

Cosmopolitan living cockroach genus represented in Chiapas amber (Blattaria: Ectobiidae: *Anaplecta vega* sp.n.) (#25104)

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I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

Cosmopolitan living cockroach genus represented in Chiapas amber (Blattaria: Ectobiidae: *Anaplecta vega* sp.n.)

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Cenozoic cockroaches were modern and with two indigenous exceptions they represent living genera. *Anaplecta vega* sp.n. – the second described cockroach from Miocene (23 Ma) Simojovel amber (Mexico: Chiapas: Los Pocitos) is characterized by slender, under 5 mm long body, prolonged mouthparts bearing long maxillary palps with distinct flattened triangular terminal palpomere, large eyes, long slender legs with distinctly long tibial spines. Some leg and palp segments differ in dimensions on left and right sides of the body, indicating (sum of left maxillar palpomeres length 65% longer than right, right cercus 13% longer than left cercus) dextro-sinistral asymmetry. Asymmetrically monstrous left palp has no equivalent. In concordance with most Cenozoic species, the present cockroach does not show any significantly primitive characters. The genus is cosmopolitan and 10 species live also in Mexico including Chiapas today. Except indigenous and those characteristic for America, this is the first Cenozoic American taxon representing living cosmopolitan genus, contrasting with living *Supella* Shelford, 1911 from the same amber, now extinct in Americas.

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ABSTRACT

**Cenozoic cockroaches were modern and with two indigenous exceptions they represent
living genera. *Anaplecta vega* sp.n. – the second described cockroach from Miocene (23 Ma)
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long body, prolonged mouthparts bearing long maxillary palps with distinct flattened
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Keywords. Fossil insect, Blattodea, new species, Simojovel, Cenozoic, Miocene

Introduction.

Order Blattodea (cockroaches) originated in Late Carboniferous (Brongniart 1885; Zhang *et al.* 2012) and during its evolution adapted to various environments gaining diverse morphological adaptations including diversification of order Mantodea (mantises) during Late Jurassic/Early Cretaceous (Vršanský 2002; Vršanský & Aristov 2014).

Works concerning cockroaches preserved in Mesozoic ambers were written by Anisyutkin & Gorochoy (2008), Bai *et al.* (2016, 2018), Grimaldi & Ross (2004), Poinar and Brown (2017), Sendi & Azar (2017), Šmídová & Lei (2017), Vršanský (2004, 2008ab, 2009, 2010), Vršanský & Bechly (2015), Vršanský & Wang (2017), Vršanský *et al.* (2011, 2013b, 2014, 2018a, 2018b), Li & Huang, (2018) and Podstrelná & Sendi (2018). In total, we know 11 families recorded in Mesozoic ambers out of which 3 are still living.

Works dealing with Cenozoic cockroaches comprise Anisyutkin & Gröhn (2012), Berendt (1836), Cockerell (1920), Foster (1891), Germar (1813), Germar & Berendt (1856), Giebel

43 (1856, 1862), Greenwalt & Vidlička (2015), Haupt (1956), Heer (1849, 1864, 1870), Heyden
 44 (1862), Hong (2002), Hörnig *et al.* (2016), Maekawa *et al.* (2003), Meunier (1921), Piton (1936,
 45 1940), Scudder (1876, 1890), Statz (1939), Vršanský *et al.* (2011, 2012ab, 2013a, 2014, 2016),
 46 Zhang (1989) and Zhang *et al.* (1994) – altogether 63 species were described according to
 47 EDNA Fossil Insect Database (active 20/11/2018) and our data:

48 *Blaberites rhenana* Statz 1939, *Blatta baltica* Germar et Berendt 1856, *B. berendti* Giebel 1856,
 49 *B. colorata* (Heer 1864), *B. didyma* Germar et Berendt 1856, *B. elliptica* Giebel 1862, *B.*
 50 *gedanensis* Germar et Berendt 1856, *B. hyperborea* Heer 1870, *B. pauperata* Heyden 1862, *B.*
 51 *ruficeps* Giebel 1862, *B. succinea* Germar 1813, *B. sundgaviensis* Foster 1891, *Blattidium fragile*
 52 Heer 1868, *Cariblattoides labandeirae* Vršanský *et al.* 2011, *Chopardia spinipes* Piton 1940,
 53 *Diploptera vladimir* Vršanský 2016, *D. gemini* Barna 2016, *D. savba* Šmídová 2016, *Ectobia*
 54 *arverniensis* Piton 1940, *E. menatensis* Piton 1940, *Ectobius glabellus* Statz 1939, *E. kohlsi*
 55 Vršanský, Oružinský, Barna, Vidlička et Labandeira 2014, *Elisama pyrula* Zhang 1989,
 56 *Erucoblatta semicaeca* Gorokhov et Anisyutkin 2007, *Gynacantha obesa* Piton 1940,
 57 *Heterogamia antiqua* Heer 1849, *Holocompsa nigra* Gorokhov et Anisyutkin 2007, *H.*
 58 *abbreviata* Gorokhov et Anisyutkin 2007, *Homeogamia ventriosa* Scudder 1876, *Isoplates*
 59 *longipennis* Haupt 1956, *Latiblatta orientalis* Hong 2002, *L. spinosa* Hong 2002, *Morphna paleo*
 60 Vršanský, Vidlička, Barna, Bugdaeva et Markevich 2013, *Nyctibora elongata* Statz 1939,
 61 *Paralatindia saussurei* Scudder 1890, *Parallelophora acuta* Haupt 1956, *P. anomala* Haupt
 62 1956, *Periplaneta eocaenica* Meunier 1921, *P. houlberti* Piton 1940, *P. hylecoeta* Zhang 1989,
 63 *P. lacera* Zhang 1989, *P. relictata* Meunier 1921, *P. sphodra* Zhang, Sun et Zhang 1994,
 64 *Phantocephalus meridionalis* Zhang 1989, *Polyzosteria parvula* Germar et Berendt 1856, *P.*
 65 *tricuspidata* (Berendt 1836), *Protectobia primordialis* Piton 1940, *Protostylopyga gigantea* Piton

1940, *Pycnoscelus gardneri* Cockerell 1920, *Supella (Nemosupella) miocenica* Vršanský, Cifuentes-Ruiz, Vidlička, Čiampor et Vega 2011, *Telmablatta impar* Haupt 1956, *Zetobora brunneri* Scudder 1890, *Zeunera madeleinae* Piton 1936, *Z. superba* Piton 1940.

The Miocene Mexican amber sourcing from resinous exudates of *Hymenaea* sp., a leguminose tree whose communities developed near the ancient coast, in estuarine environments, very similar to mangroves (Poinar 1992) is well studied with precise dating at 23Ma (Vega et al. 2009) and with over than 110 currently catalogised insect species (EDNA fossil insect database active 20/11/2018 and Vršanský et al. 2011). Cockroaches are represented with genus *Ischnoptera* Burmeister, 1838 reported by Solorzano-Kraemer (2007, although the identification needs further support) and *Supella miocenica* (Vršanský et al 2011).

The very first partial 3D extraction made from any amber organisms is formally added, comprising mostly piece of amber but also partially the inclusion presenting some advantage for the visual presentation of the organism (after presented by P. Vršanský in project SUMACO 2015).

The still living genus *Anaplecta* is today a widely distributed circumtropic taxon (see Beccaloni 2014) with very little known ecology. Fossils of genus *Anaplecta* aside from Mexican amber are also known from Eocene Baltic amber and Chinese Ambers (unpublished observation) and undescribed *Anaplecta* is also reported from Dominican amber (Gutiérrez and Pérez-Gelabert 2000, but it is unclear whether the mentioned specimens does not represent common *Plectoptera electrina* Gorokhov et Anisyutkin in Gorokhov (2007)) – locations are marked in Fig. 1.

(FIGURE 1 NEAR HERE)

Material and methods.

The studied holotype of *Anaplecta vega*, sp.n. (catalogue number IHNFG-5323) comes from Miocene (23Ma) Simojovel amber (Mexico: Chiapas), Los Pocitos (92°43'46"W, 17°08'53"N).

Specimens *Anaplecta xanthopeltis* Hebard, 1921 (**MNHN-EP-EP1398**) and *Anaplecta maronensis* Hebard, 1921 (**MNHN-EP-EP1385**), used for comparison with living *Anaplecta*, are available at the National Museum of Natural History in Paris, France.

Photographs were taken with KEYENCE digital microscope, which took many pictures from different places and focal depth and then automatically combined them into a single picture. This kind of picture was also used as a background for making a highly detailed line drawing in CorelDrawX3, where we used for additional help photographs of separate parts of the cockroach body, these were taken with LEICA MZ6 binocular loupe and LEICA EC3 camera. Dorsal drawing was manually made using the drawing ink pen applied over the transparent paper.

Abbreviations used: l= length; w= width (all in mm).

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F00B408C54E1]. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

SYSTEMATIC PALAEONTOLOGY

Order Blattodea Brunner von Wattenwyl, 1882 (= Blattaria Latreille, 1810)

Family Ectobiidae Brunner von Wattenwyl, 1865

Subfamily Anaplectinae Walker, 1868

Genus *Anaplecta* Burmeister, 1838

Type species: *Anaplecta lateralis* Burmeister, 1838

Composition. An up-to date list can be found on the online database Cockroach Species File Online, which was founded by George Beccaloni (2014) based on world catalogue of cockroaches compiled by Karlis Princis (1962, 1963, 1964, 1965, 1966, 1967, 1969).

Occurrence. Circumtropical; during Eocene also in Baltic, Dominican and China areas (in preparation by authors), which had subtropical climate that time. Stratigraphic range: Eocene-living.

Anaplecta vega sp.n.

(Figs. 2A-D, 3A-C)

Types. One complete adult specimen (Holotype kept in Paleontological Museum in Tuxtla, Mexico) with folded wings, probably male, enclosed in small piece of amber. Catalogue number IHNFG-5323.

Type horizon and locality. Lower Miocene, Mazantic Shale. Los Pocitos locality NW from Simojovel de Allende in Chiapas, Mexico. 92°43'46"W, 17°08'53"N.

Material. Types only.

Etymology. After our VEGA (VEdecká Grantová Agentúra – Research grant agency of the Slovak Republic) and also after Dr. Francisco Vega (UNAM, Mexico city) who did so much for the research progress on Chiapas amber.

Differential diagnosis. Small slender roach with body $l = 4.89$ excluding antennae and cerci and $w = 2.00$; subtriangular rounded pronotum; prolonged head with unique large eyes and huge asymmetrical maxillar palps; antennae similar length as the body; tegmina reaching apex of abdomen; long slender legs carrying long tibial spines.

Differs from all species except for *A. xanthopeltis* in having derived simplified form of pronotum and except for *A. maronensis* who has derived reticulated forewing venation.

Differs from recent species from Mexico (since this genus contains a large number of species worldwide and no other fossil species of this genus were described from this area): *A. azteca* Saussure, 1868 is bigger, its pronotum is double the length and width as pronotum of *A. vega*, pronotum length is 1/3 of tegmina length, while in *A. vega* it is 1/4.

A. fallax Saussure, 1862 has quite similar tegmina length and total body length, but pronotum is distinctly bigger, can reach almost two times the dimensions of *A. vega* pronotum; pronotum

length can be more than $1/3$ or even $1/2$ or tegmina length. Anterior margin ascending under sharper angle from the distal third of tegmen length forming a rounded angle, while in *A. vega* it is at the beginning of the distalmost fifth of tegmen length.

A. mexicana Saussure, 1868 while having similar tegmina length: pronotum length ratio, the whole body is significantly bigger and tegmina length is double the tegmina length of *A. vega*. Shape of tegmina different with anterior margin slightly sinusoid without any pronounced angulation, tegmina apex wider rounded, positioned around the middle of tegmen width.

A. nahua Saussure, 1868 is bigger, tegmina length: pronotum length ratio is quite similar as in *A. vega*.

A. otomia Saussure 1869 is bigger, dark colored, pronotum with nearly opaque lateral margins, tegmina in apical third strongly narrowing, unlike *A. vega* their anterior margin does not look angular in the apical fifth and is curved smoothly, radius area in tegmina much narrower.

A. saussurei Hebard, 1921 has similar sized and similar shaped tegmina as *A. vega*, but they reach slightly beyond cercal apices, are slightly wider, their anterior margin in the basal part is almost straight, clavus is distinctly longer and wider, pronotum is larger, pronotum length is $1/3$ of tegmina length.

A. tolteca Saussure, 1868 is bigger, tegmina length: pronotum length ratio the same as in *A. vega*.

Comparison of dimensions of *A. vega* n. sp. and mentioned Mexican species is plotted in Fig. 4, comparison of *A. vega* n. sp. dimensions and an average of mentioned Mexican species dimensions in Fig. 5.

(FIGURE 2 NEAR HERE)

(FIGURE 3 NEAR HERE)

Description. Body small and slender ($l = 4.89$, $w = 2.00$), tegmina reaching apex of abdomen, legs long and slender carrying large tibial spines, antennae similar length as the body.

Pronotum subtriangular, rounded, cranially arched over head ($l = 1.00$, $w = 1.27$), long erect setae sparsely distributed along pronotum margin and on its dorsal surface. Pronotum length is 1/4 of tegmina length.

Scutellum triangular, cranio-caudally prolonged (length of scutellum part not covered by pronotum = 0.29, $w = 0.14$).

Tegmina total $l = 4.04$, l of part not covered by pronotum = 3.89, left tegmen $w = 1.28$; visible left clavus $l = 1.16$, $w = 0.67$. Basal half of tegmina inflated with exception of anterior peripheral areas (costal area, part of radial area). Anterior margin in the apical fifth of tegmen length starts to tilt posteriad more strongly, what gives it an angular look. Apex posteroapically sharpened. Costal area wide. Radial field in apical half wide, branches of radius almost all simple (one secondary dichotomy observed in right tegmen, left tegmen veins weakly visible). Surface sclerotized, but not fully elytrized, without prominent structures. Sparsely distributed medium sized setae occur at anterior and apical margins of tegmina and medium sized to long setae on tegmina veins. Only a very small portion of right tegmen is covered by left tegmen. Clavus $l = 1.16$ (only the visible uncovered part), $w = 1.23$.

Hind wings covered by tegmina, folded in half as typical for genus.

Head with prolonged mouthparts and large eyes, which in lateral view cover almost whole head excluding mouthparts; head $w = 0.76$, length from top of vertex to distal part of mandibles = 0.91, distance from occipital foramen to top of frons = 0.47; eyes subovoid in lateral view, eye length (parallel to head length) = 0.42, eye width (perpendicular to eye l) = 0.34, interocular $w = 0.4$ mm. Between left eye ommatidia near gena observed three medium-sized setae. Vertex sparsely covered by setae sized from short to very long, frons and clypeus with few distinctly long setae, gena posteriorly with three distinct medium sized setae and smaller thin setae along eye margin. Maxillar palps long with broad triangular terminal segment; dimensions of palpomeres of right and left maxillar palp differ (right 1st palpomere $l = 0.13$, $w = 0.06$; left 1st palpomere $l = 0.13$, $w = 0.09$; right 2nd palpomere $l = 0.1$, $w = 0.05$; left 2nd palpomere $l = 0.14$, $w = 0.07$; right 3rd palpomere $l = 0.31$, $w = 0.06$; left 3rd palpomere $l = 0.4$, $w = 0.09$; right 4th palpomere $l = 0.17$, $w = 0.07$; left 4th palpomere $l = 0.29$, $w = 0.14$; right 5th palpomere $l = 0.27$, w unmeasurable due to position; left 5th palpomere $l = 0.34$, $w = 0.21$, apical contacting surface 0.34; plot of left and right palpomeres length comparison is in Fig. 6. Labial palps considerably smaller than maxillar palps, terminal palpomere triangular, distally widened. Only 2nd and 3rd left labial palpomere sufficiently visible to be measured: 2nd left palpomere $l = 0.11$, 3rd left labial palpomere $l = 1.13$.

Antennae length similar to body length. First three antennomeres only with few setae, more distal antennomeres are richly covered by distinct setae that exceed and in some parts double the width of antennomeres.

Scape large (left $l = 0.33$; right $l = 0.29$) with wide proximal half (left $w = 0.13$) and sharp transition into narrower distal half ($w = 0.09$), distal ending oblique with five setae.

212 Pedicel cylindrical (left $l = 0.21$, left $w = 0.08$; right $l = 0.2$), distal end oblique with distinct sharp
213 angle at one side and wider than proximal end. Proximal third swollen on one side. Setae very
214 few.

215 Segments of flagellum 32 in left antenna, 28 in right antenna. Each segment is more or less wider
216 in its distal part than in proximal part. Setae longer than the width of flagellar segments.

217 First flagellar segment (third antennomere) slightly elongate, length is almost two times its largest
218 width (left $l = 0.14$, $w = 0.07$). Following few basal flagellomeres are short almost square-like
219 look, being only slightly longer than their width, subsequent row of flagellomeres has a
220 lengthening trend distad.

221 Fig. 7 shows a plot that compares left and right antenna individual antennomeres length.

222 **Cerci** 7-segmented. 1st cercomere and 7th cercomere thinner than the rest while the 7th distinctly
223 tapers distad forming pointy end, cercomeres 2-6 sublenticular, being similar in shape and
224 size. Left cercus total $l = 1.00$, right cercus total $l = 1.13$; dimensions of individual cercomeres go
225 as follows (left cercomeres width was not measured due to unsuitable position): left 1st
226 cercomere $l = 0.19$; right 1st cercomere $l = 0.17$, $w = 0.10$; left 2nd cercomere $l = 0.14$; right 2nd
227 cercomere $l = 0.14$, $w = 0.17$; left 3rd cercomere $l = 0.16$; right 3rd cercomere $l = 0.21$, $w = 0.17$;
228 left 4th cercomere $l = 0.17$; right 4th cercomere $l = 0.21$, $w = 0.19$; left 5th cercomere $l = 0.21$; right
229 5th cercomere $l = 0.21$, $w = 0.21$; left 6th cercomere $l = 0.17$; right 6th cercomere $l = 0.19$, $w = 0.19$;
230 left 7th cercomere $l = 0.07$; right 7th cercomere $l = 0.23$, $w = 0.14$). Setae on cercomeres have
231 different dimensions, from small ones long as $1/3$ or $1/4$ of cercomere length, thicker prominent
232 setae approximately the size of cercomere length (maximal $l = 0.21$, but majority around 0.14)

and long thin setae the size of two or three cercomeres which occur in amount of 1 or 2 per cercomere. Whole surface of cerci also covered by very small short microsetae.

Legs slender and very long (hind legs longer than body) with large spines (longer than tarsomeres, except the 1st tarsomere) on tibia and distal end of femur.

Fore coxae subtrigonal with convex anterior margin, widest before middle of its length, more slender in distal half of its length. Few setae present along the posterior margin.

Fore trochanteri very thin, barely observable.

Fore femora slender (left fore femur $l = 1.29$, $w = 0.2$, right fore femur $l = 0.67$, maybe more, visibility obscured by damage of amber) with subparallel ventral and dorsal margin, which are being only slightly convex, narrower in proximal part and in distal third of their length. Anteroventral margin in distal half with $20 \pm$ shorter spines, posteroventral margin with 13 (observed) longer setae sparsely distributed along fore femur length, two thicker spines present on anterior surface of proximal half of fore femur. Terminally present three long serrated spines: anteroventral, posteroventral, anterodorsal. Rest of forefemoral surface covered only by a low number of shorter setae, mostly concentrated in dorsal part.

Fore tibiae distinctly more slender than fore femora, generally retaining similar width ($w = 0.07$) throughout its length (left fore tibia $l = 0.89$, right fore tibia $l = 0.73$), except the thinner arched proximalmost spineless part ($w = 0.06$), and neglectable changes of width due to elevations around large, articulated, serrate spines; these spines are up to 0.29 long and 0.01 wide, while three spines are in the middle third of tibial length, the two peripheral facing dorsad, the middle one facing posteriad, four large spines are at the distal end of tibia (1 anteroventral, 1 anterior, 1

dorsal, 1 posterior). Distribution of large spines is the same on both right and left fore tibiae.

Along dorsal and ventral side and distal half of anterior surface sparsely distributed medium-sized setae.

Fore tarsi being 5-segmented, very slender, covered by setae exceeding their width ($w = 0.04$), terminated by trilobal arolium and two thin arcuate more or less symmetrical claws with widened bases; left 1st tarsomere $l = 0.34$, right 1st tarsomere $l = 0.33$; left 2nd tarsomere $l = 0.07$, right 2nd tarsomere $l = 0.08$; left 3rd tarsomere $l = 0.06$, right 3rd tarsomere $l = 0.06$; left 4th tarsomere $l = 0.07$, right 4th tarsomere $l = 0.06$; left 5th tarsomere $l = 0.11$, right 5th tarsomere $l = 0.2$.

Middle coxae (distal part obscured by damage in amber and another leg) larger and wider than fore coxae, on posterior margin few setae present; distal end has distinct smaller lobe with 6 longer setae.

Middle trochanteri wide (width is only a little less than length), slightly curved.

Middle femora elongate with slightly convex dorsal and ventral side (ventral side being almost straight) with bigger width around the middle of length (left middle femur $l = 1.44$, $w = 0.22$ mm; right middle femur $l = 0.91$, $w = 0.17$). Setae sparsely distributed around dorsal margin, ventral margin with 6 larger thick setae and 1 – 2 medium-sized setae between each two consequent larger setae; on proximal half of middle femur present anteroventrally two longer, anterad facing spines; on distal end of middle femur present 3 large serrated spines, one anteroventrally, one posteroventrally and one dorsally.

Middle tibiae similar length (left tibia $l = 1.16$, right tibia $l = 1.11$), but left tibia being 1/6 shorter than left middle femur, right tibia being 1/5 longer than right middle femur; width varying along tibial length as result of elevations at the bases of spines (minimum $w = 0.07$, maximum $w = 0.1$);

277 10 large serrated spines (maximal $l = 0.36$, $w = 0.01$) differently facing (on left middle tibia 1
278 anteroventral, 1 posteroventral, 4 anterodorsal 4 posterodorsal) along tibial length, 4 terminal
279 large serrated spines (anteroventral, posteroventral, posterodorsal, anterodorsal) and one shorter
280 spine (posteroventral).

281 ***Middle tarsi*** 5-segmented, slender, covered by medium sized setae exceeding tarsal width ($w =$
282 0.04 mm), terminated by two arched slender claws with widened bases and trilobal arolium; left
283 1st tarsomere $l = 0.53$, right 1st tarsomere $l = 0.57$; left 2nd tarsomere $l = 0.11$, right 2nd tarsomere
284 $l = 0.12$; left 3rd tarsomere $l = 0.09$, right 3rd tarsomere $l = 0.08$; left 4th tarsomere $l = 0.07$, right
285 4th tarsomere $l = 0.04$; left 5th tarsomere $l = 0.13$, right 5th tarsomere $l = 0.18$.

286 ***Hind coxae*** badly visible.

287 ***Hind trochanteri*** slender, slightly curved with few setae, left hind trochanter $l = 0.43$, $w = 0.11$;
288 right hind trochanter $l = 0.46$, $w = 0.09$.

289 ***Hind femora*** are the largest of femora ($l = 1.4$, w of right hind femur $= 0.31$, left one in wrong
290 position to be measured) with biggest width in middle of their length, distal end slightly
291 widened, ventral side only slightly convex, dorsal side more convex. Numerous short setae
292 scattered through whole surface of femur. Setae sized from short to long present along dorsal
293 femoral margin, getting longer distad; at anterior surface setae with dark bases present at an
294 arched line subparallel to dorsal side of femur, which proximally starts around the middle of hind
295 femur width, approaching dorsal side of hind femur distad. Dorsal and anterior setae are longer
296 on left fore femur. Anteroventral edge with medium-sized setae and two large spines in the
297 middle third of hind femur length. Posteroventral edge with five long setae (left hind femur) and

298 shorter setae between them. Terminally present three long serrated spines: anteroventral,
299 posteroventral, anterodorsal.

300 **Hind tibiae** are the largest of tibiae with their length (left hind tibia $l = 1.89$, right hind tibia $l =$
301 2.13) being near double length of middle tibiae, width of hind tibiae is weakly varying due to
302 elevations at bases of larger spines, but not showing a significant narrowing or widening trend
303 (maximal $w = 0.13$), exception is the proximal 1/6 which is more slender ($w = 0.1$ mm). Each hind
304 tibia has along its length 17 long serrated spines (3 anteroventral, 2 posteroventral, 7
305 anterodorsal, 5 posterodorsal) and 5 long serrated terminal spines (1 anteroventral, 2
306 posteroventral, 1 posterodorsal, 1 anterodorsal), what makes together 22 spines on one hind tibia
307 (maximal spine $l = 0.5$ mm maximal $w = 0.02$). Medium sized setae are sparsely distributed
308 along ventral and dorsal margin (up to 4 between two spines).

309 **Hind tarsi** are the largest of tarsi, 5-segmented, slender, covered by medium sized setae most of
310 which equal or exceed tarsal width ($w = 0.06$), terminated by two arched slender claws with
311 widened bases and trilobal arolium (pulvilli absent or indistinct). 1st tarsomere very long (left $l =$
312 0.91 , right $l = 0.84$) with almost same width throughout its length, in proximal part slightly
313 thinner; covered by distinct medium sized setae, most prominent is ventral row of setae, other
314 areas have less densely distributed thinner setae; subsequent tarsomeres have the same length on
315 left and right hind leg, 2nd tarsomere $l = 0.19$, 3rd tarsomere $l = 0.11$, 4th tarsomere $l = 0.1$, 5th
316 tarsomere $l = 0.18$.

317 Comparison of length of each leg femora, tibiae and tarsomeres can be seen in Fig. 8.

318 **Occurrence.** Lower Miocene, 23Ma. Chiapas amber, Mexico.

319

320 (FIGURE 4 NEAR HERE)

321 (FIGURE 5 NEAR HERE)

322 (FIGURE 6 NEAR HERE)

323 (FIGURE 7 NEAR HERE)

324 (FIGURE 8 NEAR HERE)

325

326

327 DISCUSSION

328 Studied specimen was assigned to genus *Anaplecta* on the basis of overall body shape, shape of
 329 pronotum, smooth dorsal half of body, large axe-like terminal mandibular palpomere (however,
 330 it does not have the same length as the forelast palpomere, as mentioned in the original
 331 description of the genus), coriaceous tegmina, hind wings folded in half, arrangement of femoral
 332 setae and spines, large cerci, tarsomeres without pulvilli. The specimen was most similar and
 333 compared to holotypes of South American *A. xanthopeltis* Hebard, 1921 and *A. maronensis*
 334 Hebard, 1921, where was seen the same type of pronotum, overall tegmina shape, tegmina type
 335 of venation and hind wings folding.

336 Interesting character of the studied specimen is the distinctly larger left maxillar
 337 palpomere (Fig. 6), additionally all the legs have different dimensions at right and left side of the
 338 body (Fig. 8).

339 The coriaceous tegmina are not sclerotised enough to be considered as elytrised, being a
 340 rather primitive character (seen also in living *A. maronensis*).

In respective descriptions of living Mexican species of *Anaplecta* ecology data are missing. Diversity of the genus is very high in rainforest areas. Evangelista et al. (2015) mention 4 species in Amazonas (Venezuela), 4 species in Guyana, 10 species in Suriname, 9 species in French Guiana, 10 species in Ampa (Brazil); Vidlička (2013) mentions 10 species in Ecuador; 8 species (including the new species) are known from Mexico based on the works of Saussure (1862, 1868, 1869) and Hebard (1921).

Genus *Anaplecta* has present circumtropical distribution, and the (sub)tropical climate concerns the new described species as well. Fossil *Anaplecta* species are known also from Eocene Baltic Kaliningrad and Chinese ambers - the climate during Eocene in these areas was subtropical (Grimaldi 1996), and from the related Dominican amber (nevertheless, the Dominican species are undescribed and placement needs confirmation - see above). The palaeogeographical inferences are principal, as there has been shown that the Eocene North American fauna (major locality Green River, Colorado, U.S.A., but also more northern localities in Canada – Greenwood et al. 2005, Archibald and Mathewes 2000) and also the Miocene fauna of Chiapas amber were cosmopolitan, while younger Dominican amber contain modern, American cockroach taxa – strongly suggesting a major extinction between these two time periods (of deposition of these two sites - Vršanský et al. 2011). The present study cannot reveal information whether *Anaplecta* inhabiting Americas today is a native reminder of the original Eocene diversity or a descendant of a more recent re-invasion. This research awaits future investigators, nevertheless, *Anaplecta* is the sole such taxon.

The detailed phylogenetic study of Djernaes et al. (2014) (and also Vidlička et al. 2017) positioned the Anaplectidae into one clade together with Tryonicidae, Cryptocercidae and Isoptera, according to what it seems to be a very primitive taxon. However, according to our

morphological and taphonomical (i.e., absence in the rich Mesozoic record counting 30,000 sedimentary and over 3,000 amber specimens) observations is *Anaplecta* a modern (plesiomorphy such as non-fully elytrised tegmina of the present species are also shared with some living representatives – see above) and developed genus typical for Cenozoic.

The asymmetry of genitalia is common and appeared repeatedly during insect evolution (Huber et al. 2007), it is even part of the original groundplan in the whole order Dictyoptera. Asymmetries in left-right axis of other body parts can be also found among insects (Smith et al. 1997). The fluctuating asymmetry can predict developmental instability of the individual (Dongen, 2006). In that case the studied individual was vital and the unevenness of certain body parts did not affect the fitness/it did not affect it fatally. The difference between left and right hind legs is neglectable (Femur (F)=1.014[r]/ Tibia (T)=1.12[r]/ Tarsomere (Ta) 1=1.08[l]/ Ta2=1/ Ta3=1/ Ta4=1/ Ta5=1). It explains the importance of the hind leg in the movement (Hughes, 1951). In the contrast, the front femur leg (also important in the movement) is highly asymmetrical. The biggest difference can be found between left and right femur (the left femur is almost twice as big). Also the overall asymmetry is more evident (F= 1.93[l]/ T=1.2[l]/ Ta1= 1.03[r]/ Ta2=1.14[r]/ Ta3=1/ Ta4=1.16[l]/ Ta5=1.81[r]). The most asymmetrical tarsomeres can be observed in the middle leg (F=1.41[l]/ T=1.25[l]/ Ta1=1.65[r]/ Ta2=1.71[r]/Ta3=1.33[r]/Ta4=1.75[l]/Ta5=1.63[r]).

The expansion of extremities longitudinally could have been caused *post mortem*, by tension of polymerizing resin. The structure of resin can be modified due to conditions such as temperature, humidity change and etc. These changes can affect the state of preservation of inclusion (Poinar & Mastalerz, 2000).

The length irregularity of extremities, could have also happened while escaping after being embedded into resin, which often even leads to disarticulation (Martínez-Delclòs et al. 2004).

CONCLUSIONS

The Miocene cockroach *Anaplecta vega* sp.n. representing an extinct species of an extant genus, is consistent with cosmopolitan pattern of Cenozoic occurrences. Its closest relatives live in South America, with which shares same pronotum shape, tegmina shape and venation and hind wings folding. As well as the living representatives, *Anaplecta vega* lived in warm (sub)tropical areas. It is second cockroach species described from Chiapan amber, Mexico and it belongs to the subfamily Anaplectinae, family Ectobiidae. Described individual shows noticeable asymmetries in maxillar palpomeres length, right cercus and some leg segments. The asymmetry however remains **obscure** and needs a further study.

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641

Figure 1

Distribution map of amber *Anaplecta* spp. with the Baltic amber reaching out of the present range.

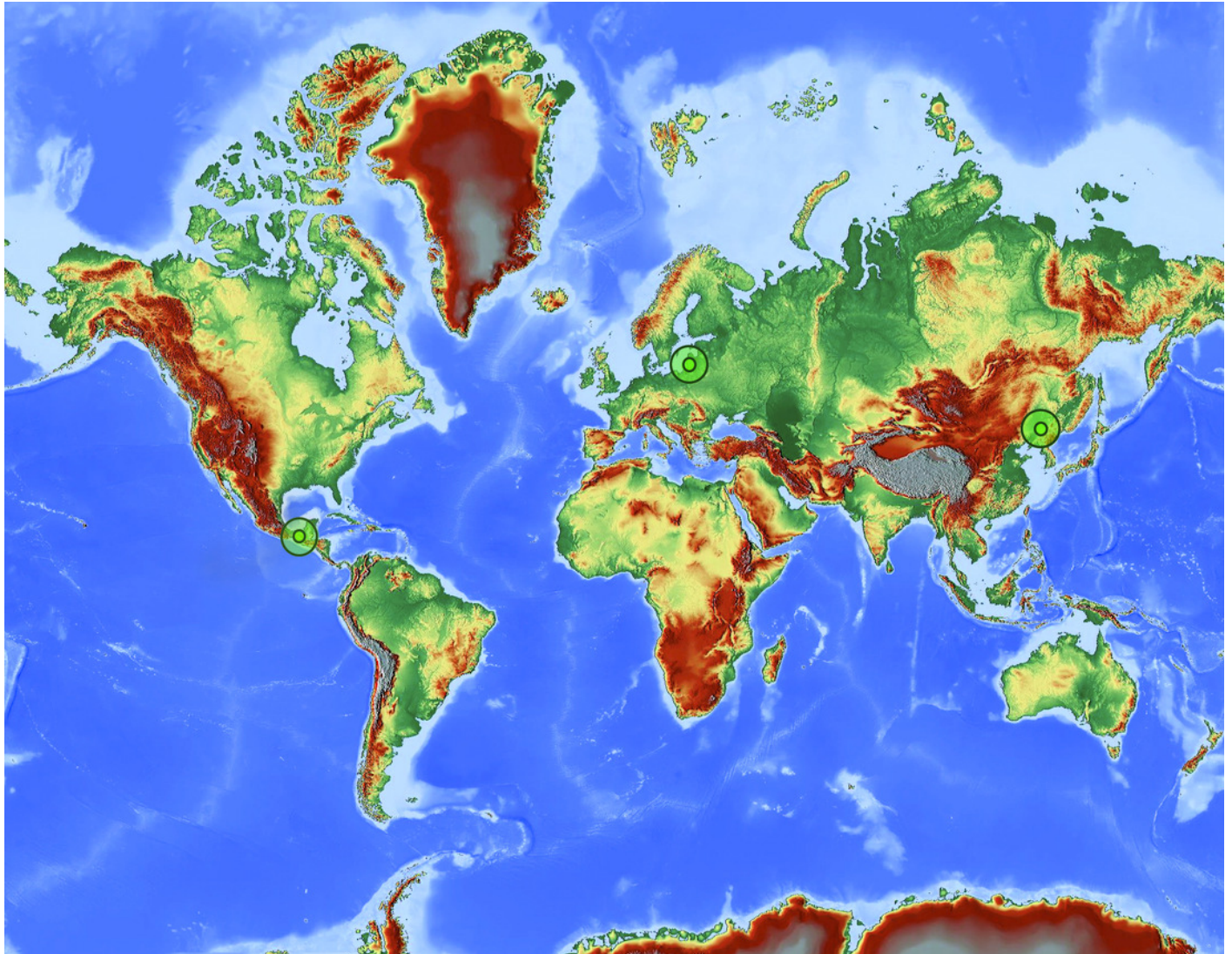


Figure 2

Anaplecta vega sp.n.

(A) Partial 3D extraction. (B) Ventral view. (C) Dorsal view. (D) Whole piece of amber, ventral view. Specimen overall length head-abdomen, 4.89mm.

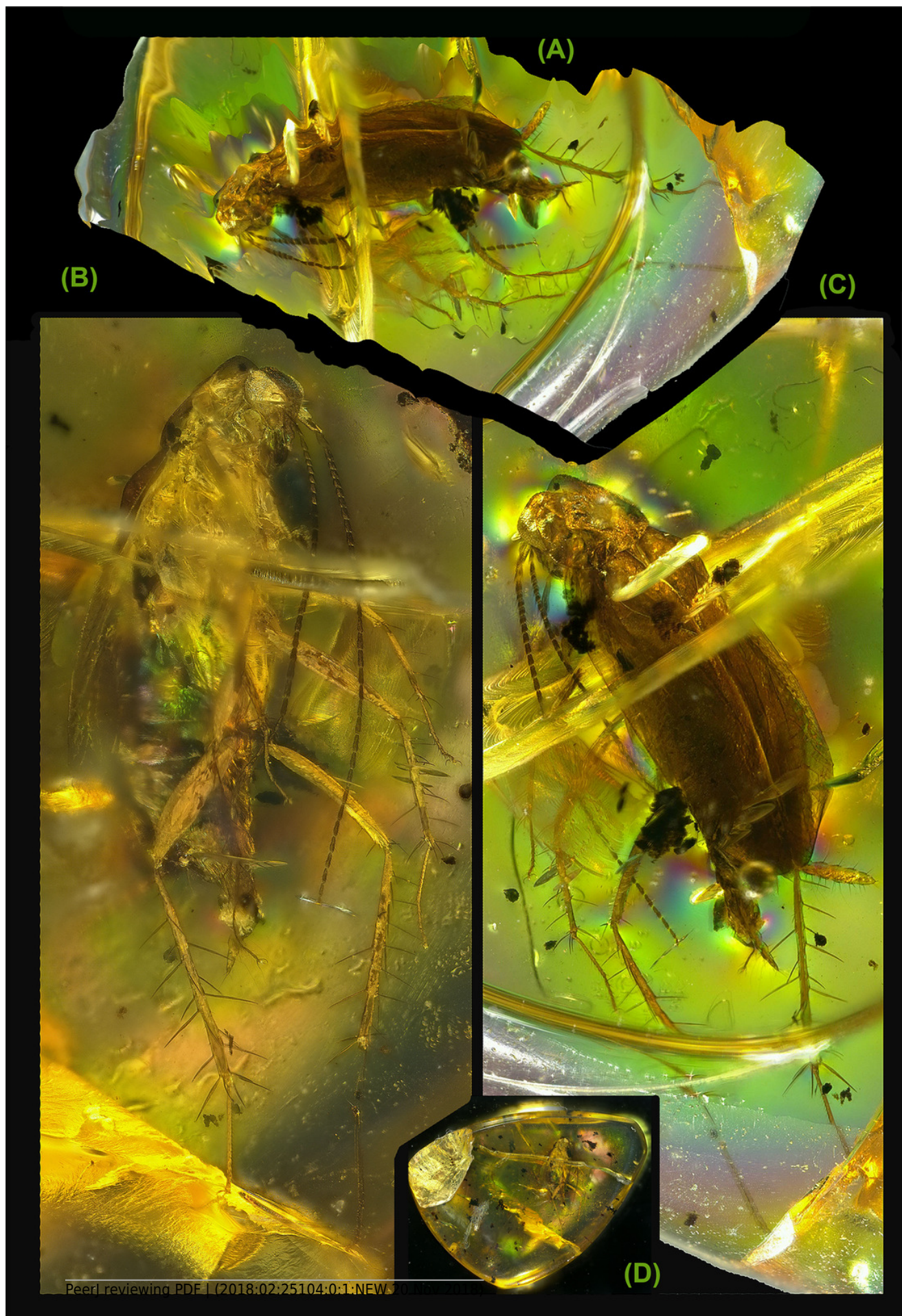


Figure 3

Line drawing of *Anaplecta vega* sp.n.

(A) Ventral view. (B) Dorsal view. (C) Head and asymmetric palps. Overall specimen length head-abdomen 4.89mm.

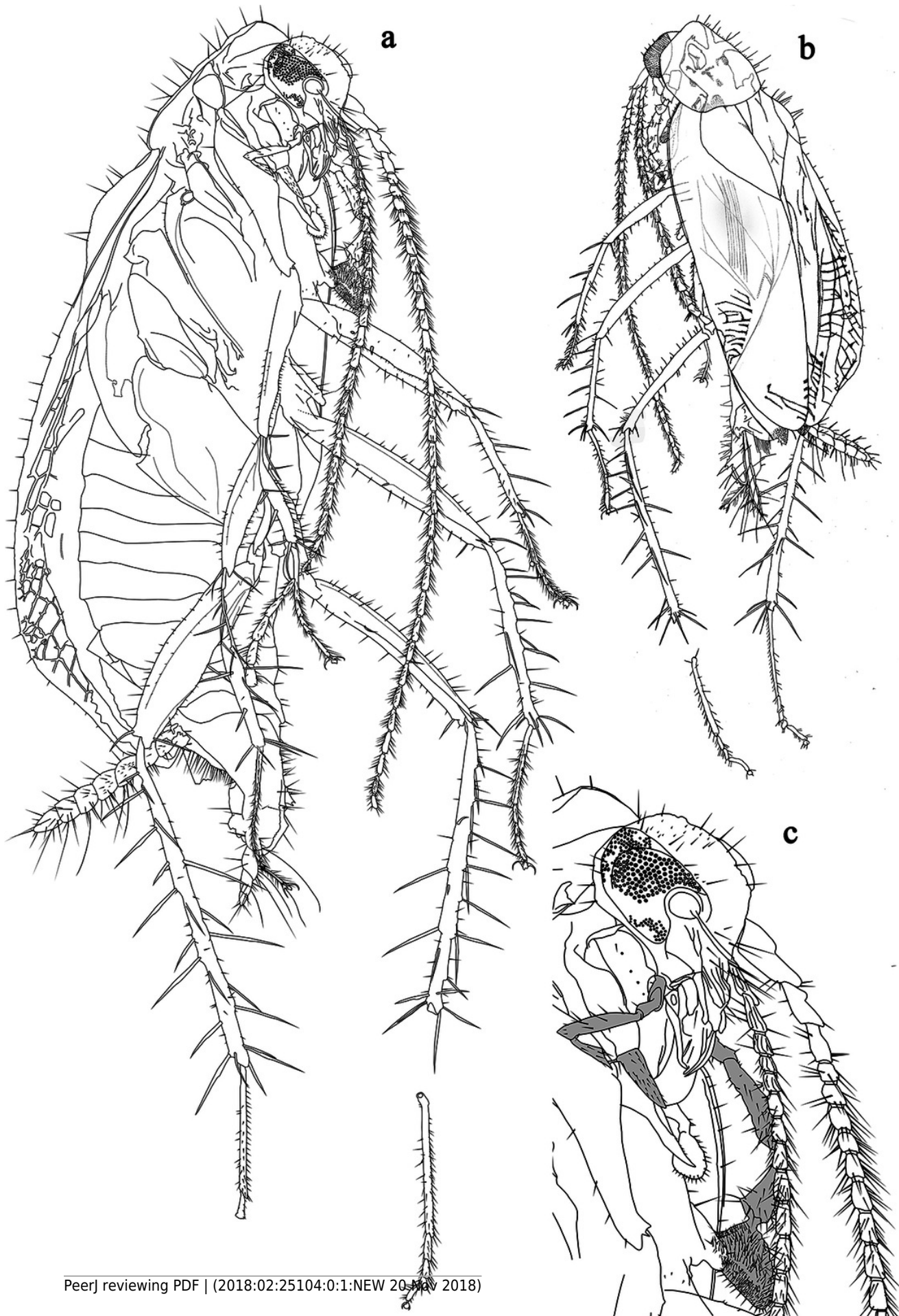


Figure 4(on next page)

Body measurements of *Anaplecta vega* sp.n. and different *Anaplecta* species.

Plot depicts comparison of dimensions of *Anaplecta vega* sp.n., *A. azteca*, *A. fallax*, *A. decipiens* (= *A. fallax*), *A. mexicana*, *A. gemma* (synonym for *A. mexicana*), *A. nahua*, *A. otomia*, *A. sausserei*, *A. tolteca* holotypes.

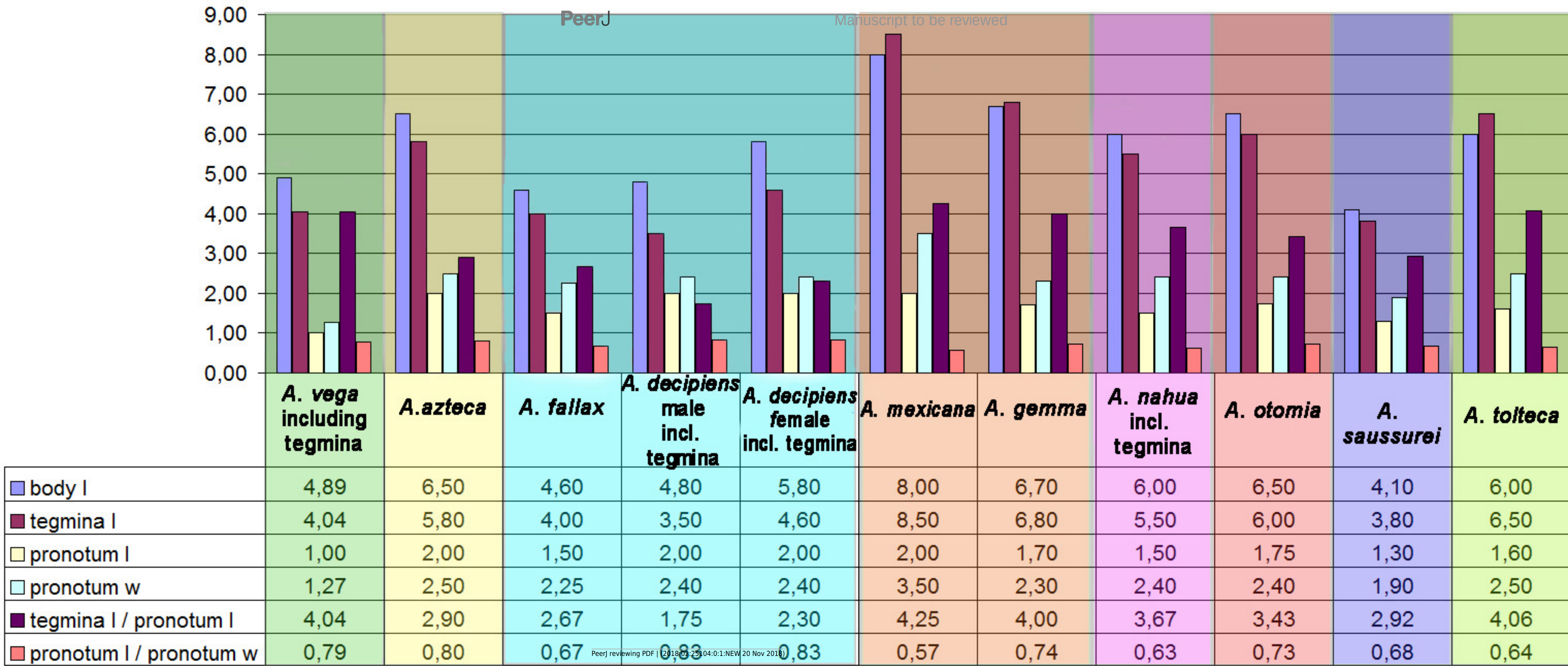


Figure 5(on next page)

Comparison of *A. vega* sp.n. dimensions (blue) and average of living Mexican *Anaplecta* species dimensions (purple).

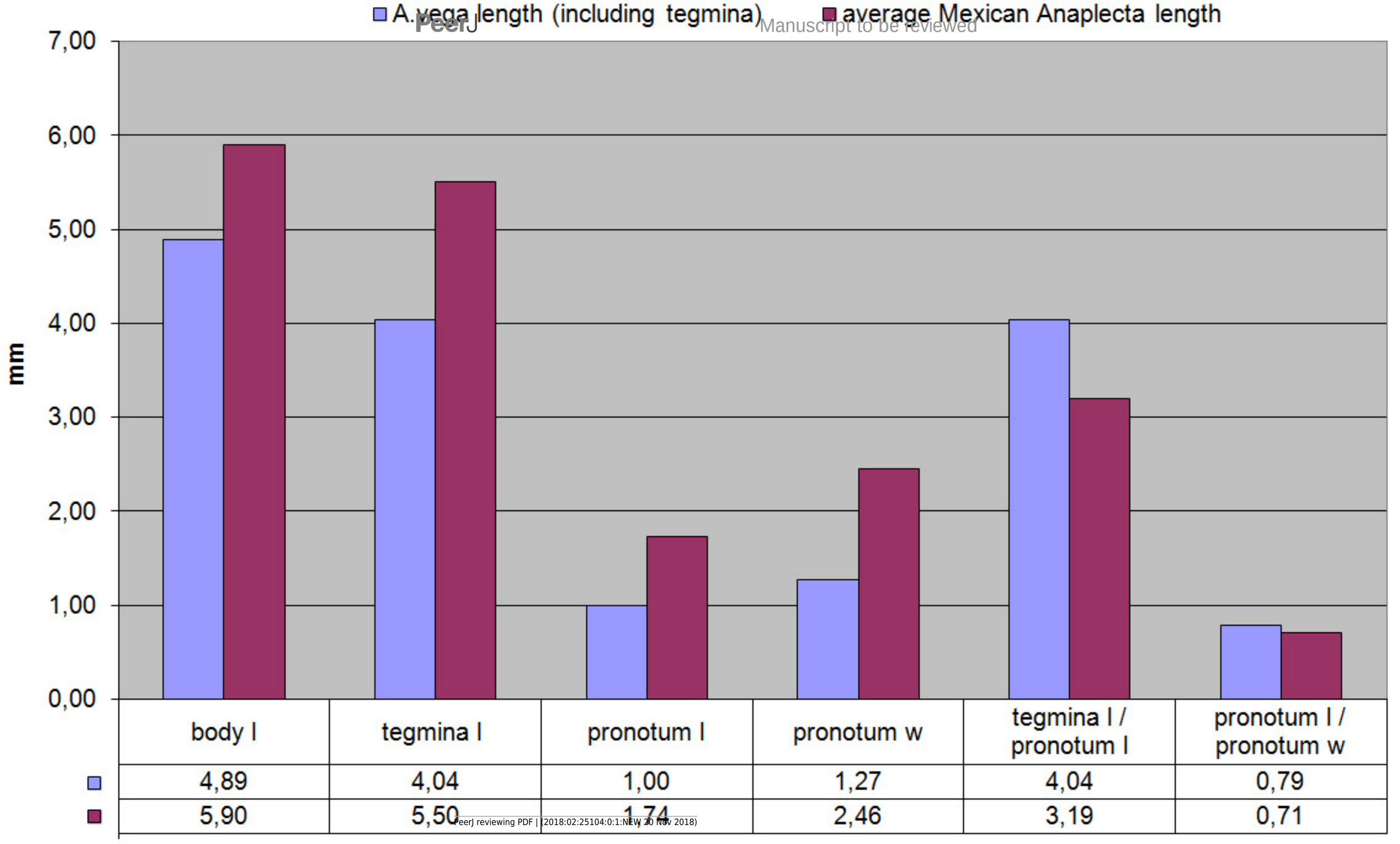


Figure 6(on next page)

Comparison of *Anaplecta vega* sp.n. left (blue) and right (purple) maxillar palpomere lengths.

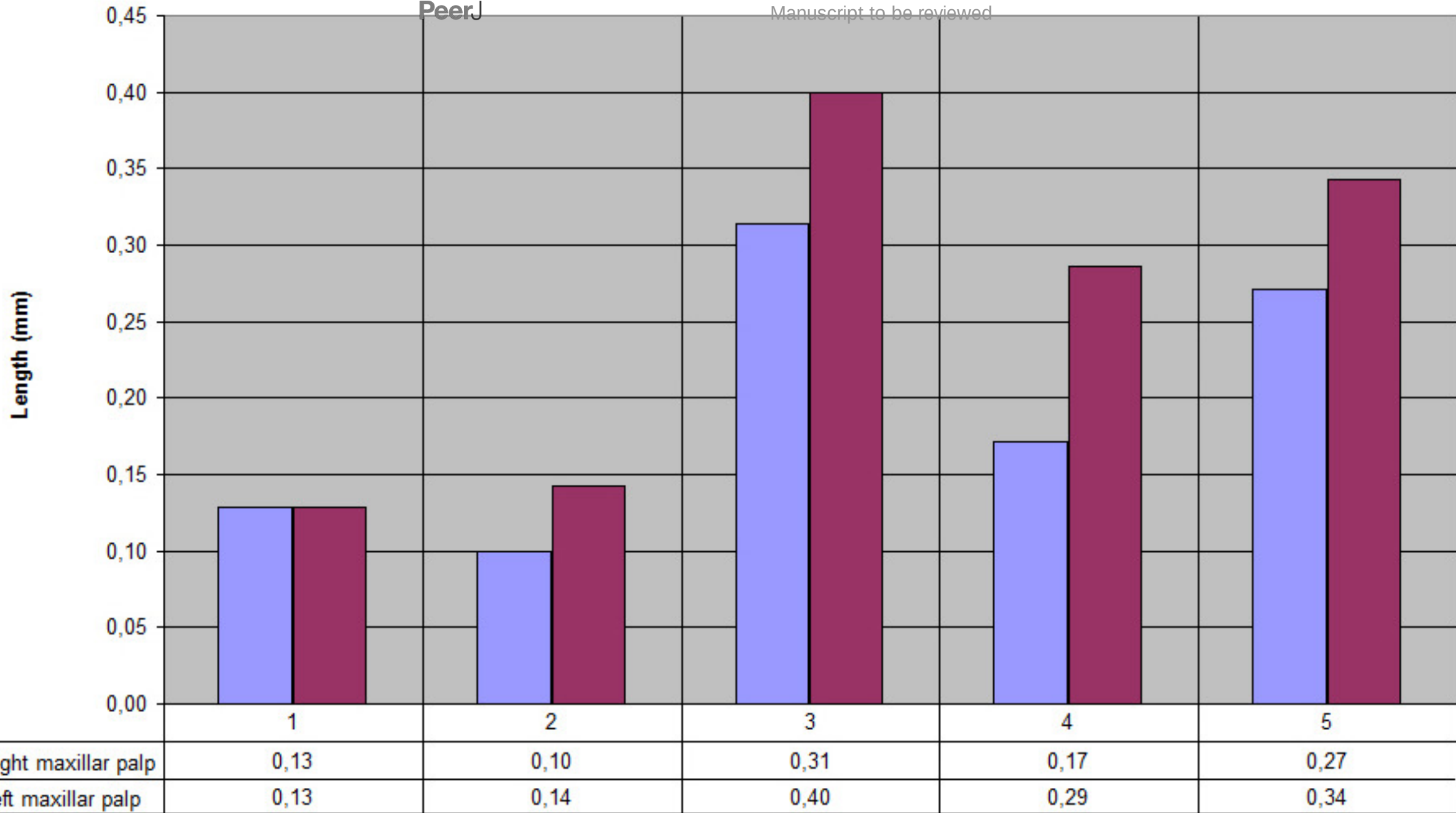


Figure 7 (on next page)

Left (blue) and right (purple) antennomeres length comparison including scape and pedicel present in *Anaplecta vega* sp.n.

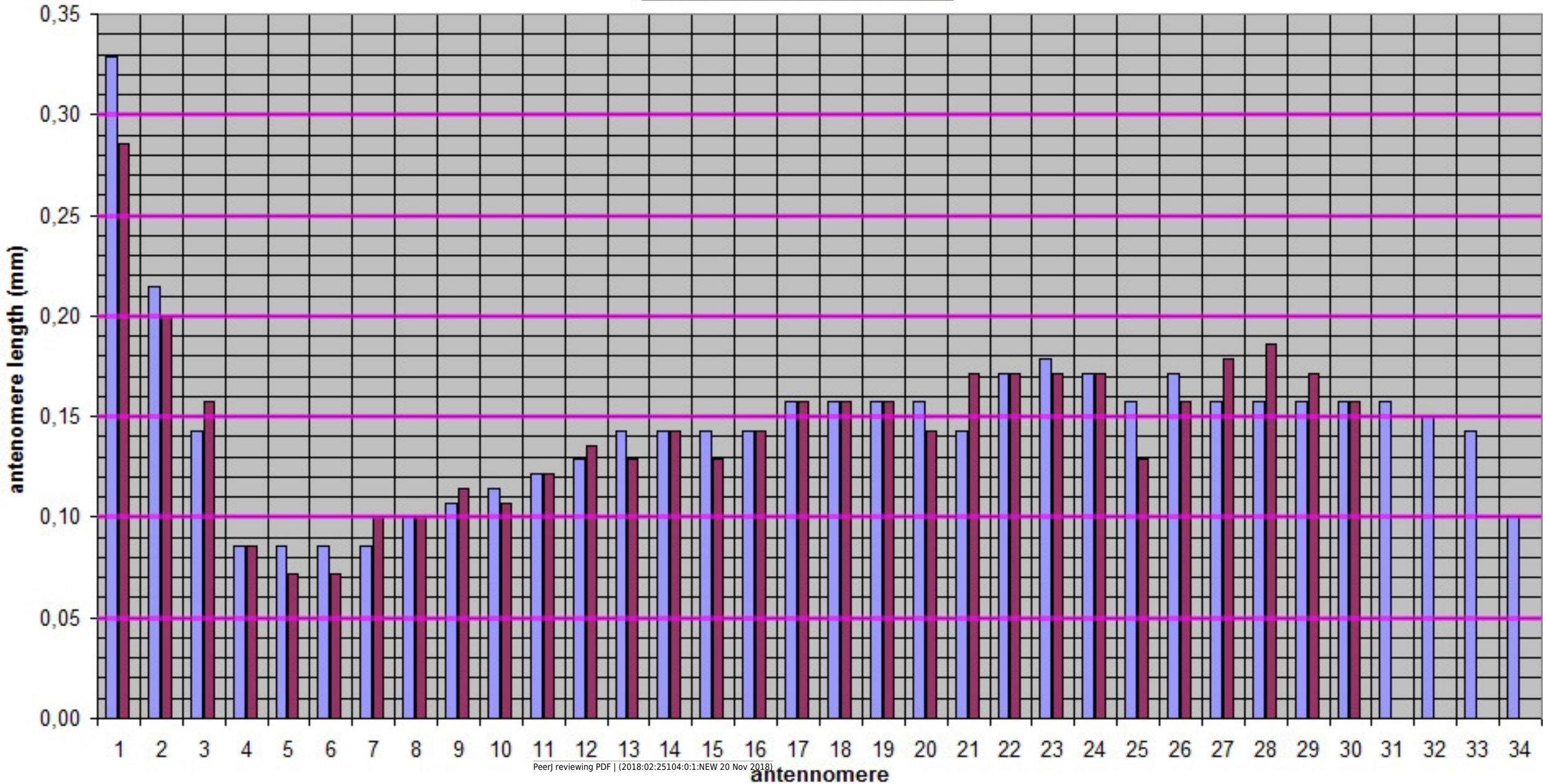


Figure 8(on next page)

Comparison of length of each leg femur, tibia and tarsomeres of *Anaplecta vega* sp.n.

