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Ancient roaches further exemplify 'no land return' in aquatic insects

Peter Vršanský [a,b,c,d,1], Hemen Sendi [e,*,1], Danil Aristov [d,f,1], Günter Bechly [g], Patrick Müller [h], Sieghard Ellenberger [i], Dany Azar [j,k], Kyoichiro Ueda [l], Peter Barna [c], Thierry Garcia [m]

[a] Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, 845 06 Bratislava, Slovakia
[b] Slovak Academy of Sciences, Institute of Physics, Research Center for Quantum Information, Dúbravská cesta 9, Bratislava 84511, Slovakia
[c] Earth Science Institute, Slovak Academy of Sciences, Dúbravská cesta 9, P.O. BOX 106, 840 05 Bratislava, Slovakia
[d] Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, 117868 Moscow, Russia
[e] Faculty of Natural Sciences, Comenius University, Ilkovičova 6, Bratislava 84215, Slovakia
[f] Cherepovets State University, Cherepovets 162600, Russia
[g] Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191 Stuttgart, Germany
[h] Friedhofstraße 9, 66894 Käshofen, Germany
[i] Bodelschwinghstraße 13, 34119 Kassel, Germany
[j] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, PR China
[k] Lebanese University, Faculty of Science II, Fanar, Natural Sciences Department, PO Box 26110217, Fanar - Matn, Lebanon
[l] Kitakyushu Museum, Japan
[m] River Bigal Conservation Project, Avenida Rafael Andrade y clotario Vargas, 220450 Loreto, Orellana, Ecuador

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ABSTRACT

Among insects, 236 families in 18 of 44 orders independently invaded water. We report living amphibiotic cockroaches from tropical streams of UNESCO BR Sumaco, Ecuador. We also describe the first fossil aquatic roach larvae (6 spp.; n = 44, 1, 1, 1, 1, 1) from the most diverse tropical Mesozoic sediments (Middle Jurassic Bakhar Fm in Mongolia, Kimmeridgian Karabastau Fm in Kazakhstan; Aptian Crato Fm in Brazil), and the Barremian Lebanese and Cenomanian Myanmar ambers. Tropic-limited occurrences are trophic- (biomass/litter-fall), structural- (diversity) and also abiotic-factor-dependent (high temperatures). Diverse Paleozoic aquatic eoblattids are here (re)described from the lower Permian sediments of Elmo, U.S.A. and Chekarda, Russia. They competed with true cockroaches to reach water prior to the Mesozoic. Due to different evolutionary rates or periodical changes in water characteristics, non-adapted terrestrial insects repeatedly invaded the aquatic realm with well adapted hydrobionts. Obscurely, most aquatic lineages still survive. In contrast with Crustacea, aquatic-terrestrial reversal is absent. A single principal lineage, namely of moths, ancestral to butterflies (origination of modern insects from ephemerans and dragonflies is questioned), possibly evolved from insects with aquatic immature stages, and none from aquatic adults. The rest of the orders are terrestrial-derived. The proposed reason for the lack of land return is the character of numerous aquatic adaptations related to reductions, which are unlikely to be resuppressed. The aquatic insect family/terrestrial insect family ratio over time reveals a sharp rise from the Late Carboniferous to Late Triassic followed by lasting stability. Diversification of aquatic insects seems consistent with a 62.05 ± 0.02 Ma periodicity.

1. Introduction

The aquatic environment might have yielded life itself (Morris and Whittington, 1979; Schopf, 2002). While it is difficult to discern marine and freshwater biomes down to the early Paleozoic period (Ponomarenko, 1996), freshwater aquatic insects or insects with aquatic immatures (Rasnitsyn, 2003) are often considered ancestral (Wootton, 1988). Originally, aquatic orders include dragonflies, ephemeras, caddisflies and possibly extinct Eoblattida, Nakridletia, Chresmodida and Coxoplectoptera (Pritchard et al., 1993; Grimaldi and Engel, 2005; Staniczek et al., 2011; Vršanský et al., 2010; Zhang et al., 2017). In 179 families, the aquatic transition occurred in immature stages; 50 families are aquatic in all stages, while 7 families have aquatic adults (Sinitshenkova, 2002; Lancaster and Downes, 2013). The aquatic mode of orthopteroid insects is limited to a few aquatic and semiaquatic orthopterans (see Derka et al., 2016) and a few groups of cockroaches (see also Figs. 1–3; Bell et al., 2007). It is generally agreed that an aquatic habit is secondary for some orders, namely Hemiptera, Diptera, and Coleoptera.

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* Corresponding author.
E-mail addresses: geolvrsa@savba.sk (P. Vršanský), sendi1@uniba.sk (H. Sendi), guenter.bechly@smns-bw.de (G. Bechly), danyazar@ul.edu.lb (D. Azar), ueda@kmnh.jp (K. Ueda), geolbarn@savba.sk (P. Barna).
[1] These authors contributed equally to this work.

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These orders invaded water multiple times (at least 14 times in the semiaquatic Hemiptera, Gerromorpha (Andersen, 1995)) and some quite recently, such as some lepidopteran species in the genus *Hyposmocoma* that began to invade water only approximately 6 Myr ago (Kawahara and Rubinoff, 2013). The aim of the present study was to describe the first extinct aquatic cockroaches, revise their aquatic relatives among the order Eoblattida and discern their ecological, paleogeographical and phylogenetic context.

2. Material and methods

Living data were extracted and photodocumented in Ecuador (Rio Bigal Conservation Area, buffer zone, UNESCO Biosphere Reserve Sumaco - http://bigalriverbiologicalreserve.org/en/).

Burmite amber specimens from Hukawng Valley of Kachin Province (Kania et al., 2015) were deposited in NIGPAS Nanjing; SNSM Stuttgart and NHM Bratislava. Cenomanian age (98.8 ± 0.6 million years) was revealed by U-Pb dating of zircons from volcanoclastic matrix (Shi et al., 2012). Extrapolation reveals 10,540–26,350 already collected insects. Additionally, ˜3500 specimens are reported in AMNH (Grimaldi and Ross, 2004) and cockroaches constitute 2–5% of the Myanmar insects collected (Grimaldi et al., 2002; Ross et al., 2010). Recent data reveal 4000 cockroach specimens (Vršanský and Wang, 2017; Li and Huang, 2018).

The Lebanese amber specimen described herein was collected from the rich Early Cretaceous locality Hammana/Mdeirij, Caza Baada, Mouhafazit Jabal Libnen, Lebanon. The amber occurs here in different geological levels in 250 m thick sandstone and clay layers. One immature specimen has been preserved, and is deposited in the Lebanese University, Faculty of Sciences II, Lebanon. Almost 60% of the entomofauna trapped in amber of the Hammana deposit are Diptera: Nematocera, mainly of the families Chironomidae, Ceratopogonidae, Psychodidae and Phlebotomidae, and are characteristic of a warm, hot and dense (sub)tropical forest (Azar et al., 2003). Cockroaches constitute, curiously, only 0.4% of all inclusions (mostly arthropods) in Lebanese amber. Amber from this locality is ascribed a Barremian age (Maksoud et al., 2017; Vršanský et al., 2017). Palynology also provided information on the paleoclimate: it was probably moderate to hot and very wet (of tropical or subtropical type) (Azar et al., 2003; see also Sendi and Azar, 2017; Podstrelena and Sendi, 2018 for cockroach data).

The Karatau specimens collected in the Kimmeridgian Upper Jurassic sediments of the Karabastau Formation in Kazakhstan (Rohdendorf, 1968) were collected and deposited in the Paleontological Institute, Moscow (PIN). Several cockroaches were described from this locality by Vishniakova (1968).

Aptian (~120 Ma) limestones of Chapada do Araripe Nova Olinda Member (Crato Formation), NE Brazil contain gymnosperms and angiosperms, fish, anurans, turtles, lizards, crocodiles, pterosaurs and birds located 10°–15°S within the tropics with ~26% of arthropod specimens represented by cockroaches (n = 3651, Lee, 2016) (Bechly, 1998; Dittmann et al., 2015; Martill et al., 2007); at Taphonomic Stage I, like 79.2% of all cockroaches (Martins-Neto et al., 2006). The studied specimens were deposited in Murata Museum, Japan and Wyoming Dinosaur Center, U.S.A.

The sediments of Chekarda were formed in a lagoon influenced by fresh water in a delta, with a lack of autochthonous inhabitants (except for undescribed fishes inhabiting both marine and freshwater - Sharov, 1999) with *Sylvonympha* and *Gurianovella* present (Zhuzhgova et al., 2015).

One eoblattid described herein was collected from Elmo, Dickinson County, Kansas, U.S.A. (Tasch, 1964). Insects collected in this locality in the deposits of Wellington Formation (Sumner Group, Lower Leonardian) are considered to correspond to the Lower Kungurian deposits of the Lower Permian (Sawin et al., 2008). The localities of the Wellington Formation (Elmo and Midco in Oklahoma) are the richest fossil insect localities of the Paleozoic. In total more than 23,000 insect fossils have been collected (Beckemeyer, 2000), with 21 orders, 53 families, 106 genera, and 194 species identified (Beckemeyer and Hall, 2007). The diversity of Eoblattida in this place is moderate.

Photographs of the amber samples were taken using a Zeiss SteREO Discovery V16 microscope system and Zen software and Olympus SZH stereomicroscope attached to an Olympus 5060 camedia 5.1Mp camera. Lighting was provided by a fiber-optic illuminator with plane polarized light and a fluorescent style ring light to capture cuticular details. Incident and transmitted light were used simultaneously. Images are digitally stacked photomicrographic composites of approximately 40 individual focal planes obtained using Combine ZP free software. Stacked photomicrographs were merged using Adobe Photoshop.

3. Results

3.1. Systematic paleoentomology

Order Blattaria Latreille, 1810
Superfamily Corydioidea Saussure, 1864
Family Liberiblattinidae Vršanský, 2002

Type species: *Liberiblattina ihringovae* Vršanský, 2002. Upper Jurassic Karabastau Formation.

Composition: see Vršanský (2002), Martin (2010), Barna (2014), Vršanský et al. (2018a, 2018b).

Geographic range: Cosmopolitan.

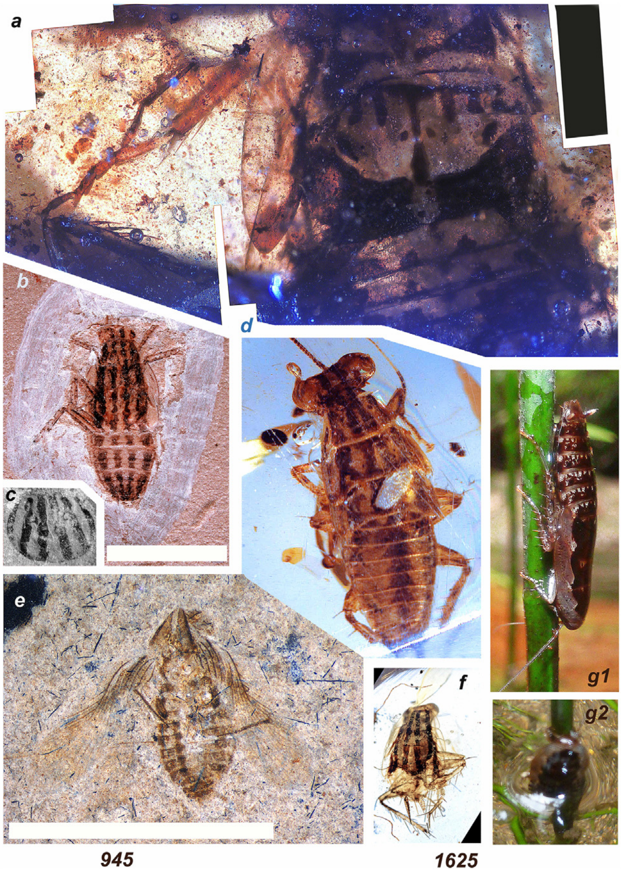

Fig. 1. Aquatic/amphibiotic cockroaches in sedimentary, amber and living record: (a) *Cryptoblatta aquatica* gen. et sp. n. from Lebanese amber (LU 444); (b) undescribed liberiblattinid cockroach (Murata private collection) from Crato Fm sediments; (c) isolated pronotum of a liberiblattinid cockroach (Bakhar specimen from PIN collection); (d) undescribed liberiblattinid cockroach with unusual adaptations (SNM Z 38916) from Burmite; (e) adult female holotype and immature of *Hydrokhoohydra aquabella* sp. n. from Karabastau Fm sediments (PIN 2452/945, abdominal width 2.6 mm, PIN 2997/1625); (f) undescribed possibly aquatic liberiblattinid cockroach (SNM Z 38619) from Burmite; (g) living undescribed blaberid cockroach from UNESCO BR Sumaco rainforest in Ecuador emerging from water. Horizontal scale 10 mm, vertical scale 1 mm.

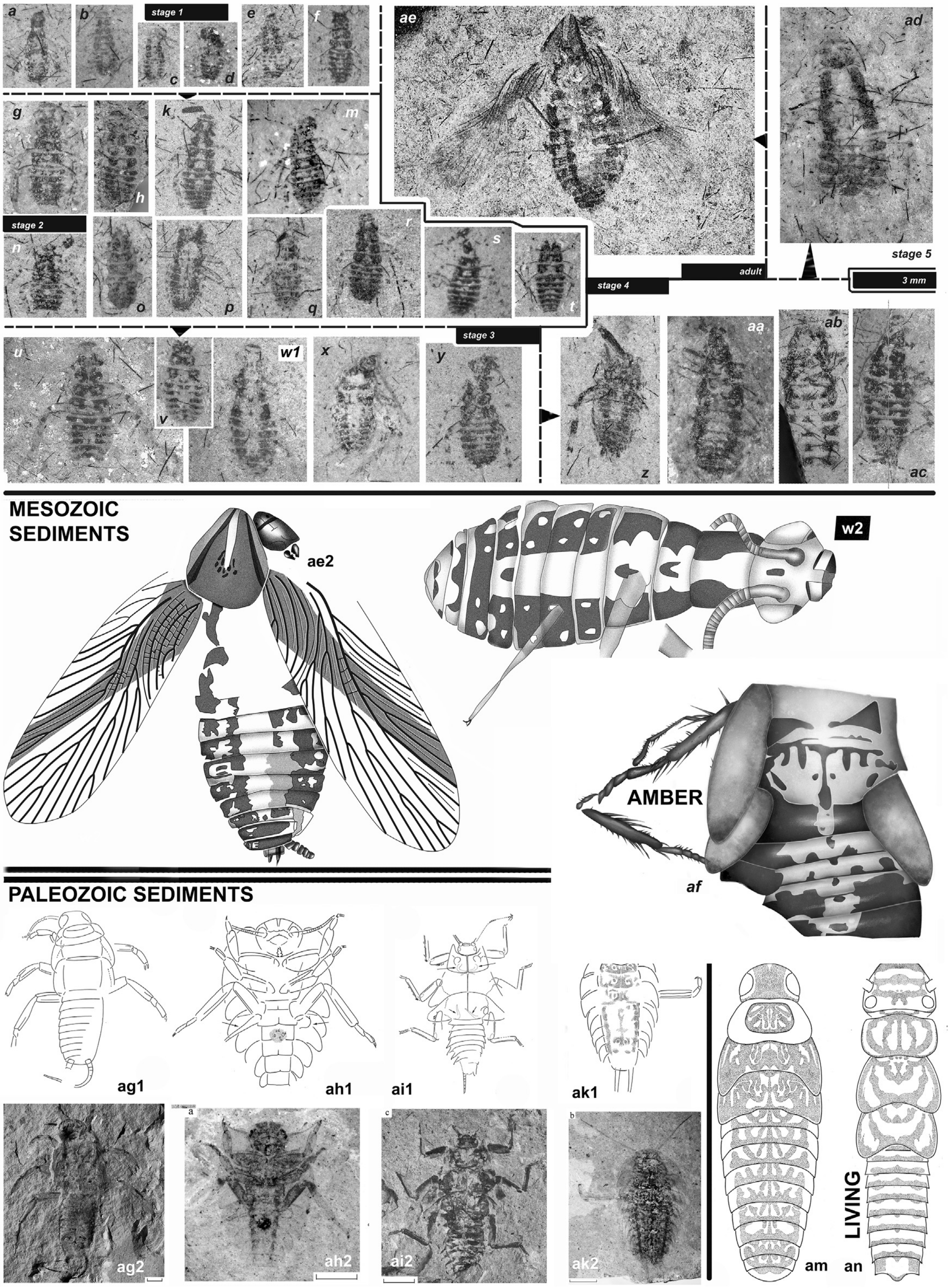

Fig. 2. Jurassic amphibiotic and/or aquatic cockroach *Hydrokhoohydra aquabella* sp. n. (a–ae, with w1–2 representing illustrated third stage); *Cryptoblatta aquatica* sp. n. (af); eoblattids (ag–am) and a plecopteran (an). Kimmeridgian Upper Jurassic sediments of Karabastau Formation, Kazakhstan with 5 immature stages and the adult female holotype (PIN; Stage 1: 2239/540; 2384/1274; 2239/327, 344; 2997/1635; 2452/239; Stage 2: 2239/692; 2997/1632; 2239/333; 2784/789; 1739/136; 2239/318, 338, 384, 366; 2452/234; 2066/541; Stage 3: 2239/316, 331; 2997/1625, 41; 2239/364; Stage 4: 2384/194; 2066/515; 2997/154; 2239/323; Stage 5: 2784/982; Adult female: 2452/945). All to scale (3 mm); (af) *Cryptoblatta aquatica* gen. et sp. n. (holotype LU 444) Lebanese amber; (ag) *Elmonympha carpenteri* sp. n. (holotype MCZ 3622) Kungurian Lower Permian of Elmo, Kansas, U.S.A. (scale 1 mm); (ah) *Gurianovella sylphidoides* Zalessky, 1939 (PIN 4987/51) (scale 3 mm); (ai) *Sylvonympha tshekardensis* Novokshonov and Paňkov, 1999 (PIN 4987/94) (scale 3 mm); (ak) *Czekardia blattoides* Martynov, 1940 (PIN 118/139) (scale 1 mm); (am) *Kirkorella mira* Zalessky, 1939 (Atactophlebiidae), reconstruction (PIN 118/104; PIN 1700/3696, 3698). Kungurian of Chekarda in Russia; (an) *Agnetina capitata* Pictet, 1841, living stonefly from Elmo, U.S.A. Origs.

Chronostratigraphic range: Early Jurassic - Late Cretaceous.

Diagnosis (modified after Vršanský, 2002): Main veins and intercalaries wide. Forewing with regular venation with terminal dichotomisation limited to the clavus. SC field narrow with SC long and branched. R field narrow with R ending prior to wing apex. M and Cu sigmoidal, M reaching wing apex. CuP strongly curved. Anal veins branched mostly in apical third. Tarsi with large arolia.

Hydrokhoohydra Vršanský, gen. n.

Type species: *Hydrokhoohydra aquabella* from Karabastau Fm described below.

Composition: undescribed species (immatures preserved) from Crato, Bakhar, Burmite, Lebanese amber.

Geographic range: Laurasia and Gondwana, circumtropical.

Stratigraphic range: Late Jurassic (Kimmeridgian) - Late Cretaceous (Cenomanian).

Differential diagnosis: differs from all representatives of the family in having a triangular pronotum in the adult stage, extremely wide FW costal field and extremely expanded FW M (while R is greatly reduced with 8–12 veins at margin). The extremely elongated clavus with reduced number of veins and the colored body of immatures are also unique. Notably, only the adult stage has the head covered by the pronotum.

Description: as for species.

Derivation of name: after Hydrokhoös (Greek name for Aquarius) and the hydra (Greek mythological water beast of Lerna, Argolida, which protected an entrance to the underworld). Gender feminine.

Remarks: The genus can be categorised within Liberiblattinidae on the basis of the characteristic head coloration, wide forewing intercalaries, branched Sc in very wide costal field, and expanded M. Autapomorphic wide costal field apparently relates to the autapomorphically narrow fore margin of pronotum. The extremely narrow clavus is characteristic of genera close to mantodean derivation and also for Eadiidae and Manipulatoridae (Vršanský and Bechly, 2015). The wide M of the holotype is a stochastic non-taxonomic character appearing due to compensation for reduced R in one of the wings. Fine cerci are autapomorphic - likely due to aquatic habits. The head is unusually preserved directing partially forwards in the holotype adult female, but also in several immature individuals (Figs. 2a, m, q, s), which might indicate partial prognathy.

Hydrokhoohydra aquabella Vršanský, sp. n.

Holotype: PIN 2452/945. Deposited in Paleontological Institute, Moscow.

Type horizon: Kimmeridgian Karabastau Fm.

Type locality: Galkino, Karatau, Kazakhstan.

Additional material (in addition to 27 specimens in label of Fig. 2): STAGE 1: 2452/355 abdomen 0.8 mm wide; 2452/575 1 mm; 2239/340 2.8 mm; 2239/341 0.9 mm; *STAGE 4*: 2465/947 5 mm; 2239/339 5.5 mm; unlabeled 5.4 mm; 2239/320 5.2 mm; 2997/4385 5.4 mm; 2339/922 6 mm; *ADULT*: 2384/186 a forewing; 2997/4368 body fragment.

Description: Immature stage 1 (Fig. 2a–f): Very large for initial instar, elaborate coloration already formed. Abdomen width 0.8–1.15 mm. Immature stage 2 (Fig. 2g–t): Abdomen width 1–1.6 mm. Immature stage 3 (Fig. 2u–y, and also drawing 2w2): Abdomen width 1.5–1.73 mm. Immature stage 4 (Fig. 2z–ac): Coloration most differentiated among all stages. Legs apparently natatorial. Abdomen width 1.7–2 mm. Immature stage 5 (Fig. 2ad): The sole preserved specimen has the head directed forwards, more globular than in the adult and not covered by pronotum. Coloration simplified compared to previous instars, wing pads not distinct. Abdomen width ca. 2.2 mm. Adult (Fig. 2ae1–2): Abdomen width ca. 2.6–2.8 mm. Head large, elongated, globular (ca. 1.3/0.6 mm), dark with black pattern apparent at base. Pronotum triangular, with longitudinal medial stripe and two lateral longitudinal dark stripes, and also with central puncturation. Forewing narrow (ca. 6–6.2 mm/2.3 mm; area 9.6 mm^2), but with parallel margins and oval wide apex (with oblique dark stripe). Costal field extremely wide, but not very long (shorter than clavus) with branched (3) Sc. RS barely differentiated, whole R system highly reduced with 8–12 veins at margin. M in 2 cases highly reduced (4–5) while in one case also reduced (7), but compensating reduction in R. CuA symmetrical with 7–10 veins. CuP slightly curved, clavus very long, reaching nearly half of the wing. A branched (4–7). Body standard, wide, with unique disruptive coloration with sharp edges (see Fig. 2ae). Cerci multisegmented, segment not wide. Styli not observed on a female. Ovipositor protruding externally, short, but very strong and sharp.

Remarks: The immatures were sorted to the above size groups (instars 1–5) on the basis of general habitus (see all-to-scale Fig. 2). The coloration pattern is too small for representation of an aposematic signal and is regarded as cryptic. The forewing areas are consistent with the exponential function of forewing area averages in Oružinský and Vršanský (2017).

Derivation of name: after *aquabella* (water-athlete). Gender feminine.

Cryptoblatta Sendi et Azar, gen. n.

Type species: *Cryptoblatta aquatica* Sendi et Azar, sp. n. described below from Lebanese amber; by monotypy.

Differential diagnosis: The genus is categorised within Liberiblattinidae based on the large arolium, medium- sized body, narrowed pronotum, coloration of wing pads (present also in descendant but modified beetle-like and wasp-like Umenocoleoidea). It differs from all known representatives by the elaborate coloration and modified legs.

Description: as for species.

Remarks: The coloration is similar to an aposematic pattern, but is disruptive in water, as in long-legged insects such as phantom crane flies Ptychopteridae and some mosquitoes which have banded legs that might render the insect less conspicuous (Adler, 2009; see also Fig. 2am–an). The extremities are characteristic of an aquatic lifestyle, and along with the adjacent spurs are partially adapted for swimming (autapomorphic within cockroaches).

Derivation of name: after *crypsis* (the coloration pattern on this specimen) and Blattaria. Gender feminine.

Cryptoblatta aquatica Sendi et Azar, sp. n. (Fig. 2af).

Holotype: Nymph (final moult - preadult stage), LU444, Azar Collection deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

Type locality: Hammana/Mdeirij, Caza Baada, Mouhafazit Jabal Libnen, Lebanon.

Type Horizon: Barremian.

Description: Maxillary palp 1.1 mm long (segments 1–3 ca. 0.4 mm; 0.5 mm; 0.3 mm) and laterally densely covered by sensilla chaetica. Body width ca. 2 mm, with distinct slightly asymmetrical contrast coloration. Prothorax large (length/width 1.4/1.7 mm), lightly pigmented with a complex contrasting dark pattern. Metathorax large, mostly dark-colored. Abdomen also robust, with color patterns. Width of black coloration increases towards apex of abdomen. Fore- and hindwing pads fully developed, rigid, elongated and transparent with dark tip. Venation invisible. Left forewing pads length/width 2.0/0.4 mm. Left hindwing pads length/width 1.3/0.4 mm. Right hindwing pads length/width 1.5/0.4 mm. The extremities natatorial/cursorial; massive, very wide, tibia laterally densely covered with long strong spurs adjacent to tibia and dorsally with irregularly placed tiny chaetica. Fore femur length/width 1.6/0.4 mm. Fore tibiae length/width 1.1/0.2 mm and mid tibiae length/width 0.9/0.2 mm. Fore tarsus 1.1 mm long. First tarsomere length/width ca. 0.5/0.1 mm, second 0.2/0.1 mm, third 0.2/0.1 mm, fourth 0.2/0.1 mm, fifth 0.3/0.05 mm. Mid tarsus 1.0 mm long. First tarsomere length/width ca. 0.4/0.1 mm, second 0.1/0.1 mm, third 0.1/0.1 mm, fourth 0.1/0.1 mm.

Remarks: Amber piece is honey-colored, with a few irregular orange-brown spots, partially opaque with frequent contamination and a sharp fractured area.

Derivation of name: after *aquaticus*, the Latin word for ‘found in water’. Gender feminine.

Character of preservation: complete cockroach without head, antennae, labial palps, left maxillary palp, compound eyes, ocelli, mandibles, maxilla, labium, labrum, coxa's, trochanters, right mid-, hindfemur, left fore-, mid-, hindfemur, right hind tibia, left fore-, mid-, hind tibia, right hind tarsus, left fore-, mid-, hind tarsus, right mid tarsus- fifth segment, pretarsus, tarsal claws, arolium, cerci; the abdomen consists of 4 segments due to post-burial processes.

Order Eoblattida Handlirsch, 1906

Family incertae sedis

Elmonympha Aristov, gen. n.

Type species: *E. carpenteri* sp. n.; by monotypy.

Differential diagnosis: The new genus is categorised within Eoblattida on the basis of resemblance to *Kirkorella* and *Gurianovella*. Paranotal circle differentiated from pronotum and absence of wide lateral tergal extensions is identical with *Kirkorella*; tarsi are identical with *Gurianovella* (foretarsi are simple, the rest 2-segmented). Both taxa differ in not having all tibiae directed forwards.

Description: as for species.

Derivation of name: After the locality Elmo.

Elmonympha carpenteri Aristov, sp. n.

Holotype: MCZ 3622 ab - positive and negative imprints.

Type locality: USA, Kansas, Dickinson County, Banner Township, 5 km SE from Elmo.

Type horizon: Lower Permian, Leonardian (Lower Kungurian) Stage, Sumner Group, Wellington Fm., Karlton Mb.

Description (Fig. 2ag): Head very large, transverse, 1.7 mm wide, with huge eyes and short antenna. Antenna shorter than notum, narrowing with antennomere elongation towards apex. Pronotum transversal, short and as wide as head, widening basally along with the paranotal circle; Mesonotum transversal, metanotum quadrate. Paranotal circle narrowed anteriorly, wide at base and in the middle. Wing pads with concave anterior margins. Fore legs shortest, hind legs longest. Legs flattened, all 3 pairs directed with tibiae posteriorly. Tibiae widened in distal half, fore tarsi simple, the rest pairs 2-segmented (first segments short, second segment as long as claw). Abdomen as long as notum (total body length/maximal width 8.3/3.4 mm). Tergites with insignificant lateral protrusions. Cerci short, steeply narrowed.

Derivation of name: after F. M. Carpenter.

Czekardia Martynov, 1940, nom. resurr.

Czekardia: Martynov, 1940: 27; *Czekardia blattoides*: Martynov, 1940: 27, fig. 26–31, Tabl 8, fig. 3

=*Gurianovella*: syn. Sharov, 1961: 134; *Gurianovella silphidoides*: syn. Sharov, 1961: 134

Type species: *Czekardia blattoides* Martynov, 1940. Monotypic.

Czekardia blattoides Martynov, 1940, nom. resurr.

Material: holotype PIN 118/139 positive and negative imprints. Russia, Permian territory, Suksun Area, right bank of the River Sylva near Chekarda village; Lower Permian (Kungurian), Irenian horizon, Kochelev Formation.

Remarks: Nymphs with wide oval body, individual length ca. 15 mm; width 6 mm. Head transverse, with small eyes. Antenna shorter than body, width near base twice as wide as apex. Nota elongate, twice as long as wide. Paranotalia as wide as notal segments. Hind legs longer than notum, tibia without armature. Coloration (stripes and maculae) restricted to tergites (lateral extensions also without coloration). Tarsus 3-segmented, second tarsomere shortest, first and third ones (with strong claws) subequal. Cerci wide, likely elongated. Thus *Czekardia* differs from *Kirkorella* in having a wider body, unarmed tibia and long first tarsomere. Additionally, *Kirkorella* has body twice as long as wide (Fig. 2am). *Tshekardushka* differs in absence of lateral tergal extensions. *Czekardia*, *Kirkorella*, *Peremella* and *Mariella* were synonymised with *Gurianovella* by Sharov (1961). Gurianovella and *Kirkorella* appear to represent separate genera, and *Peremella* with *Mariella* were synonymised with *Kirkorella* (Aristov, 2004). Reexaminaton of *Czekardia blattoides* revealed significant differences from *Kirkorella*, and *Czekardia* is reestablished.

4. Discussion

An aquatic mode of life in extant cockroaches is evidenced by direct field observations in UNESCO BR Sumaco (Fig. 1g). The living cockroaches of the subfamily Epilamprinae are abundant in water in all stages in numerous localities in Ecuador, and numerous researchers have reported this phenomenon (Bishop, 1973; Ward, 1992; Hutchinson (1993: 569); Dudgeon (1999: 511–512) without detailed study. We focus on the history of the freshwater biome as a habitat for cockroaches, and their aquatic mode of life, already demonstrated for living species. It must nevertheless be stressed, that no superficially visible aquatic adaptations are present in living semiaquatic cockroaches. And this is in spite of the fact they can swim submerged with a speed of approximately 1 m per second.

Proof for an aquatic mode of life in *Hydrokhoohydra aquabella* sp. n. fossils is partially based on the very different morphology with the unique triangular shape of the adult pronotum. Although this shape is not unequivocally advantageous in water, it is clearly different from all known living or fossil cockroaches. The coloration, which might appear aposematic on the ground (as in the similarly colored Harlequin cockroach and its relatives), is also unique, but was apparently cryptic in the here-reported aquatic fossil species. This pattern of cryptic coloration has already been demonstrated in aquatic environments (Adler, 2009). Otherwise, unlike in immature individuals (identified as belonging to this species on the basis of identical coloration), at least stages 2–4, with swimming hind and mid legs, the adult does not seem specifically modified and was likely not fully aquatic. Indirect evidence comes from the distribution pattern of the Karabastau species. There is only a single complete adult (and one isolated forewing and one isolated body) among 1332 Karatau winged cockroach specimens. Nevertheless, there are 38 unambiguously identified immature specimens, which is 36% of all 96 larvae documented from Karatau. It is the most common species in terms of the number of preserved immatures in sediments in the 320 Ma history of the order. Distribution of immature stages (stage 1–5) is as follows: (10, 12, 5, 10, 1, 3). Notably, the second stage is the most common in terms of number. This distribution of juvenile stages is common for amber and the sedimentary record (Vršanský, 1997; Šmídová and Lei, 2017). It must be noted that the first immature stage is disproportionally large (according to Hörnig et al., 2016 and Mlynský et al., 2018 and first stage immatures of *Jantaropterix* sp. from Myanmar amber, this huge size in immatures might really represent the first stage), but also with another growth parameter, Dyar's rule is highly modified and the growth stage multiplication towards the next larval stage of *Hydrokhoohydra aquabella* sp. n. is 1.2 (1.16/1.23/1.12/1.23/1.34) instead of the standard 1.4. Average size and also visual distribution of instars (abdominal average width 0.99/1.33/1.63/1.83/2.25/2.6 mm) thus do not conform to Dyar's rule. Other specimens were collected from: Crato (Fig. 1b), and are characteristic because of the swimming position of legs; Myanmar amber (Fig. 1d, f), characteristic for its significantly modified legs and ventral side of the body; Lebanese amber, with *Cryptoblatta aquatica*, which is described in detail above (Figs. 1a, 2af).

The occurrence of Mesozoic aquatic cockroaches is limited to history's hottest Mesozoic localities, Bakhar, Karatau, Myanmar, Lebanese amber and Crato, disregarding their age. Crato was a tropical biome with (NB) low diversity of cockroaches (Lee, 2016). The Middle Jurassic Bakhar in Mongolia, the locality with the highest diversity in history, contains primarily hardly attributable forewings, although liberiblattinid forewings are known. Lebanon is a site with very high diversity, but not as extreme as the previous four. On the other hand, the cohort is completely absent from all other localities, which is a significant negative evidence as Bon Tsagaan, Baissa and other Cretaceous sites together provide a huge amount of cockroach samples. Apparently the taxon is limited to high temperature freshwater biomes, probably freshwater lakes of tropical type. Unfortunately, gut contents have not been preserved, so the diet is obscure. Nevertheless, the absence of aposematic coloration and a potentially partially prognathous head might indicate a predatory way of life. If they were predatory, it would not be on insects, as fine cuticular remnants would be preserved as in most Karatau predatory cockroaches. The undescribed cockroach in

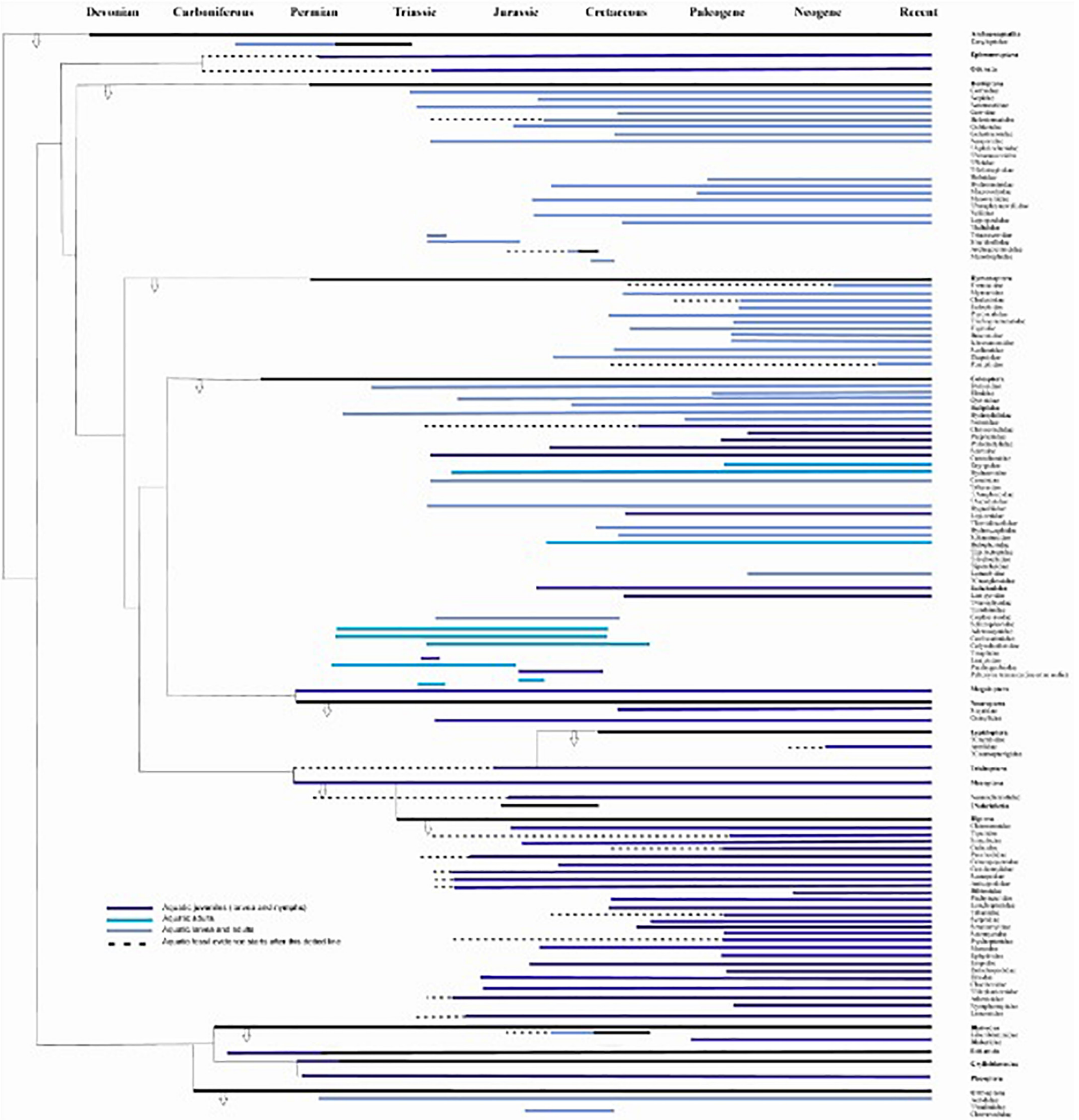

Fig. 3. "Waves" of insect invasions to aquatic realm, without a single reversal. Insect orders with attached arrows are partially aquatic with its aquatic families described below. Otherwise the insect orders are fully aquatic. Insect families with question marks are absent in the fossil record. Plecoptera contains mostly aquatic juveniles, but *Capnia lacustra* Jewett, 1965; *Baikaloperla* Zapekina-Dulkeit et Zhiltzova, 1973; Notonemouridae Ricker, 1950 is aquatic from birth to death (Holst, 2000).
Data obtained from Sinitshenkova (2002), Lancaster and Downes (2013), Nicholson et al. (2015), and Rasnitsyn and Strelnikova (2018).

Fig. SI2 shows superficial resemblance to the herein studied group, including characteristic coloration. Its raptorial legs show that it was a predator, despite the fact that the abdomen with its gut content is not preserved. Notably, likely due to acting of homeotic genes, the fore and also mid and hindlegs had strong femoral spines, like as *Santanmantis axelrodi* Grimaldi, 2003 (see Hörnig et al., 2013, 2017) although the raptorial function of its mid and hindlegs was obscured (Brannoch and Svenson, 2017).

Cockroaches and eoblattids were directly related. Their hypothetical shared ancestor connects the families Archimylacridae (Blattaria) and Eoblattidae (Eoblattida - fore details see Aristov, 2015, 2017) through the prognathous head, SC ending at R, M5 falling into CuA main stem, CuA further branched in intercubital field and clavus. Ecologically, the shared ancestor was a saprophagous and facultative stratobiont connected to plants. Cockroaches immediately further specialized as obligatory stratobionts with an uncarved pronotum, SC falling into C, undifferentiated RS, reduced M5. Nevertheless, a carved pronotum was retained in *Miroblatta costalis* Laurentiaux-Vieira et Laurentiaux, 1987 (Rieu-du-Coeur, Belgium). SC also ends in R in *Archimylacris johnsoni* (Woodward 1887) (Coseley, UK). *Qilianiblatta namurensis* Zhang et al., 2012 retained M5 and intercubital CuA.

Paleozoic nymphs regarded here as belonging to Eoblattida, are ancestral to true cockroaches (before revision they belonged to Grylloblattida (Storozhenko, 1998, Aristov, 2005, 2014, 2015)). They competed with true cockroaches, and possibly prevented them from reaching water prior to the Mesozoic. This nevertheless, cannot be confirmed, as they apparently differed in ecological niches. Ecology of the larvae is indicated by a characteristic wide and flat body. The body of *Gurianovella* is widened due to lateral tergite extensions reaching half of the total pronotal and two-thirds of the abdominal width and form a continual surface. Such a flat body is functional for adherence, which helps to cope with flowing streams. The fore margin of the pronotum from *Sylvonympha* is deeply excavated and the lateral sides of the excavation protect the head. The body is also flattened. Meso- and metawing pads are laid at an angle, making the body surface larger and the substrate-binding force bigger. The abdominal tergite growths are thin. Legs are attached with widely laid coxae, fore-directed tibiae (characteristic for phytophiles and reophiles) and numerous rows of dense chaeta. *Sylvonympha* is a typical ritrobiont (reobiont inhabitating rapid/mountain streams) (Sinitshenkova, 1987) similarly to the plecopteran *Barathronympha* from Chekarda. *Sylvonympha* was apparently a free-living reophile inhabiting open environments on rocks in rapid streams. Coxal gills in *Gurianovella* and *Sylvonympha* directly indicate water habitats. *Gurianovella* was a less specialized reophile, possibly with a less open way of life (Paňkov, 2010), with only the mid legs directed forwards. *Elmonympha* larva with all three pairs of legs directed backwards with widened tibiae and natatorial tarsi, is a characteristic swimming limnophile, common in sediments ($n = 82$; Carpenter, 1935). Ecology of *Kirkorella*, *Tataronympha*, *Czekardia*, *Tchekardushka*, *Iblatta*, *Sylvatorialies* and *Permedax*, all without reophile adaptations, is less apparent. *Kirkorella* and *Tataronympha* were apparently amphibiotic in alluvia ($n = 50$, 50 including exuvia indicating moulting in or near freshwater bodies). Its flattened body suggests a hidden way of life, possibly temporarily in the litter. At the same time *Kirkorella* and *Czekardia* have camouflage coloration, characteristic of species living at least a part of their life in open habitats. Such coloration was also present in some species of aquatic beetle larvae *Coptoclava* (Zhang et al., 2010) and stratobiont Silphidae (*Kemerovia* was probably also a stratobiont due to the opened pronotum allowing a panoramatic view), eoblattids (Fig. 2ag–am), stoneflies (Fig. 2an) and cockroaches (Figs. 1, 2a–ae, af).

Morphologically, paranotalia were absent in knemidolestids and present in eoblattids and reculids. Lateral extensions on the tergites are characteristic for eoblattids and certain reculids. In Atactobhlebidae with archimetaboly, the number of tarsomeres varies from 1 to 5, depending on the immature stage. Eoblattida and Cnemiodolestida (except Sojanoraphidiidae) and Reculida (except Probnidae) always have five tarsomeres. *Kirkorella mira* (Atactophlebiidae) is characterized by a moderately wide flat body and armed tibiae, while *Czekardia* (and also *Iblatta* with smaller head) is wider, with unarmed tibiae, which was possibly also an aquatic adaptation. The middle and hind tibiae are directed backwards in all three taxa - a character trait occurring in both limnophiles (unknown in Chekarda) and in terrestrial insects. Other aquatic adaptations were not preserved.

Based on the new material, we distinguish four formal adaptive stages: (1) Terrestrial nymphs periodically feeding on littoral without aquatic adaptations, known from isolated specimens *Sylvalitoralis*, *Permedax*, possibly *Tshekardushka*; (2) terrestrial and/or amphibiotic nymphs frequently visiting the littoral and entering water without distinct aquatic adaptations, common in the sedimentary record and with inorganic particles in the gut, known from *Kirkorella* and all water-related cockroaches. These might occur in alluvia during lowstands and consequently permanently (Paňkov, 2010); (3) aquatic, reophiles with attaching legs and subcoxal gills, known from *Sylvonympha* and *Gurianovella*; (4) aquatic, actively swimming limnophiles with swimming legs, known from *Elmonympha* (possibly predatory, all others saprobionts).

Surveying the aquatic way of life through insects, we see that 236 lineages independently produced at least some aquatic descendants, but not one returned to the land (see Fig. 3). Only a single principal lineage of moths (ancestral to butterflies; the origin of modern insects from ephemerans and dragonflies is questioned) hypothetically evolved from an insect with aquatic immature stages, and no terrestrial lineage evolved from aquatic adults. This is surprising because to-land reversal is common in numerous other vertebrate (such as fish, amphibians, reptilomorphs, and mammals (Ashley-Ross et al., 2013)) and invertebrate crustaceans (Spicer et al., 1987). The absence of an aquatic terrestrial reversal puts the hypothesis of the earliest water-emerging insects into doubt. Most aquatic insect orders had terrestrial ancestors based on the fossil record. Furthermore, the fact that most lineages of aquatic insects have no direct marine members (Hynes, 1984; Ward, 1992), indicates that transition from land to freshwater must have occurred more frequent than transitions from land or freshwater to the sea. In general, invasions of fresh water from the land or from the sea are more frequent than invasions via fresh water between land and sea (Vermeij and Dudley, 2000). Up to 16% of fossil insects are represented by aquatic ones. A possible reason for the lack of land return is the character of numerous aquatic adaptations related with reductions, which are unlikely to be resuppressed. Transitions to freshwater from terrestrial environments could lead to fewer physiological difficulties (Pritchard et al., 1993), taking into account morphological changes, such as reduction of limbs. On the other hand, some mammalian lineages in marine environments, such as sea lions (with their tails, supporting locomotion on land) might tend towards becoming terrestrial again. Furthermore, the transition to freshwater required adaptations, such as thermo- and osmo-regulation, respiration, feeding and locomotion in insects (Dijkstra et al., 2014). Unadapted organisms might respond to new physical circumstances in evolutionary transitions between aquatic and terrestrial ecosystems by shutting down their metabolic mechanisms, a disadvantage for these organisms in contrast with other well adapted organisms. Freshwater environments, however, are thought to offer less biotic resistance than terrestrial or marine environments (Vermeij and Dudley, 2000). For example, the first abundant insects in the Carboniferous freshwater, such as eoblattids and notopterans, were phytophagous (Aristov, 2015). In this respect the low abundance of predatory odonatans (Lancaster and Downes, 2013) is also remarkable.

Aquatic habitats in insects do not form a distinct taxonomic cohort. Aquatic insects can spend one or more stages of their life cycle in freshwater; they can be aquatic as juveniles, adult or both (see Fig. 3). The majority (ca. 75%), however, become terrestrial in the adult stage (Fig. 3). Therefore, it is not surprising that the family diversity of aquatic insect families shows some similar patterns with the entire insect family diversity, although these synchronicities are less abrupt in aquatic insects (Fig. 4a–b). It is obscure if the latter is due to the smaller number of aquatic insect families, or possibly a more stable aquatic environment with less short or long-term environmental stress. Freshwater bodies are in general shallow and sensitive to environmental changes. However, in contrast with soil or air, freshwaters today have more stable daily and seasonal temperatures (Dijkstra et al., 2014). Freshwater bodies can be divided into lentic (standing) or lotic (running) waters and most aquatic insects are limited to one of these habitats (Lancaster and Downes, 2013). The dataset of strictly aquatic insects is compared with the dataset from Nicholson et al. (2015), consisting of 1454 insect families from the fossil record. Proportion of diversity between aquatic insect families and all insect families through time follows a square-function ($r2 \approx 0.6$) with a sharp rise from Late Carboniferous to Late Triassic with still lasting stability (Fig. 4e).

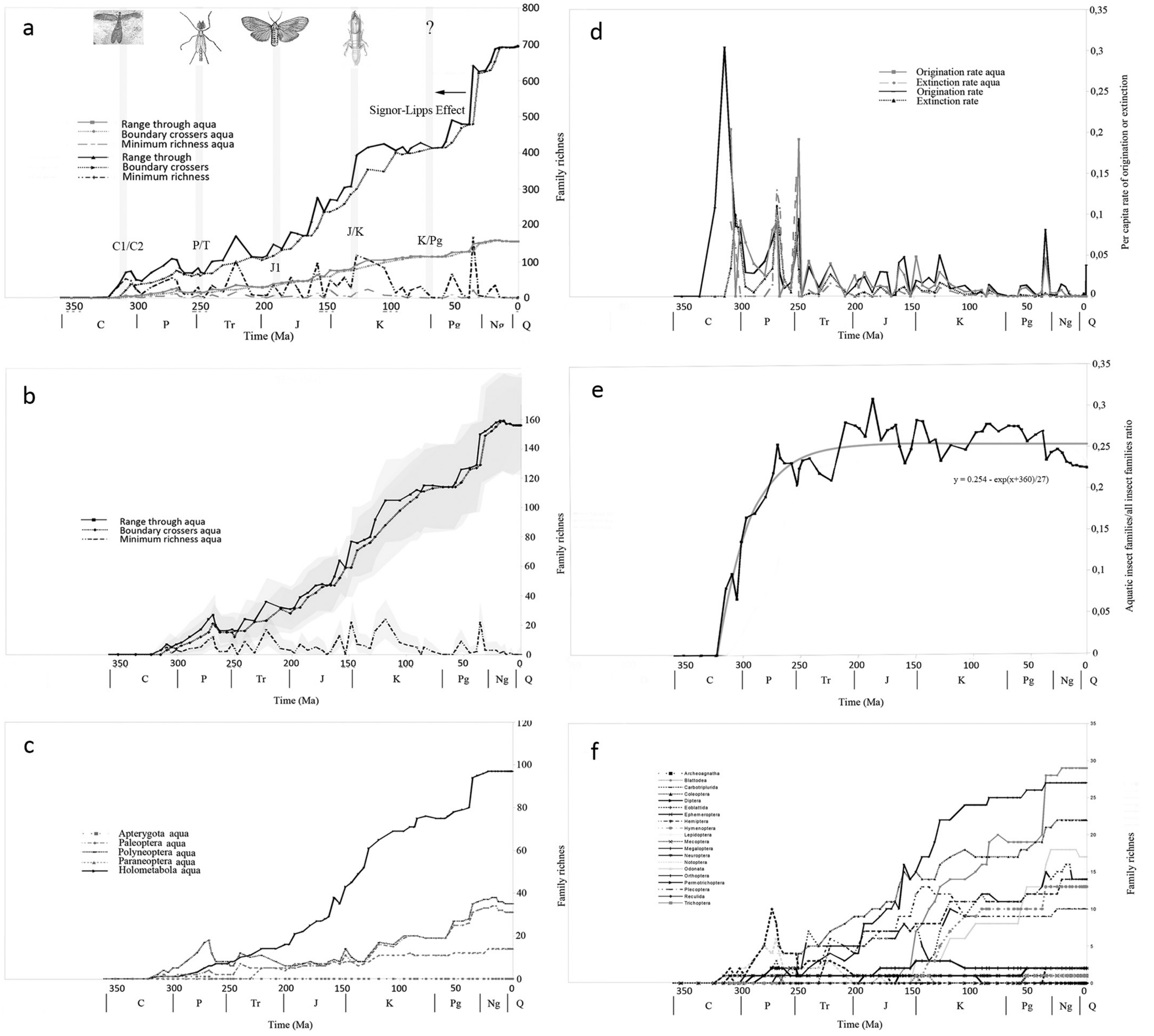

Fig. 4. Changes in aquatic insect diversity through time. (a) Family richness of aquatic insects and all insects from the fossil record though time. Gray lines show 62.05 Ma periodicity; (b) family richness of aquatic insect from the fossil record through time; (c) family richness in major aquatic insect groups through time. Gray shading is 95% confidence interval; (d) estimated per capita rates of origination and extinction of aquatic insects and all insects from the fossil record; (e) aquatic insect families/all insect families ratio from the fossil record trough time. The gray line is a trendline; (f) family richness of aquatic insect orders from the fossil record through time. Range through = first, last, single interval occurrence taxa, and taxa originating and continuing after stage boundaries. Boundary crossers = last occurrence taxa, and taxa originating and continuing after stage boundaries. Minimum richness = first, last and single interval taxa records within stage boundaries. Aqua = aquatic taxa. Family richness of all insects from the fossil record is used from Nicholson et al., 2015. Rest of data is obtained from Sinitshenkova, 2002; Lancaster and Downes, 2013; Rasnitsyn and Strelnikova, 2018.

Between extinction and origination rates for both aquatic and all insect families, a narrow correlation can be seen with five main originations and four main extinctions. In general, originations exceed extinctions, and explains the rise of family diversity through time (Fig. 4a–c, f). Notably, also the synchronicity between the main separate and unrelated insect groups over geological time, which, unless resulting from biases in collections, directly indicate that environmental changes affected entire freshwater ecosystems globally. Paleozoic origination and extinction rates are distinctly higher than in the Mesozoic (Fig. 4d). Comparing the comparatively low Paleozoic diversity (Fig. 4a–b), the high rates could be due to the appearance of numerous short-lived families.

In the Carboniferous, the first aquatic insects are known from the Moscovian. The Late Carboniferous (Bashkirian-Moscovian) has the highest origination rate for all insects, probably as result of the first appearance of winged insects (including Polyneoptera and Paleoptera) and colonization of ecosystems (Nicholson et al., 2015). With the rise of winged insects and large terrestrial arthropods since the Middle Carboniferous, continental terrestrial ecosystems have offered biological (i.e. competitors) and physical barriers for aquatic organisms to enter the continent (Vermeij and Dudley, 2000). Extinctions in all insects in this period are according to Labandeira (2005) caused by changes in plant communities and trophic structure. The shift of origination and extinction rates towards the Carboniferous/Permian (C/P) boundary in aquatic insect families could possibly be attributed to the Signor-Lipps effect. Carboniferous forests might have yielded shallow reservoirs with organic matter overgrown by helophytes inhabited by a few active swimmers, such as molluscs, horseshoe crabs and cirripeds

(Ponomarenko, 1996). The earliest known insect families belong to Apterygota and contribute little to aquatic insect diversity, or to entire insect diversity. Polyneoptera, of which mostly eoblattids, followed by notopterans, from this period were, based on the current state of the fossil record, the most abundant of all insects in Carboniferous freshwaters (Fig. 4c, f), follow the same pattern as the general aquatic insect diversity.

The Early Permian (Kungurian) origination rate peak could be attributed to the colonization of wider environments (Nicholson et al., 2015). Notably, only Polyneoptera contribute to the high diversity peak for aquatic insects in the Permian as well with an even higher diversity, still mostly consisting of eoblattids, followed by notopterans (Fig. 4c, f). Extinction rates per capita in all insects are relatively high in this period and caused by hot dry climates on land (Benton, 2003). Both extinction (which is higher than origination) and origination rates per-capita are higher at the Permian-Triassic (P/T) boundary for aquatic insects, compared to all insect families. These high rates however might be exaggerated by the poor pre-Ladinian record (Dmitriev and Ponomarenko, 2002). There is no evidence for a large mass extinction at the P/T boundary. More probably, only reorganization of the biota's structure took place, rather than a catastrophic extinction (Aristov et al., 2013).

In the Triassic, a large peak in both origination and extinction is visible, which is likely to be an attribute of sampling bias. Polyneoptera still contribute the most, together with Paleoptera, to the diversity peak of aquatic insects in this period. The diversity of eoblattids and notopterans, however becomes smaller, while ephemeropterans start to dominate in the fossil record (Fig. 4c, f). For the first time, aquatic insect assemblages appear, which are more numerous than terrestrial ones. Mesozoic freshwaters are overgrown by helophytes, which extracted and accumulated biogens and presumably attracted dragonflies, stoneflies, and mayflies.

Late Jurassic (Oxfordian) high origination rates of insects could be due to the radiation of communities on advanced seed plants (Nicholson et al., 2015). Extinction rates are a result of competitive turnover during simultaneous radiation (Labandeira, 2005). The Jurassic/Cretaceous (J/K) boundary is significant for aquatic insects, as their origination rate per-capita overtakes the general origination rate per-capita of insects. Holometabola, dominated mostly by dipterans (Fig. 4c, f), starts to contribute mostly to the general aquatic insect diversity from the Jurassic to the present (instead of Polyneoptera and Paleoptera before). The first aquatic liberiblattinid cockroaches originated in the Oxfordian (when no eoblattids are known) and become extinct in the Cenomanian (Fig. 3).

Early Cretaceous (Barremian) extinction rate peaks of terrestrial insects are caused by competitive turnover adapting to new environments, including angiosperms (Ross et al., 2000). No evidence of the Cretaceous/Paleogene (K/Pg) extinction seems to be related to insects or specifically aquatic insects at family-level, but unfortunately the fossil record of the Maastrichtian contains a sparse amount of fossil insects to rule this out. Origination peak rates are a result of radiations in decomposer and freshwater systems (Nicholson et al., 2015). Due to periodic changes of water characteristics or different evolutionary rates, unadapted terrestrial insects repeatedly invaded the aquatic realm with well adapted hydrobionts. Until the Eocene, Mesozoic freshwaters had a low abundance of angiosperm macrophytes. The presence of only clarophytes caused less consumption of biogens, which resulted in eutrophication, and subsequent oxygen depletion, which changed the water characteristics (Ponomarenko, 1996). In addition, Cretaceous freshwaters might have had more detritus from the abundant terrestrial angiosperm plants, which might have attracted some insect groups feeding on this. Primarily trichopterans, dipterans, hymenopterans, odonatans (remarkably also exclusively aquatic), and later also ephemeropterans, had a comparatively large increase in diversity in the fossil record. Moderate diversity rises are observable in coleopterans and hemipterans, while no significant changes occur in the diversity of megalopterans, mecopterans, archeoagnathans, cockroaches, and eoblattids (Fig. 4f). In exclusively aquatic larvae, such as lotic ephemeropterans and plecopterans (today restricted mostly to cooler habitats), in this period, a decrease of diversity is visible in the fossil record (Fig. 4f). Lotic species are mostly bad dispersers, and their species diversification peaks mostly in periods of stability (Dijkstra et al., 2014). Changes in some orders, however, might have occurred (faster) more significantly at lower taxonomic-level, simply because of the ‘conservativeness’ of some orders (e.g. cockroaches have only 34 families compared with ca. 300 beetle families). Floating mats on lycopsid and moss frames were major producers and particularly attracted insects (Ponomarenko, 1996).

The Eocene (Priabonian) origination rate is probably caused by extensive finds of Baltic amber, Green River, and Florissant formations (Labandeira, 2005). However, in general, during the Cenozoic, origination and extinction rates are almost zero, possibly due to high species and genus per family ratio of Cenozoic insects. The second aquatic, extant cockroach family Blaberidae appear in the first half of the Eocene (Ypresian) (see Fig. 3). In aquatic environments the first half of the Eocene was warm, with warm-water reservoirs spreading around the globe that resulted in eutrophic reservoirs, while cooling down in the latter half of the Eocene brought seasonal water turnovers improving oxygen supply and expansion of grasslands that decreased erosion. The stability of aquatic ecosystems has increased since (Ponomarenko, 1996). In the Neogene, trichopterans contributed most to the aquatic insect diversity (replacing dipterans), following the diversity patterns of aquatic fossil insect families (Fig. 4f). Both orders have a large feeding niche diversity, which may explain their high species diversification (Dijkstra et al., 2014). Decline in diversity of aquatic insect families from the Paleogene/Neogene (Pg/Ng) boundary towards the present (Fig. 4b) is possibly biased by poor preservation of fossils from these periods. If living aquatic insect families, unknown in the fossil record were included, a sharp rise would be visible instead.

The diversity dynamics of aquatic insects correlates with that of the entire freshwater biota. A major contribution to the rise of general diversity is made by arthropods, particularly insects (Ponomarenko, 1996). Furthermore, the basic pattern of low insect diversification rate in the Paleozoic is observable besides the freshwater biota (Dmitriev and Ponomarenko, 2002) in non-marine tetrapods (Alekseev et al., 2001), non-marine dinosaurs (Benton, 1993), and also in marine animals and their subgroups. Other trends, like P/Tr extinction and a slightly minimum diversity at Triassic/Jurassic (Tr/J) boundary are known from insect families and all other biota, but evidence is lacking in aquatic (freshwater) insects. This is characteristic for non-marine reservoirs where extinctions are less significant, occur earlier, and are presumably related to the isolation of non-marine reservoirs and their more immediate response to the environment (Ponomarenko, 1996). Very important is the stability of groups with exclusively aquatic larvae, such as ephemerans and dragonflies, while stabilization of terrestrial insect families coincides with the origin of angiosperms.

Diversification of aquatic insects seems consistent with a 62.05 ± 0.02 Ma periodicity (Fig. 4a) diversification of cockroach families (Vršanský et al., 2017). The first (C1/C2) peak is probably present, but shifted due to imprecise datings of fossils from this period. It corresponds among others to the origins of aquatic Eoblattida and Odonata (Rasnitsyn and Quicke, 2002) (both with the first aquatic family occurrences in the Bashkirian). This period is also attributed to the diversification of Holometabola (Labandeira, 2011). The C/P transition, with a small peak after the initial C1/C2 peak, gave rise to among others Hemiptera (with first aquatic occurrences in the Carnian), Coleoptera (with first aquatic occurrences in Capitanian), Megaloptera (with first aquatic occurrence in the Carnian), Neuroptera (with first aquatic occurrence in the Sinemurian), Trichoptera (with first aquatic occurrence in the Toarcian), and Plecoptera (with first aquatic occurrence in the Roadian) (Vršanský et al., 2017). The P/T peak is indistinct, because this period is not fully evaluated (Aristov et al., 2013). The P/T peak is known for its wide range of new families and includes, among others, the origin of the order Diptera (with first aquatic family occurrence in the Roadian) (Vršanský et al., 2017). The J1 peak is probably invisible due to the fact that different orders have different ranks of families. J1 corresponds to the origin of Lepidoptera (with the first aquatic family known from the Rupelian) (Vršanský et al., 2017). The J/K peak corresponds with the periodicity without the influence of Signor-Lipps effect, because of a comprehensive fossil record from this period. Events within the J/K peak, associated with angiosperm origin, might all be associated with the peak around 127 Ma (Vršanský et al., 2017) and ants that originated in this time interval (Engel et al., 2009; Wilson et al., 1967). The high peak at the Pg/Ng boundary is consistent due to extensive finds of Baltic amber, Green River, and Florissant formations, and is probably shifted from the K/Pg due to the Signor-Lipps effect. The fossil record from the Paleocene is not extensive. The last peak at 3.95 ± 0.2 Ma is absent due to non-analysed consequent fossil record and exclusion of exclusively extant families from the analysis.

Among cockroaches, the earliest aquatic fossil specimen appears in the Jurassic, after the waters were dominated by Paleozoic aquatic eoblattids, while there is no significantly evaluated Triassic collection. Systematically, the aquatic realm transition occurred in only two cockroach families, in the Mesozoic Liberiblattinidae and within the Cenozoic to still living Blaberidae. Both groups are characteristic for their high evolutionary potential, high variability and high disparity of forms. Liberiblattinidae gave birth to eusocial Socialidae and termites, numerous predatory lineages, and beetle and wasp mimicking umenocoleids/alienopterids (and to the water skimming cockroaches, possibly Chresmodidae); Blaberidae gave rise to viviparous Diplopteridae (Vršanský, 2002, 2003, 2010; Vršanský et al., 2016, 2017, 2018a, 2018b; Bai et al., 2016, 2018; Kočárek, 2018a, 2018b). In the 320 million years of the history of the order of cockroaches, only one other lineage, Mesoblattinidae have similar phylogenetic potential, but did not produce any known aquatic representatives.

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Author contributions

We organised fieldwork (T.G.) collected the material (K.U., D.A., P.M., S.E.) and data (H.S.) performed the research (G.B. - Crato; D.A. - Paleozoic localities, H.S. - Lebanese amber; P.V., P.M. - Myanmar; P.V. - Kazakhstan, Mongolia); designed research (P.V., D.A., D.A.) and wrote the paper (P. V., H.S.). All authors commented on the MS.

Author information

The authors declare no competing financial interests.

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