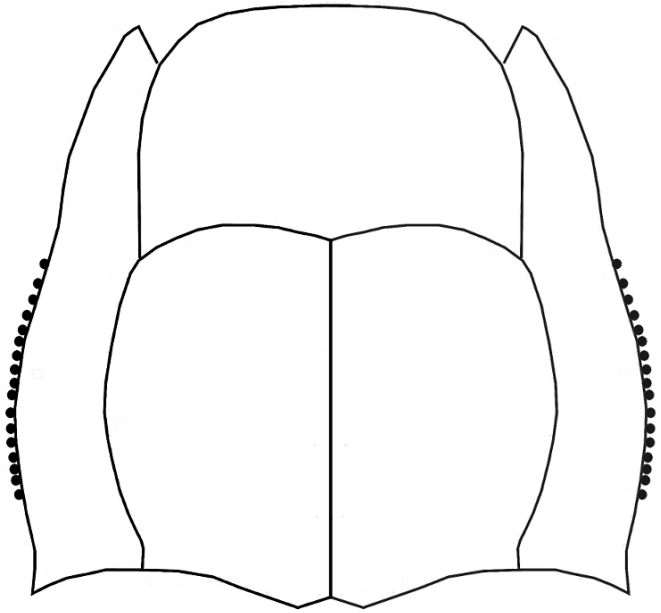

Figure 1. *Neocylloepus*, adult, pronotum dorsal, schematic. The form and perceptibility of both the transverse as well the longitudinal impressions vary not only between species but also between individuals of certain species.