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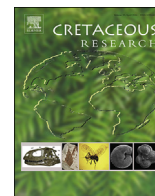


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Ptismidae fam. nov. (Coleoptera, Staphyliniformia) from the Lower Cretaceous Lebanese amber



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ABSTRACT

Ptisma zasukhae gen et sp. nov. is described from the Lower Cretaceous Lebanese amber and attributed to a new family Ptismidae fam. nov. with unclear position within the infraorder Staphyliniformia, hypothetically in the superfamily Staphylinoidae. This species is characterized by the rather small body size (0.59 mm) and structural similarities with different staphylinoid groups. The particular development of the legs of the new taxa shows some similarities with those of small and medium-sized jumping beetles from the superfamilies Scirtoidea, Buprestoidea, Tenebrionoidea, Chrysomeloidea and Curculionoidea. However, jumping beetles of these groups have strong femora and tibiae with large spurs and thick apical setae only on the posterior legs while *P. zasukhae* sp. nov. demonstrates such features on both mid and posterior legs. Another particularity of *P. zasukhae* sp. nov. is the unusual large femoral plate of metacoxae extending behind the suture between ventrites 2 and 3. Strong development of these structures are rare among Coleoptera and occurs in different taxonomic groups without close relationship. The studies were carried out with the usage of usual conventional light microscopy and confocal laser scanning microscopy.

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1. Introduction

Staphylinoidae and Curculionoidea represent the largest animal superfamilies. However coleopterists currently recognize only six families within Staphylinoidae (Lawrence and Ślipiński, 2014: Ptiliidae Heer, 1843, Hydraenidae Mulsant, 1844, Agyrtidae C. Thomson, 1859, Leiodidae Fleming, 1821, Silphidae Latreille, 1807, Staphylinidae Latreille, 1802). Newton and Thayer (1992) defined twelve families uniting the same taxa but partly with other ranks. Most representatives of the superfamily are currently Staphylinidae that are most structurally diverse within the superfamily and currently divided into 32 subfamilies (Gebennikov and Newton, 2009; Lawrence and Ślipiński, 2014; etc.). These subfamilies

include the groups with characters somehow spread in different staphylinid groups and not infrequently demonstrating an intermediate condition between the characteristic features of separate suprageneric groups.

Kirejtshuk and Azar (2013) summarized the data on beetles recovered from the study of materials from the Lower Cretaceous Lebanese amber and published the list of beetle families found in this resource. In that publication, as an aberrant member of the family Ptiliidae, it was mentioned the “specimen has the 4-segmented long tarsi, not strongly reduced membrane of hindwings fringed along their margin and some characters (long palpi) which are reminiscent of those of Hydraenidae (this specimen could be described as a member of the new family)”. The latest studies of this specimen supported the previous opinion on its very isolated but still unclear position. In this paper we describe a new species and propose a new genus and a new family.

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2. Materials and methods

The specimen examined (holotype) is housed in the collection of the Museum of Natural History in the Department of Natural Sciences of the Lebanese University, Fanar. The specimens of different groups of Coleoptera for comparison were used from the collection of the Zoological Institute of the Russian Academy of Sciences. Basic optical equipment was used, including a Leica MZ 16.0 stereomicroscope in the St. Petersburg Institute and an Olympus SCX9 stereomicroscope in the Paris Museum. In addition, the specimens were studied with a confocal laser scanning microscope (CLSM) in the St. Petersburg State University (see below). The method of preparation of the specimens was described in [Azar et al. \(2003\)](#).

CLSM technique and 3-D modelling. CLSM acquisition was carried out using Spectral confocal & multiphoton system Leica TCS SP2 with objectives 40× N.A. 1.25–0.75 Oil CS HCX PL APO and 63× N.A. 1.4–0.60 Oil IBL HCX PL APO with the same adjustments of the confocal laser system as described by [Kirejtshuk et al. \(2015\)](#). Black and white CLSM images are maximum intensity projections (MIP) obtained with ImageJ free software (<http://rsb.info.nih.gov/ij/>). The coloured CLSM images are pseudovolume images obtained as a result of combination of two different modules (Orthoslice and Voltex® 5.3.2 software which helped to accentuate the structures of interest (provided by Voltex module) against the background (provided by Orthoslice module) (see for details in [Chetverikov, 2014](#); [Chetverikov et al., 2014](#)).

Strata. Lower Cretaceous; ante Jezzinian ([Maksoud et al., 2014](#)) i.e. ante Late Barremian (circa 130) most likely Lower Barremian, after the most recent geological and stratigraphical data.

Locality. Nabaa Es-Sukkar – Brissa, details on this amber outcrop could be found in [Kirejtshuk and Azar \(2013\)](#). This outcrop visited only two times for less than half an hour each, have yielded to date to 24 inclusions (members of rachiberothid neuropteran; trichocerid, chironomid and ceratopogonid dipterans; thysanopteran; aleyrodid hemipterans; and trogossitid, monotomid, silvanid-like, aderid and our herein described coleopteran) distributed in 7 amber pieces.

3. Systematic paleontology

Superfamily Staphylinoidea

Family Ptismidae A. Kirejtshuk et Azar, fam. nov.

Type genus: *Ptisma* gen. nov.

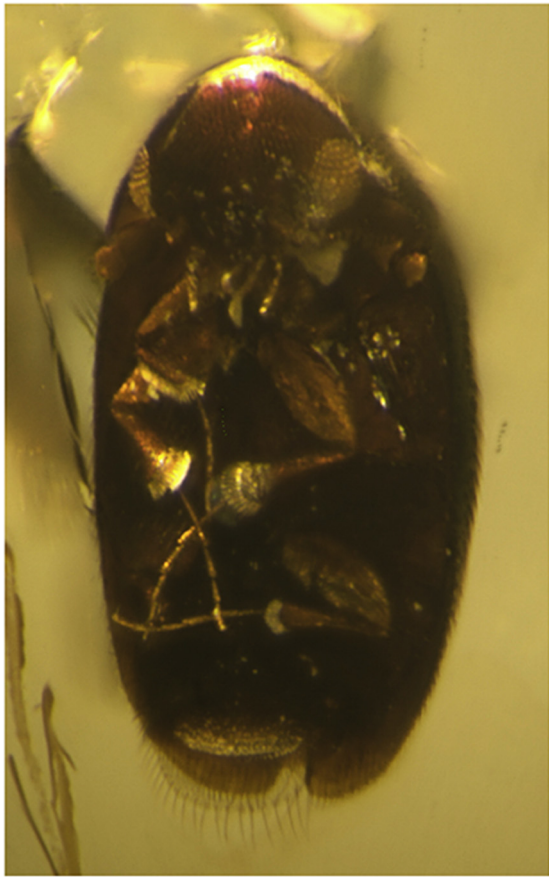
Composition. The type genus only.

Diagnosis. Body very small (circa 0.6 mm), oval and moderately convex. Integument smoothed, finely punctured, finely and slightly conspicuously pubescent. Head short, without trace of frontoclypeal suture, not constricted at base, with clubbed 10-segmented antennae bearing scape (antennomere 1) and pedicel (antennomere 2) larger than flagellomeres, compact club with columella-like sensilla on subtruncate apex of ultimate antennomere and sensilla like short elliptic cylinders at side of apex of antennomeres 8 and 9 ([Figs. 1B, 2A, 2C, 4A–B](#)), maxillary palpi about half as long as antennae and with very long subcylindrical ultimate palpomere ([Fig. 3C](#)). Prothorax with dilated sides, with distinct lateral carina. Pronotum slightly convex, gently sloping at sides, widest at base and its anterior part extended above head base. Procoxal cavities apparently narrowly separated (or contiguous). Mesocoxal cavities apparently (sub)-contiguous, open laterally, widely transverse and oblique, mesocoxae with exposed trochantin ([Fig. 2E](#)). Metaventrite comparable in length with prosternum and mesoventrite. Metacoxal cavities very wide and conjoined, with large femoral plates covering metacoxae. Abdomen with seven exposed ventrites,

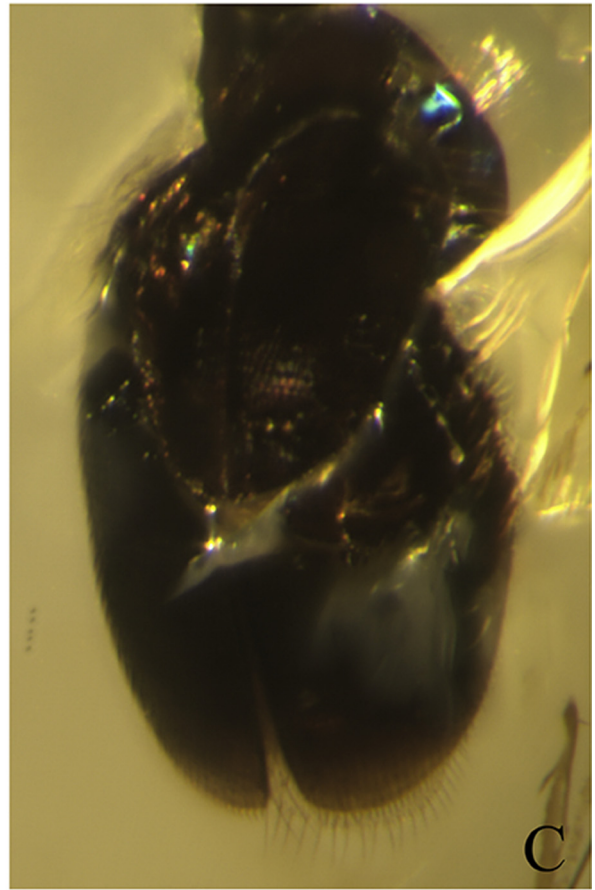
lateral part of ventrite 1 (derivate of sternite 2) exposed externally from outer edge of femoral plate of metacoxae ([Fig. 3E](#)), ventrites 2–6 comparable in length, and ventrite 7 (hypopygidium) longer and rounded at apex, three last segments (ultimate and penultimate) partly retracted into previous segments. Elytra complete and with epipleura not expressed. Hindwings with fringed margins. Trochanters very large and transverse, “large and mobile” type (after [Crowson, 1981](#)). Femora of usual shape. Protibia dilated, with long fine and dense setae along outer edge and stout setae at apex; meso- and metatibiae not dilated, thickening distally and with very long and stout setae around oval posterior plane and very strong two apical spurs ([Figs. 1B, 2E and 2F](#)). Tarsi 4-segmented and very long, all tarsomeres subcylindrical very long and tarsomeres 1–3 spinose at apex, claws simple, without empodium ([Fig. 2B](#)).

Notes. The usage of confocal microscopy gives a possibility to see lateral end of the most proximal suture on the ventral surface of the abdomen, the most part of which is covered with the femoral plates of metacoxae ([Figs. 3E, 4C](#)), but can be traced in separate slides after laser scanning. Besides, the frons of *Ptisma zasukhae* sp. nov. ([Fig. 3C](#)) looks quite different from that characteristic of many staphylinoid groups by the dilatations over the antennal insertions as well as narrowed and partly separated by its anterior portion.

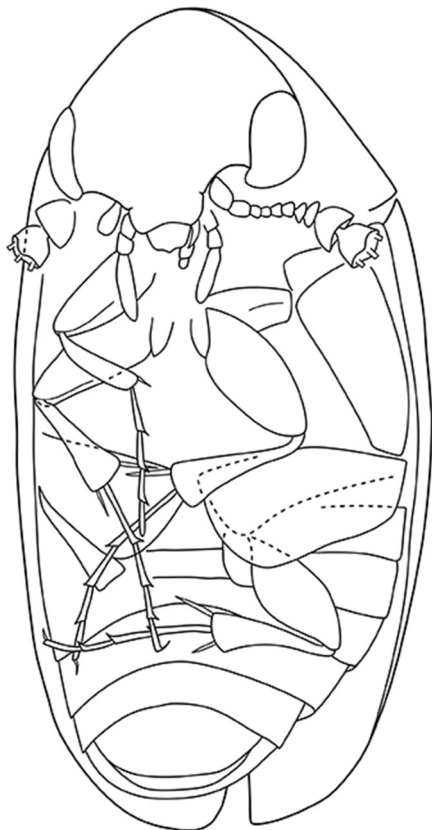
Comparison. This new family is currently connected with other groups of the superfamily Staphylinoidea because *Ptisma* gen. nov. shares similarities with some members of staphylinoid groups having small body in the general appearance and many organs, including the structure of all coxae and abdomen (see the below [Discussion](#)). The particularly distinctive structural characters of the new family are represented by the peculiar structure of all legs, the stout columella-like sensilla on the subtruncate apex of the ultimate antennomere and the sensilla like short elliptic cylinders on the apex of antennomeres 8 and 9 (see above), which are not characteristic of most staphylinoids (see a more detailed comparison below in the [Discussion](#)). The comparative length of the tibial spurs and corolla of very long and stout setae on tibial apex in Ptismidae fam. nov. are unique among staphylinoids, although the apices of tibiae of many psephenines have a corolla of setae of a structure different from that of setae in other tibial parts ([Kurbatov, pers. comm.](#)). By the small and regularly oval body, fringed hindwings, large trochanters, metacoxal femoral plates, reduced elytral epipleura, seven free abdominal ventrites and sometimes mesocoxal cavities open laterally the type species of Ptismidae fam. nov. is most reminiscent of some representatives of Ptiliidae. However, the new family is rather distinct from the latter in the following: long palpi, large and transverse mesocoxae, wide metepisterna, derivatives of the abdominal sternites 2 and 3 separated by a suture, widened apices of meso- and metatibiae with the crown of thick setae and the very long apical spurs (about third as long as tibiae), 4-segmented very long tarsi and the lack of tarsal empodium. Besides, the general appearance and many characters of *Ptisma zasukhae* sp. nov. allow comparing it with some representatives of Hydraenidae (particularly with *Limnebius* Leach, 1815). *Ptisma zasukhae* sp. nov. differs from the members of this family in the: lack of clear “frontoclypeal” suture, much longer 10-segmented antennae, comparatively shorter palpi, fringed hindwings, flattened and transverse mesocoxae, wide metepisterna, large metacoxal femoral plates, larger trochanters, wider femora, lack of elytral epipleura, widened apices of meso- and metatibiae with the crown of thick setae and the very long apical spurs (about third as long as tibiae), and long 4-segmented tarsi with the shortest ultimate tarsomere. The groups of other staphylinoid families (Agyrtidae, Leiodidae, Silphidae and Staphylinidae) differ from the new family in many characteristics including: body-size, mouthparts,



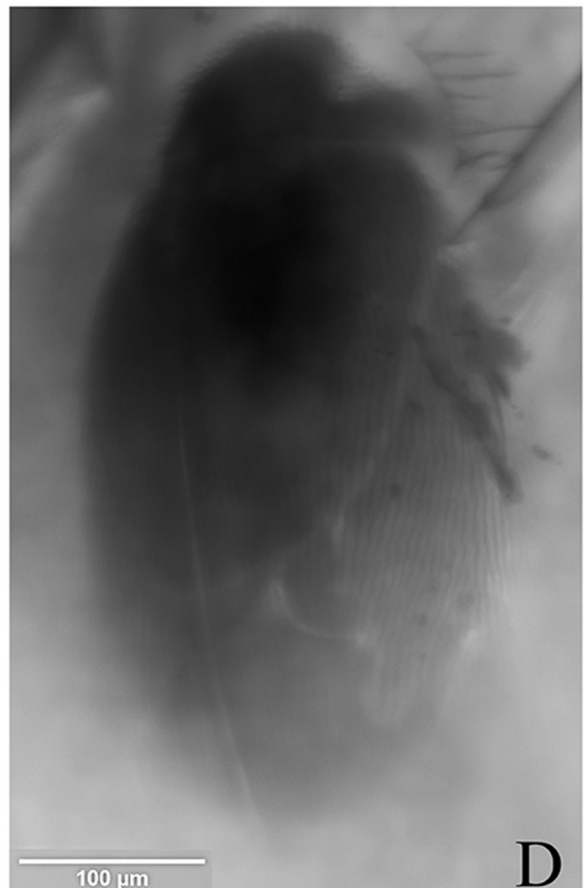
A



C



B



D

Fig. 1. *Ptisma zasukhae* gen et sp. nov., holotype, NBS-2E (Lebanese University, Department of Natural Sciences, Fanar); Lower Cretaceous, Lebanese amber. Length of body 0.59 mm. **A.** Body, ventral, photos under Olympus SCX9 with camera Olympus. **B.** *ibid.*, drawing reconstruction. **C.** Body, dorsal, photos under Olympus SCX9 with camera Olympus. **D.** *ibid.*, reconstruction; CLSM image (maximum intensity projection).

antennae, metacoxae, if present, with not large femoral plates, tarsi, etc. (see recent family characteristics in Lawrence and Ślipiński, 2014). In contrast to Ptismidae fam. nov., Agyrtidae, Leiodidae, Silphidae and usually Staphylinidae have the bisetose tarsal empodium, and also their hindwings are very rarely slightly fringed. Some staphylinid groups also demonstrate similarities in various organs with *Ptisma zasukhae* sp. nov., although in most cases the members of this family have the major characteristic of long body with the strongly shortened elytra. Among staphylinids with small body-size, most similarities shared with this fossil falls into the recent Nearctic species from the monotypic Empelinae Newton et Thayer, 1992 (after Abdullah, 1969), particularly expressed in the: general outline, shape of head without “frontoclypeal” suture, long palpi, long elytra with obliquely arcuate apices, comparatively long ultimate maxillary palpomeres, short prosternum, all pairs of coxae (sub)-contiguous. However *Ptisma zasukhae* sp. nov. differs from *Empelus brunnipennis* (Mannerheim, 1852) in the: convex anterior edge of the pronotum extending on the head base, metepisterna widened anteriorly, fringed hindwings, extremely large femoral plates of metacoxae, abdomen with seven free ventrites, strongly thickened tibial apices with strong spurs and thick setae, very long 4-segmented tarsi and the lack of raised empodium. Another group of small staphylinids shares similarities with the new family in the appearance including: short prosternum, lack of elytral epipleura, conjoining metacoxae with raised femoral plates, 4-segmented tarsi is represented by the recent species of *Silphotelus* Broun, 1895 (Proteininae Erichson, 1839: *Silphotelini* Newton and Thayer, 1995: see Steel, 1966) from New Zealand. *Silphotelus* differs from *Ptisma* gen. nov. in the wide frons with the deep lateral excisions for antennal base, long subfiliform 11-segmented antennae, very narrow metepisterna (but widening anteriorly), six abdominal ventrites, smaller and separated mesocoxae, and short tarsi with lobed tarsomeres 1–3. Considerable external similarities of the new species can be also traced with the small members of *Microsilpha* Broun, 1886 (omaliine *Microsilphini* or *Microsilphinae* Crowson, 1950), including similarities in the: smoothed dorsal integument, (almost) complete elytra, clubbed antennae, subacute ultimate palpomeres, sometimes widened tibiae with spurs and so on; but *Ptisma* gen. nov. has a smaller body, a head strongly inclined and oriented posteriorly, much larger eyes, no ocelli, 10-segmented antennae, conjoined meso- and metacoxae, clear and very large femoral plates of metacoxae, lack of elytral epipleura, seven ventrites of abdomen and very long 4-segmented tarsi with subcylindrical palpomeres. Some small staphylinids of the subfamily Scydmaeninae Leach, 1815 also need to be compared with the new taxa because some of them are similar to it in the general body outline, the clubbed antennae and the large mesocoxae (for example, species of *Cephennodes* Reitter, 1884 (including *Chelonoidum* Strand, 1935), *Trurlia* Jałoszyński, 2009 and *Cephennococcus* Jałoszyński, 2011 from Cephenniini Reitter, 1882), the reduced elytral epipleura, although these staphylinids differs from *Ptisma* gen. nov. in the structure of mouthparts and particularly in the structure of maxillary palps, 11-segmented antennae with 3-segmented loose club, narrow metepisterna, separated meso- and metacoxae, lack of metacoxal femoral plates, six abdominal ventrites, short 5-5-5-tarsi and many other characters. Finally, *Ptisma* gen. nov. has a more or less considerable similarity with *Semiclaviger* Wasmann, 1893 (Pselaphinae Latreille, 1802), probable member of the supertribe *Clavigeritae* Leach 1815 (according to Hlaváč et al., 2013, p. 273: “pronotum widened posteriorly ... is apparent only for *Semiclaviger* and *Madara* Dajoz, 1982...” in the shape of its small and wide body, the wide pronotum with widely dilated sides and posterior angles projecting lateroposteriad, the presence of femoral plates of metacoxae, however these pselaphines demonstrate the very different structure of head and mouthparts, 4-segmented antennae with

very long and subcylindrical ultimate antennomere, short elytra remaining about half of the abdomen uncovered, small oval mesocoxae, the separated meso- and metacoxae, long sclerite exposed behind elytral apices (fused three tergites), quite narrow femora and tibiae, 3-segmented tarsi etc. As to other similarities among staphylinids beyond the above-considered subfamilies, the 4-4-4 tarsi are known in the omaliine *Metacoraeolabium* Steel, 1950 (Corneolabiini Steel, 1950), oxyteline *Bledius* Samouelle, 1819 (Oxyteliini Fleming, 1821, including *Thinobiini* J. Sahlberg, 1876), the aleocharine tribes Corotocini Fenyes, 1918 and Hypocyphtini Laporte, 1835, and in most Euaesthetinae C. Thomson, 1859 as well, although their structure and that of other organs are completely different from those of the new family and species described herein. The staphylinid abdomen is rather variable: usually with six free ventrites, although with seven ventrites in most Oxytelinae Fleming, 1821, in some pselaphine males, or sometimes with only five ventrites in some pselaphine females and in Scaphidiinae Latreille, 1806, even with three ventrites in some pselaphines. The staphylinid antennae are usually moderately long and 11-segmented, although in some Aleocharinae Fleming, 1821 they are 10-segmented, in some Euaesthetinae 9- or 10-segmented, in Pselaphinae from 3- to 11-segmented; filiform, moniliform or incrassate-clavate, or weakly clubbed, though the usually elongate antennal club is strongly developed in the glypholomatine *Glypholoma* Jeannel, 1962, megalopsidiine *Megalopinus* Eichelbaum, 1915, and some Pselaphinae, Scaphidiinae, Scydmaeninae, Euaesthetinae and Leptotyphlinae Fauvel, 1874. Finally, all tarsomeres of *Ptisma* gen. nov. are very narrow and long reminiscent of those in some scaphidiines, however the members of the latter group in addition to other distinguishing characters mentioned above have the very long ventrite 1, the oval mesocoxal cavities, the separated meso- and metacoxae, the lack of large femoral plates of metacoxae, the narrow femora and tibiae, the expressed adsutural lines on elytra and 5-segmented tarsi. The detailed comparison with other staphylinids demonstrating the comparatively wide metepisterna not widening posteriorly, large and transverse mesocoxal cavities and other similarities with the new species is considered in the “Discussion” below.

Genus *Ptisma* A. Kirejtshuk et Azar, gen. nov.

Type species: *Ptisma zasukhae* sp. nov.

Etymology. The name of the new genus was borrowed from the Greek “πτισμα” = *ptisma* (grain; pure seed, peeled corn, barley). Gender feminine.

Composition. The type species only.

Diagnosis. As that in the family.

Ptisma zhasukhai A. Kirejtshuk et Azar, gen. et sp. nov.

Figs. 1–4.

Etymology. The epithet of this new species devoted to Lyudmila Mikhailovna Zasukha, the class teacher of the first author in the Kharkov secondary school № 59 during 1967–1969.

Holotype. “NBS-2E”, sex unknown; flat and elongate piece of light yellow and clear amber with some small cracks around the complete beetle placed in Canada balsam inside elongate and flat bar made of microscope glasses (20 × 4 × 1.5 mm). The amber piece contains a crack along the dorsal surface of the beetle separating a resin layer making it difficult to observe the outlines of sclerites and integument of the dorsum of the specimen under both usual optic and confocal microscope. The specimen examined is missing the most part of left anterior leg and right posterior tarsus.

Description. Body length 0.59, width 0.32, height apparently about 0.05 mm. Elongate oval, moderately convex dorsally and slightly

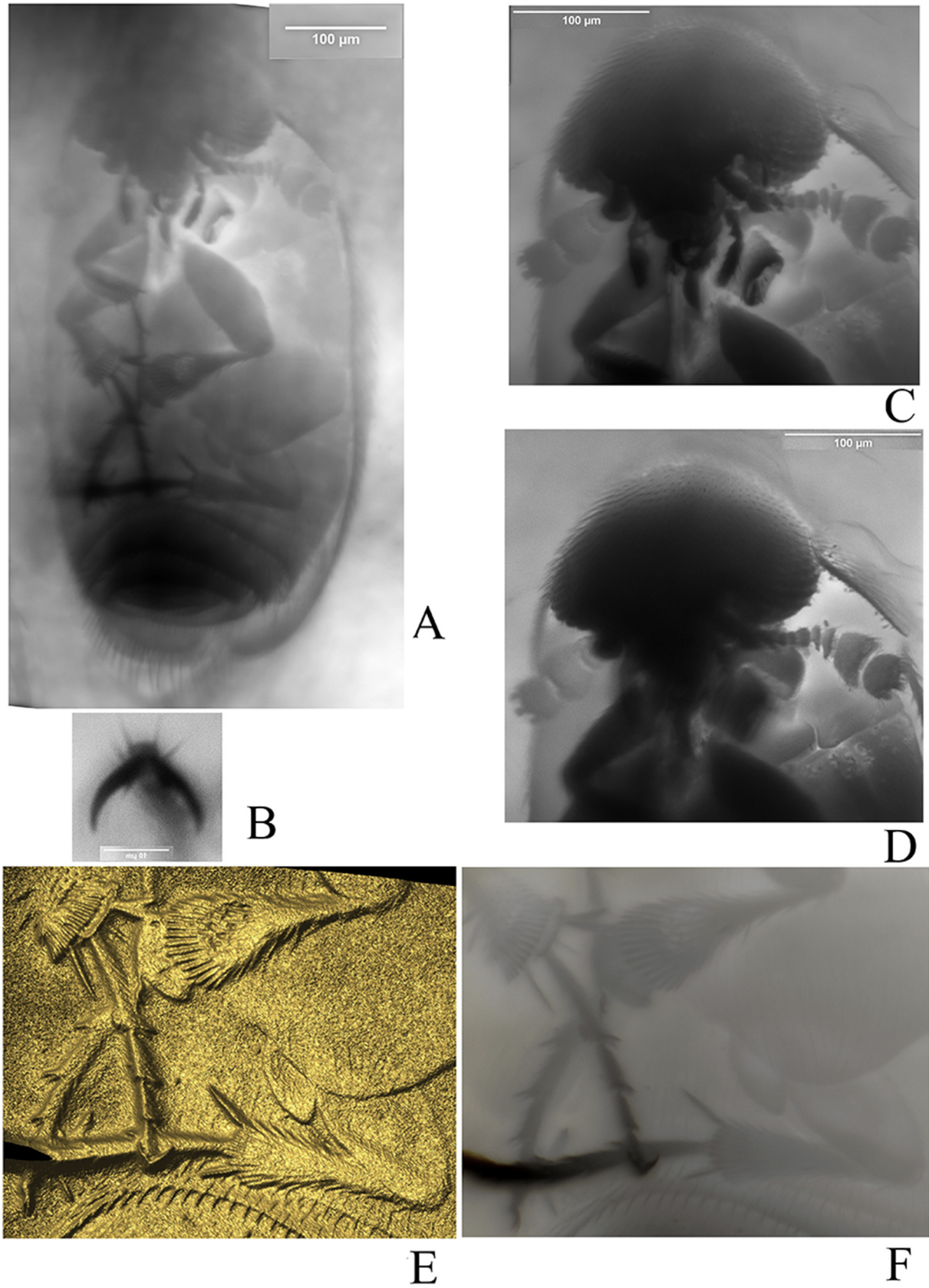


Fig. 2. CLSM images (A–D, F – maximum intensity projections, E – isosurface) of *Ptisma zasukhae* gen et sp. nov., holotype, NBS-2E (Lebanese University, Department of Natural Sciences, Fanar); Lower Cretaceous, Lebanese amber. Length of body 0.59 mm. **A.** Body, ventral. **B.** Tarsal claws. **C, D.** Head with appendages and anterior thoracic sclerites, ventral. **E, F.** Meso- and metatibiae and tarsi.

convex ventrally; dorsum chestnut brown; ventral thoracic sclerites lighter, appendages and abdominal apex reddish; dorsum with recumbent, slightly conspicuous and very short hairs becoming not visible on pronotum and head; pterothorax and abdomen with not visible hairs, pronotal and elytral sides ciliate. Dorsum with extremely fine and diffuse punctures and alutaceous, underside without clear punctures.

Head transverse and declined ventrally, slightly convex dorsally, narrower than pronotum, temples not projecting, with very large and oval, coarsely faceted eyes (longitudinal diameter of eyes about half as great as entire length of head); antennal insertions covered by dilated fold of frons and located at the middle of edge of lateral frons between eye and anterior edge. Labrum well exposed, transverse, wide than long and truncate at apex. Mandibles narrow and rather long, gently curved and sharply acuminate at apices. Antennae about as long as distance between eyes, 10-segmented, scape (antennomere 1) about 1.5 times as long as wide and somehow longer than each of flagellomeres; pedicel (antennomere 2) large and smaller than scape; antennomeres 3–8 elongate or nearly subequal in length and width, antennomeres 7 and 8 rather transverse; club rather compact and slightly dorsoventrally compressed, 2-segmented, about 2/5 of total antennal length, penultimate and ultimate antennomeres (9 and 10) transverse, subequal in length, antennomere 8 with one sensillum like a short elliptic cylinder, penultimate antennomere with two sensilla like short elliptic cylinders and ultimate antennomere truncate at apex and with three stout columella-like sensilla. Pronotum evenly convex and smoothed, gently sloping at sides, widest at base (as wide as elytra) and arcuately narrowing anteriorly, posterior edge shallowly emarginate, anterior edge convex and partly covered head; posterior angles with distinct top and anterior ones arcuate. Scutellum shaped as equilateral triangle and with narrowly rounded apex. Elytra nearly 1.7 times as long as wide combined, longest at suture and broadly arcuate along sides, moderately convex along the middle and steeply sloping at lateral edges, conjointly rounded at apices, with weak shoulders, adsutural lines not visible. Pygidium widely rounded at apex and not exposed from under elytral apices.

Underside of head and prosternum not visible. Maxillary palpi apparently 4-segmented, with not transverse palpomeres and ultimate palpomere about three times as long as thick and narrowing anteriorly. Ultimate and penultimate labial apparently elongate and ultimate palpomere apparently narrowing anteriorly. Procoxae not visible and apparently contiguous. Mesocoxal cavities large and widely transverse. Metaventricle medially convex. Metacoxae contiguous, transverse, with large femoral plate arcuate at posterior edge and extending beyond posterior edge of abdominal ventrite 2. Abdomen with 7 exposed ventrites, ventrite 7 (hypopygidium) longer and widely rounded at apex, together with pygidium partly retracted into previous abdominal segment.

Legs moderately narrow and long. Trochanters very large and transverse. Protibia about 2/3 as wide as antennal club, dilated and subparallel-sided, with long and stout setae along outer and apical edge; meso- and metatibiae only slightly narrower than antennal club. Pro- and mesofemora widest at base and metafemur with subarcuate at anterior and posterior edges (widest in middle). Setae on apex of mesotibiae much stronger than those on apex of metatibiae. Tarsi very long and very narrow, about 1.5 times as long as corresponding tibiae, all tarsomeres subequally narrow and subcylindrical, tarsomeres 1–3 spined at apex, tarsomere 1 about as long as tarsomeres 2 and 3 combined; claws simple and about 2/3 as long as ultimate tarsomere.

4. Discussion

On similarities of Ptisma gen. nov. with other staphylinoids

Ptisma zasukhae sp. nov. could be attributed to the superfamily Staphylinioidea (infraorder Staphyliniformia) because of the rather large and transverse mesocoxal cavities open laterally (occurring in many staphyliniformians, but rarely beyond this infraorder). Besides, it shares many other structural similarities with ptiliids, hydraenids and some subfamilies of Staphylinidae (see the above Comparison). A considerable number of characters of the new species is shared with several ptiliids without any clear systematic or phylogenetic preference, although there is no member of the family Ptiliidae that accumulates the whole set or even a considerable number of similarities of *Ptisma* gen. nov. For instance, the conjoined metacoxae are known also in the members of *Bambara* Vuillet, 1911, *Cylindroselloides* Hall, 1999 and many other genera of Nanosellini (*Discheramocephalus* Johnson, 2007, *Eurygyne* Dybas, 1966, *Porophila* Dybas, 1956, etc.); the conjoined mesocoxae in species of *Africoptilium* Johnson, 1967, *Bambara*, *Eurygyne*, *Macdonaldium* Abdullah, 1967, *Nanosella* Motshulsky, 1868, *Porophila*, *Ptiliopycna* Casey, 1924, *Rioneta* Johnson, 1975, *Urotriainus* Silvestri, 1945, etc.; the clubbed antennae in species of *Baronowskiella* Sörensson, 1997, *Cylindrosella* Barber, 1924, *Cylindroselloides*, *Discheramocephalus*, *Nanosella*, *Primorskiella* Polilov, 2008, etc; the large femoral plates of metacoxae in species of *Africoptilium*, *Bambara*, *Discheramocephalus*, *Eurygyne*, *Macdonaldium*, *Ptiliopycna*, *Smicrus* Matthew, 1872, *Urotriainus*, *Skidmorella* Johnson, 1971, etc.; the very large eyes among representatives of *Baronowskiella*, *Cisidium* Motshulsky, 1855, *Discheramocephalus*, *Nanosella*, etc. (Dybas, 1955, 1978; Johnson, 1967; Sörensson, 1997; Hall, 1999; Sawada and Hirowatari, 2003; Sörensson and Johnson, 2004; Grebennikov, 2008; Polilov and Beutel, 2009; Darby 2013; etc.). The very large femoral plates of metacoxae almost reaching the lateral edge of abdomen are present in the recent ptiliid species from *Eurygyne*, *Mikado*, *Nanosella* among others, however the femoral plates of *Ptisma* gen. nov. are much larger and with a long lateral portion covering the ventrite 1 (derivate of sternite 2), what remains visible as a narrow stripe at the very lateral edge of the abdomen. The tibiae of ptiliids are usually very narrow, not or rarely slightly widening distally and without or sometimes only with short spurs while the meso- and metatibiae of *Ptisma zasukhae* sp. nov. are strongly thickening apically with crown of thick setae and two very long spurs. Most ptiliids have 11-segmented antennae, although the ptiliid genera *Baronowskiella*, *Rodwayia* Lea, 1907 and many Nanosellini are characterized by 10-segmented antennae (as in the new species). The ultimate maxillary palpomere in *Ptisma* gen. nov. is not so thin as in most ptiliids and more reminiscent of some staphylinids than ptiliids.

The combination of the widely transverse and oblique mesocoxal cavities open laterally, the mesocoxae with exposed trochantin and the wide metepisterna are characteristic of silphids and agyrtids, although in some silphids and in agyrtid *Lyrosoma* Mannerheim, 1853 the body is much larger and with more or less wide elytral epipleura and the metepisterna are narrow, also in addition some silphids have the very large oval mesocoxal cavities open laterally. The agyrtid abdomen includes 5–6 ventrites (abdominal sternite 2 can be concealed or partly exposed) and the silphid abdomen have seven ventrites (sometimes with sexual dimorphism in number of ventrites and with abdominal sternite 2 exposed or completely concealed by the projecting distal part of metepisternum). Another very diverse staphylinoid family is Leiodidae which in general is characterized by the narrow metepisterna and the large transversely oval mesocoxal cavities open laterally (although sometimes rather small), and also the long

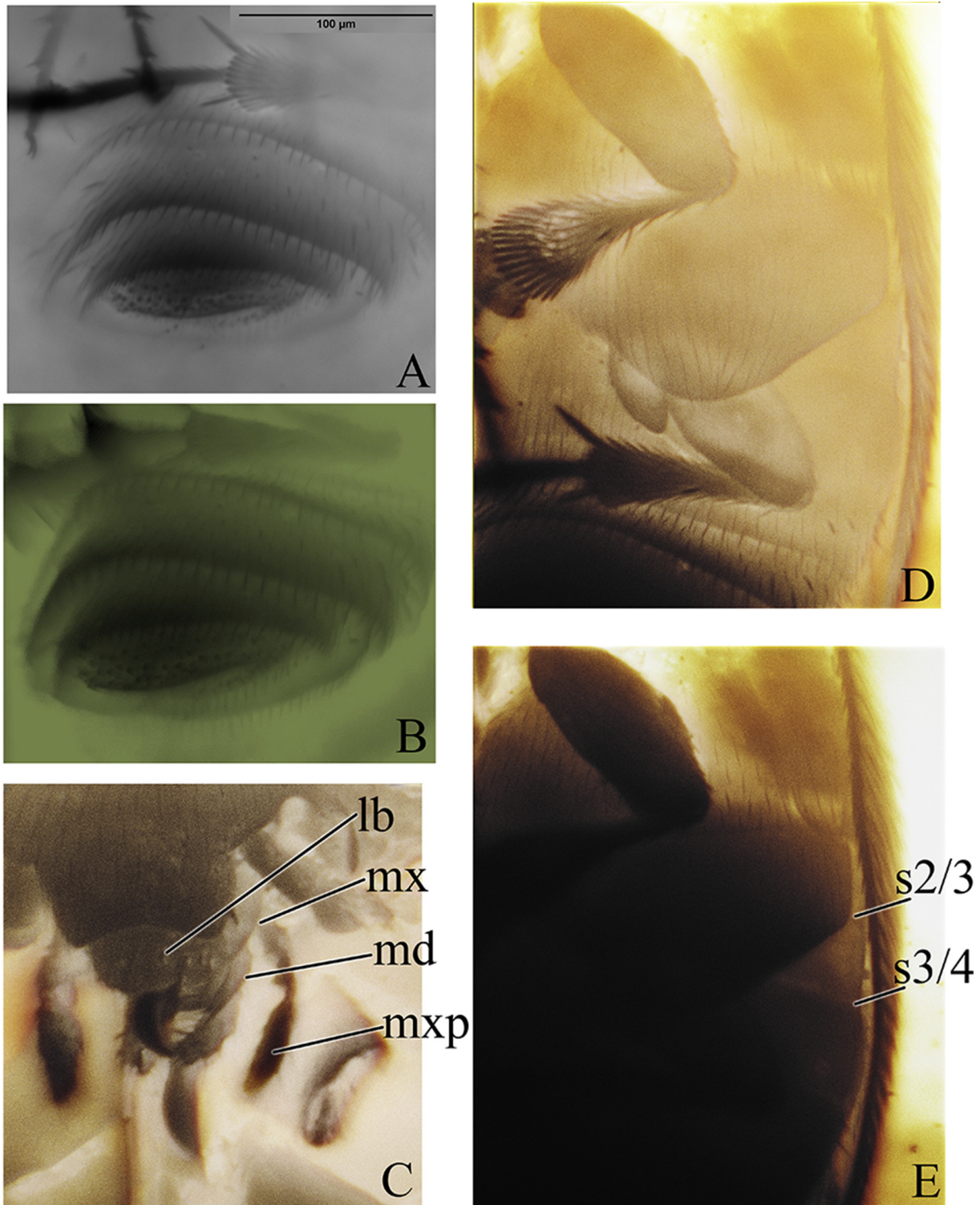


Fig. 3. CLSM images (A – maximum intensity projection, B–E – combined Orthoslice & Voltex pseudovolume images) of *Ptisma zasukhae* gen et sp. nov., holotype, NBS-2E (Lebanese University, Department of Natural Sciences, Fanar); Lower Cretaceous, Lebanese amber. Length of body 0.59 mm. **A, B.** Body, abdominal apex, ventral. **C.** Body, anterior part of frons with mouthparts; ventral. **D.** Right part of metaventricle, metacoxa with femoral plate, abdominal base, mid and posterior legs, ventral. **E.** ibid, ventral. Abbreviations: lb – labrum, md – mandible, mx – maxilla, mxp – maxillary palpomere, s2/3 – suture between ventrites 1 and 2 (derivates of sternites 2 and 3), s3/4 – suture between ventrites 2 and 3 (derivates of sternites 3 and 4).

ultimate maxillary palpomere (as that in *Ptisma* gen. nov.), but they have almost always 11-segmented antennae, the metacoxae without femoral plates or rarely only with very small femoral plates, usually the separated meso- and metacoxae, 4–6 abdominal ventrites (never seven), the metatarsi variable but never of the 4-4-

4 type. The leioidids are frequently with antennal club (if present) including more than two segments and in these cases the antennomere 8 is usually shorter and narrower than antennomeres 7 and 9. The recent species of *Platyptysyllus* Ritsema, 1869 (*Platyptysyllinae* Ritsema, 1869) have a smaller number of antennomeres and the

compact club, however, in contrast to *Ptisma* gen. nov., they are also characterized (in addition to the above-mentioned features) by the strongly modified head without eyes and with the strongly modified mouthparts, the long prosternum, the short elytra, the lack of hindwings and other different features.

The staphylinids present many features of *Ptisma* gen. nov. that can be found among its different groups, but not only among the groups with small body-size (see the above Comparison). However, there is no staphylinid with structure of tibiae and long spurs as those in the new genus. The metepisterna of many staphylinids are comparatively wide in the posterior part and more or less narrowing apically. In addition to the groups considered in the above comparison, it is worthy to mention that there are some staphylinid groups with more or less long elytra and comparatively large femoral plates of metacoxae. For example, *Anacyptus testaceus* (LeConte, 1863) (Mesoporini Cameron, 1959: Aleocharinae) has extremely long femoral plates of metacoxae, however these plates are oblique and far from reaching the lateral edge of the abdomen, and this aleocharine demonstrates the rather short elytra, the separate metacoxae, the metepisterna wide at posterior edge and strongly narrowing anteriorly, and the short 5-segmented tarsi. Some recent omaliine species of *Eusphalerum* Kraatz, 1857 (*Eusphalerini* Hatch, 1957) and *Anthophagini* C. Thomson, 1859 (including *Brathinini* LeConte, 1861) not only have the long elytra and sometimes the raised femoral plates of metacoxae, but also their metepisterna occasionally are widening anteriorly and reminiscent of those in this fossil, nevertheless they have the raised ocelli on their head (with few exceptions when they are weakly or not raised), the filiform or moniliform 11-segmented antennae, the prothorax with moderately or very long prosternum and the explanate pronotal sides (or without lateral carinae of prothorax in *Brathinus* LeConte, 1852), the short 5-segmented tarsi with more or less lobed tarsomeres 1–4, their femoral plates of metacoxae, if raised, are not projecting at the lateral part and the mesal lobes of the latter do not extend posteriorly, and elytra usually with more or less wide elytral epipleura (but not in *Brathinus*).

Among staphylinids with small body-size, there exist several groups of the subfamily Pselaphinae which are very distinct from the new species in the general characteristic of body shape and many other features, the head of different type with constricted neck and rather different mouthparts, the pronotum narrowed at base and without lateral carina (except some species of *Clavigeritae* – see above), the more or less shortened elytra, usually narrowing anteriorly (although some species of the tribe *Iniocyphini* O. Park, 1951 with the long elytra), the very narrow metepisterna, the lack of large femoral plates of metacoxae, which are usually relatively separated, and usually the rather short and at most 3-segmented tarsi (although sometimes the tarsi in this subfamily could consist of two or even three long and narrow terminal tarsomeres) (representatives of *Arthromelus* Jeannel, 1949 and *Batrasiella* Raffray, 1904: *Batrisini* Reitter, 1882; *Ergasteriocerus* Leleup, 1973: *Brachyglutini* Raffray, 1904; *Morphogenia* Parker, 2014: *Jubini* Raffray, 1904; *Tmesiphorinus* Leleup, 1971: *Tmesiphorini* Jeannel, 1949; etc.) while the antennomere 1 of these psephenine species is short. The recent staphylinids of the subfamily *Apateticinae* also have long elytra, comparatively wide metepisterna, large and transversely oblique mesocoxae, but they have much larger body, different shape of head, rather long prosternum, wide elytral epipleura, six exposed abdominal ventrites, short 5-segmented tarsi and many other different features.

As to the characteristic stout columella-like sensilla on the subtruncate apex of the ultimate and penultimate antennomeres of the new taxa, some peculiar sensilla are also known among different staphylinid groups, particularly in Pselaphinae Latreille, 1802 (Jeannel, 1956; Bañar & Hlaváč, 2014; Chandler et al., 2015;

etc.), but when they are raised, these sensilla are rather different from those in the new species. A columella-like sensillum in or at a depression at the base of the ultimate antennomere are found in the recent pselaphine *Ambicocerus* (Batrisini Reitter, 1882) [described by Leleup, 1970] and in some other relatives. The similar location of sensilla of other types is known in other recent pselaphines (Leleup, 1976a). However the sensilla-like short elliptic cylinders on apex of antennomeres 8 and 9 are not known among other groups. The members of *Mayetia* Mulsant et Rey, 1875 (*Mayetiini* Winkler, 1925), *Euplectini* Streubel, 1839 and *Trichonychini* Reitter, 1882 have the ultimate antennomere with long lanceolate sensilla around the middle of this antennomere (Jeannel, 1956; Besuchet, 1985; etc.), in contrast, other pselaphines show such or different sensilla in different places (Leleup and Celis, 1968; Leleup, 1973, 1976b; Yin et al., 2011; etc.). Different groups of the supertribe *Clavigeritae* (Nomura, 1997; Hlaváč, 2005; etc.) have subtruncate apex of the ultimate antennomere and types of sensilla different from those in the new species. Some scydmaenines from the supertribe *Cephenniitae* Reitter, 1882 have stout sensilla concentrated in invaginated membraneous pockets or separate flat spatulate sensilla on antennomeres 9–11 (club) (Jajoszyński, 2014: “sensory organ”).

On similarities of Ptisma gen. nov. with other coleopterans

A certain level of similarity of *Ptismidae* fam. nov. could be traced with scirtoids, namely with *Eucinetidae* Lacordaire, 1857 and *Clambidae* Fischer, 1821. The eucinetids (among others) share with the new family the following: hypognathous head, shortened prosternum, conjoined meso- and metacoxae, large femoral plates of metacoxae, transverse and oblique mesocoxal cavities, widened apices of meso- and metatibiae with a crown of thick setae, simple subcylindrical metatarsomeres with acuminate spinose projections at apex and very long apical spurs. In contrast to the new genus, the eucinetids have: long and filiform 11-segmented antennae, “frontoclypeal” suture, separated mesocoxae, very short short metaventrite, five abdominal ventrites, more consolidated abdomen, usually raised elytral epipleura, heteromeroid type of trochanters (not very large and transverse, “large and mobile” type), and long 5-segmented tarsi. The similarities of eucinetids and *Ptisma* gen. nov. could be a result of convergence in structural adaptations for jumping. However, both groups demonstrate important differences in the metacoxae and their femoral plates. The clambids are similar to the new genus by: usually 10-segmented antennae with distinct club, transverse mesocoxae open laterally, large femoral plates of metacoxae, usually 4–4–4 tarsi. Nonetheless, clambids have small and not transverse eyes, very short metaventrite, separate mesocoxae, very narrow metepisterna, five exposed ventrites of abdomen, not enlarged and transverse trochanter, simple tibiae without both strong spurs and thick setae, and lobed tarsomeres 1–3. The scirtoid members of *Scirtidae* Fleming, 1821 and *Mesocinetidae* Kirejtshuk et Ponomarenko, 2010 differs from the new genus in the: larger body, 11-segmented antennae without clear club, smaller femoral plates of metacoxae, abdomen with five ventrites and 5-segmented tarsi with lobed tarsomere 4.

Among other elateriformians, many groups have the conjoined meso- and metacoxae with a raised femoral plates and a wide metepisterna widening anteriorly, however, the structure of head, thorax and abdomen cannot be compared with the new family. Particularly no one of them have: a large and wide femoral plates of transverse metacoxae, tibiae with dense thick setae and very long spurs, and 4-segmented very long tarsi similar to those in *Ptisma zasukhae* sp. nov. The jumping recent *Eucinetus*-like byrrhids from *Thaumastodinae* Champion 1924 with the small or

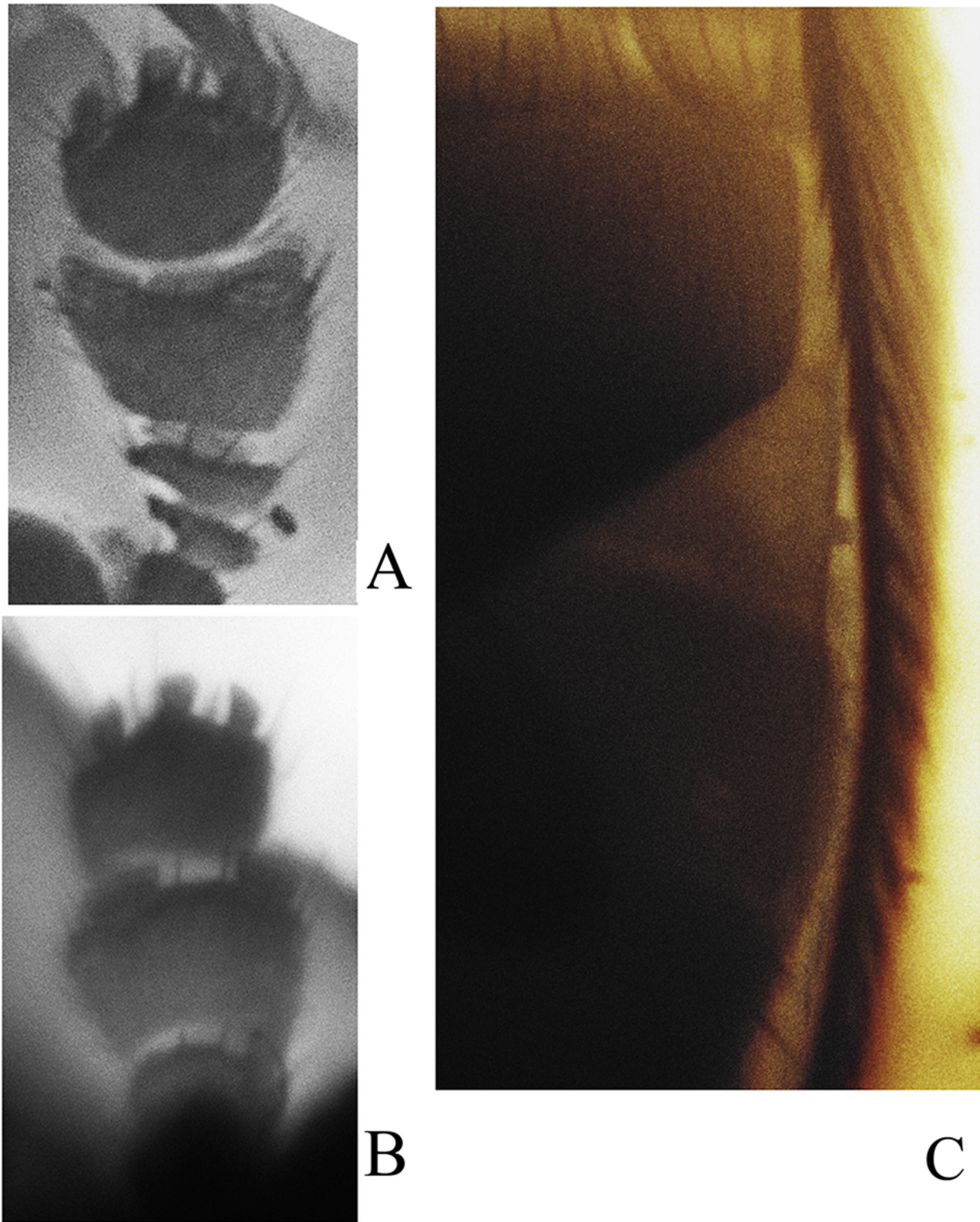


Fig. 4. CLSM images (A, B – maximum intensity projections, C – combined Orthoslice & Voltex pseudovolume image) of *Ptisma zasukhae* gen et sp. nov., holotype, NBS-2E (Lebanese University, Department of Natural Sciences, Fanar); Lower Cretaceous, Lebanese amber. Length of body 0.59 mm. **A.** Right antennal club with columella-like sensilla on subtruncate apex of ultimate antennomere and sensilla like short elliptic cylinders on apex of antennomeres 8 and 9, ventral. **B.** Left antennal club with above mentioned sensilla, ventral. **C.** Right part of femoral plate and abdominal base, ventral.

medium-sized body have hypognathous head, large pedicel, conjoined metacoxae with the femoral plates, spined posterior legs with strong spurs, and sometimes the 4-4-4 tarsi with long and simple metatarsomeres. Still, they differ from *Ptisma* gen. nov. in: different structure of the head with large and dorsally placed

eyes and another type of mouthparts, long prosternum, widely separated procoxae and suboval mesocoxae, short metaventricle, strongly oblique metacoxae, elytral epipleura wide at least at base, abdomen with five ventrites, etc. The jumping recent buprestids *Anthaxomorphus* Deyrolle, 1864 and *Endelomorphus* Bílý, 2007

(Aphanisticini Jacquelin du Val, 1859) have a small body with a very thick metafemora, but their metatibiae are without very strong spurs and stout apical setae, etc. (Williams and Weir, 1992; Bílý, 2007). Other jumping buprestids (Furth and Suzuki, 1992) do not show special structural differences from non-jumping relatives (as a rule with larger body, like members of *Hippomelas* Laporte et Gory, 1837 (Chrysochroini Laporte, 1835) or *Chalcogenia* Saunders, 1871 (Melanophilini Bedel, 1921)) while others have at least the enlarged metafemora (as a rule with medium or small body size, like *Pseudagrilus* Laporte, 1835 (Agrilini Laporte, 1835)). The numerous buprestids of the genera *Sambus* Deyrolle, 1864 (Agrilini) and particularly *Anthaxia* Eschscholtz, 1829 (Anthaxiini Gory and Laporte, 1839) with medium or rather small body size studied by Furth and Suzuki (1992) as jumping, demonstrate wide ranges in development of metafemurs. In the latter many species are without special peculiar structures, although some species have enlarged metafemora.

Some tenebrionoids, representatives of Melandryidae Leach, 1815, Mordellidae Latreille, 1802, Scraphiidae Mulsant, 1856, Ripiphoridae Gemminger in Gemminger & Harold, 1870, may have similar structures, at least of the metatibiae with both dense stout setae and very long spurs at apex, simple segments of metatarsi, large and obliquely transverse mesocoxal cavities open laterally, flat coxae, enlarged metafemora and wide metepisterna widening anteriorly. Nevertheless, these members of the mentioned families differ from *Ptisma* gen. nov. in the: larger body which is elongate and curved from lateral view, usually securiform ultimate maxillary palpomere, 11-segmented antennae of very different structure, convex underside, large metacoxae without femoral plates, five ventrites of abdomen, 5-5-4 tarsi with different structure of meso- and metatarsomeres, and other distinguishing characters. Crowson (1981) reported that a spring behaviour for *Propalticus* Sharp, 1879 did not demonstrate any clear adaptation in structure for jumping; however, many cucujoids from different families with large metafemora are not considered as jumpers (Propalticidae Crowson, 1952). Some similarities in body shape and size of some sclerites can be found between Ptismidae fam. nov. and Corylophidae LeConte, 1852, including sometimes 10-segmented antennae with large pedicel and distinct club, short prosternum, transverse mesocoxal cavities, metepisterna widening anteriorly, fringed hindwings, 4-segmented tarsi etc. In contrast to Ptismidae fam. nov., Corylophidae LeConte, 1852 are characterized by the: short and thick palpomeres, widely separated meso- and metacoxae, lack of femoral plates of metacoxae, abdomen never with seven ventrites (derivate of sternite 2 completely fused with that of sternite 3), raised elytral epipleura, tibiae never with large spurs and stout apical setae, lobed tarsomeres 1–3 and very short tarsomere 3, etc.

The body-size, general appearance, large metacoxal femoral plates, clubbed antennae, short prosternum, metepisterna widening anteriorly, mesocoxal cavities open laterally, conjoined metacoxae, fringed hindwings of the new species herein described can be compared with representatives of Sphaeriusidae Erichson, 1845 (Myxophaga). Nevertheless, Sphaeriusidae are easily distinguished by: the subspherical body, shorter head with smaller oval eyes and short frons, labrum slightly exposed (if exposed) from under frons and other mouthparts, abdomen with three ventrites, very small trochanters, and short 3-3-3-tarsi.

The structural features of legs of *Ptisma* gen. nov. can be compared also with those of jumping chrysomelids [Galerucinae Latreille, 1802 and Eubaptini Bridwell, 1932 (Bruchinae Latreille, 1802)] and weevils [Choragini Kirby, 1819 (Anthribidae Billberg, 1820); Acalyptini C. Thomson, 1859 and Ceratopodini Lacordaire, 1863 and Ramphini Rafinesque, 1815 (Curculioninae Latreille, 1802); Lechriopini Lacordaire, 1865 and Zygopini Lacordaire, 1865

(Conoderinae Schoenherr, 1833) and some tribes of Ceutorhynchinae Gistel, 1848] (Furth and Suzuki, 1990, 1992; Morimoto and Miyakawa, 1996; etc.). All last mentioned phytophagous groups have the enlarged metafemora, however, the long and strong spurs are known only in chrysomelids while in weevils only the weak spurs and rather thin apical setae are found. Instead of tibial spurs some of these beetles frequently have a strong extension of inner edge of metatibiae (like that in alticine *Psylliodes* Berthold, 1827 or in some Ramphini). Nonetheless, these cucujiform groups are very distinct from this fossil in the structure of many organs of their head, mouthparts, thorax, unfringed hindwings, different type of tarsi (usually pseudoquadrimerous with lobbed tarsomeres 1–3), etc.

If the structural features, which could be associate with adaptation for jumping, are skipped, it is possible to estimate to trace relationship of Ptismidae fam. nov. to any group of the order by drawing attention to the abdomen with free (not connate) seven ventrites and the mesocoxae open laterally, not conical and not strongly oblique. This set of features of the general body structure is rather stable and important, although independent progressive increase in the number of abdominal ventrites as a consequence of pedomorphous transformations (larvalization of adults) can be traced in different groups mostly among the infraorders Staphiliniformia (including Scarabaeoidea sometimes regarded as a separate infraorder Scarabaeiformia) and Elateriformia. The only exception of possession of the mentioned set beyond Staphiliniformia and Elateriformia, is the dermestid *Egidyella* Reitter, 1899 (Bostrichiformia; Egidyellini Semenov-Tian-Shanskij, 1915) with the: medium-sized body, metepisterna widening anteriorly, abdomen with seven abdominal ventrites, contiguous metacoxae with femoral plates moderately developed; but in contrast to *Ptisma* gen. nov., it has a head with simple ocellus, long 11-segmented antennae without club, separated mesocoxae, moderately raised femoral plates of metacoxae, 5-5-5-tarsi, etc. Some similarities in thoracic sclerites of the new family and some other Dermestidae Latreille, 1807 are expressed in the structure of metepisterna and metacoxae with femoral plates, and in frequently clubbed antennae. In contrast to the new family, the latter is characterized by 11-segmented antennae (except *Thylophorus* Motschoulsky, 1839: Thelydriini Semenov-Tian-Shanskij, 1909 with antennae bearing only nine antennomeres and not forming a club), five abdominal ventrites (except anelytrous females of *Thylophorus* with eight ventrites), and 5-5-5 tarsi, etc. Besides, none of dermestids has so small body, so large femoral plates of metacoxae, and tibiae and tarsi as those in *Ptisma* gen. nov.

The elateriform groups with seven abdominal ventrites (males of Drilidae Lacordaire, 1857 and elaterid Cebrioninae Latreille, 1802) have also the metepisterna widening anteriorly but differ from the new genus in the: markedly larger and elongate body with different sculpture of integument, short anterior part of the frons, oval eyes, filiform or pectinate antennae with comparatively small pedicel, pronotum not widening posteriorly, narrow femora and tibiae, at most a weak femoral plates of metacoxae and 5-5-5 tarsi. Besides, Drilidae are distinct from the new genus in the: antennal insertions located laterodorsally and visible anterodorsally, smaller mesocoxae, narrow femora and tibiae without spurs and thick apical setae, lobed tarsomere 4, etc.; and Cebrioninae are distinct also in the: very convex underside, prothorax without wide lateral dilatations, convex and not strongly shortened prosternum, etc.

Some scarabaeid representatives of Trichiini Fleming, 1821 (Cetoniinae Leach, 1915) with seven abdominal ventrites, similar metepisterna, and large mesocoxae open laterally. Most other scarabaeoids differ from the new genus in the: much larger body with usually rather convex underside, head with wide frons and “frontoclypeal suture”, usually smaller suboval eyes and

characteristic lamellate antennal club, convex and not strongly shortened prosternum, lack of femoral plates of metacoxae, much shorter trochanters (not “large and mobile” type), another type of tibial structure, 5-5-5 tarsi, etc.

Ptisma gen. nov. shares few similarities with the groups of the superfamilies Hydrophiloidea and Histeroidea in the clubbed antennae and the wide metepisterna etc., however, they differ by the: moderately long or slightly short prosternum, abdomen with five ventrites (very rarely six) and its distal segments not retracted inside previous ones, different type of structure of the trochanter and tibiae, 5-5-5 or 5-5-4 and very rarely 4-4-4 tarsi. Groups of Hydrophiloidea also differ from *Ptisma* gen. nov. in the head with wide frons showing “frontoclypeal suture” and maxillary palpi often longer than antennae; the underside often with fine and dense (hydrofuge) pubescence. Members of Histeroidea differ from *Ptisma* gen. nov. by the usually geniculate antennae with compact club, the separated coxae of all pairs and the abdomen only with five tightly articulated ventrites.

On miniaturization

It is noted that fringed hindwings occur in different unrelated groups with small body size, at least in *Nossidium* Erichson, 1845 (Ptiliidae), some pselaphines, myxophagans, clambids, throscids, corylophids (Kirejtshuk & Azar, 2008; Kovalev & Kirejtshuk, 2013; etc., including the information from S. Nomura and P. Jałoszyński, pers. comm.). Kurbatov (pers. comm.) found that the level of the hindwing fringing in different pselaphines depends upon body-size; longer fringe occurs among the smaller species. It seems to be one of the regular structural transformations as a result of miniaturization that is manifested in different organs. However, in many other cases the characters of very small beetles are not evident whether any of them appeared as a consequence to miniaturization or other reason. The studies on comparative morphology of small beetles and their development make it possible to conclude that the organs less important for feeding, locomotion and reproduction are more subject to transformations associated with decreasing of body size (Grebennikov, 2008; Polilov and Beutel, 2009, 2010; Lawrence et al., 2011; etc.). As a result, progressive miniaturization of the related groups could bring a considerable difference in them depending on even not great distinction in ecological circumstances and mode of life of these groups. Kirejtshuk and Poinar (2013) proposed that this explanation can be applied on great differences between the families of Myxophaga. Probably such processes occurred in evolution of staphylinoids with small body showing a mosaic in distribution of characters. In addition, it could be proposed that the parthenogenesis known among small and medium-sized staphylinoids (Coiffait, 1984; Taylor, 2012; etc.) could promote quick and more mosaic diversifications and strengthen effects of miniaturization.

On probable bionomy of *Ptisma* gen. nov.

As to bionomic features of the new species, it can be admitted that it had like other probable relatives of Staphyliniformia with small body, a mode of life inside substrate or hidden habitats. The unique structure of sensilla on three apical antennomeres of *Ptisma* gen. nov. (Figs. 4A, 4B) can be used for an assumption of some analogies with the mode of life of psephenines. A development of structural adaptations similar to those in jumping beetles could be explained by some probable similarities in a peculiar behaviour of the new species. However, it is still unclear why such adaptations affected both mid and posterior legs of the new species and not only the posterior ones as in other jumping beetles.

On probable phylogenetic relation of *Ptisma* gen. nov.

Thus, even if the position of Ptismidae fam. nov. is unclear, its probable placement could be within or near the superfamily Staphylinioidea taking into consideration that many members of this group demonstrate a high rate of similarities with the new genus in different parts of the body.

Staphylinioidea is one of the oldest polyphagan superfamilies and the earliest staphylinid-like prints were obtained from the Uppermost Permian of Babii Kamen' (Western Siberia), where also the earliest polyphagan hydrophiloid, elateroid and byrrhid forms (Volkov, 2012; Ponomarenko et al., 2014) as well as the earliest adephagan were recorded (Ponomarenko and Volkov, 2013), although the oldest representative attributed to the Staphylinidae was described from the Upper Triassic of Cascade near Martinsville (Virginia) (Chatzimanolis et al., 2012) after Gore (1988) and Fraser et al. (1996) on three specimens of staphylinids from Culpeper Basin (Virginia). Chatzimanolis et al. (2012) supposed that the origin of the family Staphylinidae at least is hypothesized in the beginning of the Middle Triassic. Nevertheless, till the late Mesozoic this infraorder had been quite rare in deposits, and during the Jurassic and Cretaceous the number of its representatives had been gradually increasing (Kirejtshuk and Ponomarenko, 2015). The staphylinoids with small body are known mostly from amber. Their earliest representatives were recorded from the Lower Cretaceous Lebanese amber (Crowson, 1981; Poinar, 1992; Lefebvre et al., 2005; Kirejtshuk and Azar, 2013) and there are known as well from the Cretaceous Alawa (Spain), Burmese and New Jersey amber (O'Keefe et al., 1997; Clarke and Chatzimanolis, 2009; Chatzimanolis et al., 2010; Peris et al., 2014; etc.). The traditional interpretation of a silphid-like ancestor of the recent staphylinoids had been discussed during long time. Jeannel and Jarrige (1949) placed the family Silphidae into “section Brachyptera” including also the groups currently united into the Staphylinidae. Subsequently Grebennikov & Newton (2012) put Agyrtidae and Leiodidae in their analysis as out-groups to the pair Silphidae + Staphylinidae. The earliest silphid fossils have been recorded from the Middle Jurassic of Daohugou (Inner Mongolia) (Cai et al. 2014) [*Sinosilphia punctata* Hong et Wang, 1990 described as a member of Silphidae from Lower Cretaceous of Laiyang (Shandong) scarcely belongs to both Silphidae and Staphylinioidea because of its long and not clubbed antennae and its rather short pronotum – this taxon should be regarded without family attribution till a further re-examination], while the earliest Leiodid-like *Mesagyrtoides* Perkovsky, 1999 is known from the Upper Jurassic of Sharteg (Mongolia) and earliest agyrtid-like *Ponomarenkia* Perkovsky, 2001 has been found in the deposits from the Lower Cretaceous of Turga (Transbaikalia) (Kirejtshuk and Ponomarenko, 2015)

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