



***Baetis zdenkae* sp. nov., a new representative of the *Baetis buceratus* species-group (Ephemeroptera: Baetidae) from Rhodos (Greece) with notes to species-grouping of the subgenus *Baetis* Leach, 1815 s. str.**

TOMÁŠ SOLDÁN<sup>1,2</sup> & ROMAN J. GODUNKO<sup>1,3,4</sup>

<sup>1</sup>Biology Centre of the Academy of Science of the Czech Republic, Institute of Entomology and <sup>2</sup>Biological Faculty, University of South Bohemia, Branišovská 31, CZ–37005 České Budějovice, Czech Republic. E-mail: soldan@entu.cas.cz

<sup>3</sup>State Museum of Natural History, National Academy of Sciences of Ukraine, Teatralna 18, 79008 Lviv, Ukraine. E-mail: godunko@museum.lviv.net; godunko@seznam.cz

<sup>4</sup>Corresponding author

## Abstract

The male and female imago (subimago of both sexes unknown), and larva of a new species belonging to the *Baetis buceratus* species-group, namely *Baetis (Baetis) zdenkae* sp. nov. from Rhodos Island are described and illustrated in detail. Substantial diagnostic characters of males and larvae of the whole *B. buceratus* species-group are summarized and its position relative to other species groups is discussed. Critical characters distinguishing *B. zdenkae* sp. nov. from all other representatives of the *B. buceratus* species-group are emphasized and a discussion of 22 characters of the remaining 6 European species-groups of the subgenus *Baetis* Leach, 1815 s. str. and their relationships is offered. Available data on the biology of *B. zdenkae* sp. nov. (vertical distribution, habitat, current and substrate preference, abundance and density, possible life cycle type, and mating flight and oviposition patterns) and distribution with respect to possible endemism are given. Basic data on biology and area of distribution of Westpalaeartic species *Baetis (Baetis) buceratus* Eaton, 1870, *B. (B.) nexus* Navás, 1918 and *B. (B.) spei* Thomas & Dia, 1985 known only from Lebanon are summarized and compared to those of *B. zdenkae* sp. nov.

**Key words:** Ephemeroptera, Baetidae, Rhodos, new species, *Baetis buceratus* species-group, taxonomy, biology, distribution

## Introduction

As far as we know, any special data concerning mayfly occurrence on Rhodos Island (Greece) in the East Mediterranean have never been published, and only two species have been mentioned in the literature. Sowa (1985) described a new species of the genus *Pseudocentropilum* Bogoescu, 1947 (Bogoescu 1947) of the family Baetidae Leach, 1815 (Leach, 1815) on the basis of a rather incidental sample of 11 adults and a single damaged larva collected by Dr. H. Malicky near Kallithia in 1975 and the species was subsequently treated by Belfiore and D'Antonio (1990), and Jacob (1991) from the taxonomical point of view. Besides *Procloeon (Pseudocentropilum) fascicaudale* (Sowa, 1985), Soldán and Godunko (2008) mentioned the occurrence of *Baetis mirkae* Soldán & Godunko, 2008 from the *B. lutheri* species group recently described from Cyprus also at a single locality on Rhodos.

In May of 2005, a rather incidental but extensive survey of mayflies was conducted at 19 freshwater localities and lenitic habitats of the island. The localities, studied only in the spring-summer seasonal aspect, were selected in order to cover all altitudinal zones, all types of aquatic habitats with regard to as much as possible an even distribution throughout the island. Including *P. fascicaudale* found at several localities in considerable

number of both adults and larvae, altogether approximately 10 Ephemeroptera species have been determined. These belong to the genera *Baetis* Leach, 1815 (subgenera *Baetis* Leach, 1815, *Rhodobaetis* Jacob, 2003 and *Nigrobaetis* Novikova & Kluge, 1987, *Cloeon* Leach, 1815 (subgenus *Cloeon* Leach, 1815 s. str.) and *Centroptilum* Eaton, 1869 of the family Baetidae and *Caenis* Stephens, 1836 (family Caenidae Newman, 1853) (Stephens 1836; Newman 1853; Eaton 1869; Novikova & Kluge 1987).

The objective of the present contribution is to (i) describe a new species, namely *B. zdenkae* **sp. nov.** of the *B. buceratus* species-group as defined by Müller-Liebenau (1969) and Jacob (2003) in both larval and imaginal stages, (ii) discuss in detail its affinities to larvae and imagines of all Palearctic representatives of the respective species-group with emphasis on critical diagnostic characters, (iii) discuss selected and critical distinguishing characters of the remaining 6 European species groups of the subgenus *Baetis* Leach, 1815 s. str. in order to characterize their affinities and relationships and (iii) briefly summarize and discuss available data on the biology of *B. zdenkae* **sp. nov.** and its distribution with regard to possible endemism.

***Baetis (Baetis) zdenkae* Soldán and Godunko, sp. nov.**

(Figs 1–29)

**Description.** *Male imago.* Size: body length: 5.8–6.3 mm; fore wings length: 5.6–6.2 mm; cerci length: 10.6–13.8 mm; tarsal segments: T1 = 0.68–0.72 mm; T2 = 0.54–0.57 mm; T3 = 0.32–0.34 mm; T4 = 0.23–0.25 mm; general relative tarsal segments length ratio: 1>2>3>4.

General body color light, yellowish-brown to brown. Head brown with darker smudges laterally. Antennae brown, flagellum slightly paler. Ocelli whitish-brown at the apex with brown bases. Eyes black, surrounded by a light ring, occasionally with some yellowish smudges basally. Turbinate eyes oval in dorsal view with convex external margins. Faceted surface yellowish-brown to light brown. Distal part of stalk with narrow yellow ring; central part slightly darker, dirty-yellow, basal brown ring well distinguished (Figs. 1, 2). Thorax darker than head, yellowish-brown to brown, with light to dark brown maculation along sutures. Pronotum and distal part of mesonotum yellowish-brown to brown, proximal part distinctly brown. Thoracic sterna light brown to brown. Wings hyaline, transparent. Fore wings with slightly opaque pterostigma. Hind wings with costal process small, acute and rounded at apex with three simple longitudinal veins with two free veins in the third field, second vein occasionally with distal bifurcation, third vein relatively short, length about 0.38–0.40 of wing (Figs. 3, 4). Fore legs light brown, femora with diffuse smudges distally, middle and hind legs yellow to yellowish-brown.

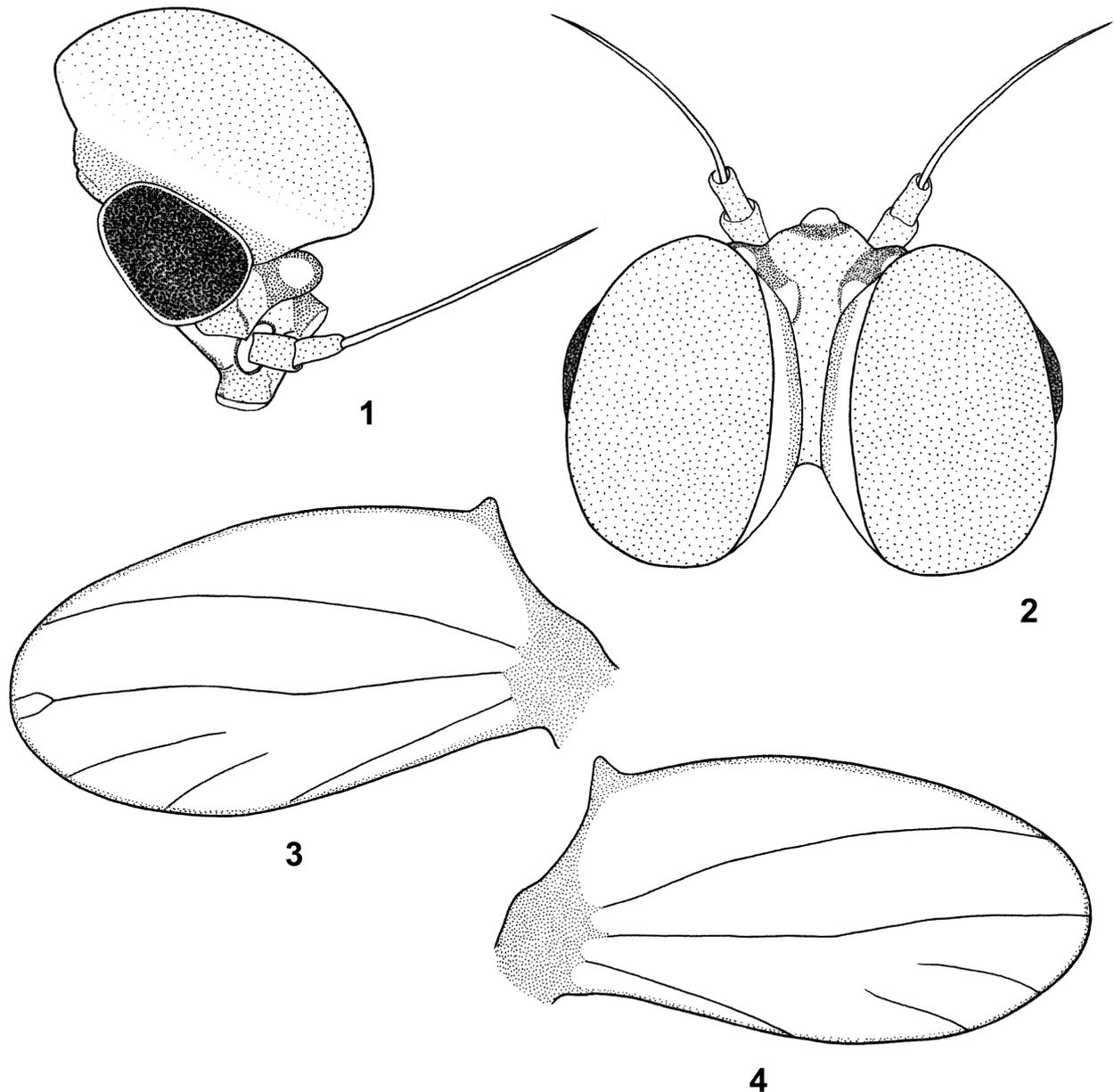
Abdominal terga with small brownish lateral smudges. Tergum I brown, terga II–VI whitish-yellow with a pair of diffuse central brownish smudges, terga VII–X distinctly darker, yellowish-brown, with narrow elongate central spots. Sterna whitish-yellow to dirty yellow with elongate whitish central spot on segments VII–VIII.

Genitalia pale, yellowish-white to dirty yellow. Forceps distinctly bent up at approximately 45° angle in lateral view (Fig. 7). Basal segment about as long as wide without a posteromedial projection, segment 1 elongate conical with slightly convex external margin, segment 2 narrow at the base, slightly expanded distally (widened part as long as 2/3–3/4 of the segment length), segment 3 elongate, slightly longer than wide (Figs. 5, 6). Cerci whitish-grey to dirty yellow, first 4–7 segments light brown.

*Female imago.* Size: body length: 6.5 mm; fore wings length: 6.2 mm; cerci length: 13.2–13.4 mm.

General body color yellowish-brown to brown. Head uniformly brown. Eyes black with yellowish maculations. Ocelli yellowish with black bases, antennae brown.

Thorax yellowish-brown to brown with dark brown smudges on mesonotum. Sterna whitish-yellow to light brown. Legs yellowish-brown to light brown, fore legs darker. Wings transparent, hyaline, fore wings with distinct yellowish-brown venation, hind wings similar to male, veins darker.



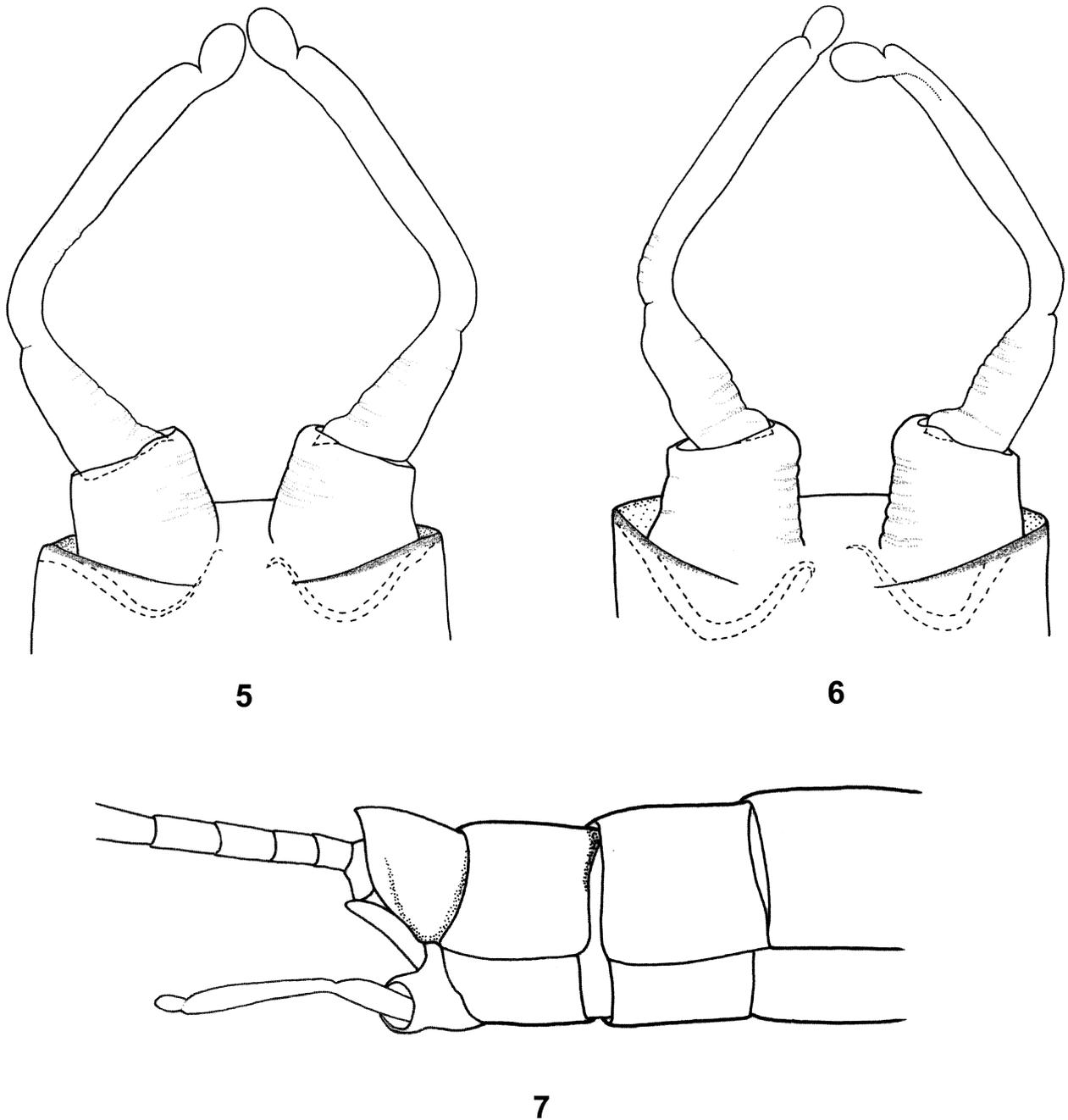
**FIGURES 1–4.** *Baetis zdenkai* sp. nov., male imagoes, paratypes: 1, head (lateral view); 2, head (dorsal view); 3, hind right wing (dorsal view); 4, hind left wing (dorsal view).

Abdominal terga uniform, yellowish-brown to light brown, sterna paler. Cerci light brown to whitish-yellow, darker at bases.

*Mature larva.* Size: body length: 5.4–7.5 mm (male), 5.8–8.5 mm (female); cerci length: 2.0–3.3 mm.

General body color dark, light brown to dark brown. Head yellowish-brown to brown, frons and clypeus paler. The whole head surface covered with short setae and solitary bases of setae. Surface of clypeus with numerous setae. Eyes black, developing turbinate eyes light brown to brown, surrounded by a narrow yellowish ring. Antennae whitish-yellow to light brown, flagellum paler than pedicel and scape, with numerous fine hairs. Pedicel surface with short setae only, scape surface with solitary setae concentrated distally. Labrum relatively wide (width/length ratio 1.52–1.55), with 1 + 4–7 long submarginal bristles and a few pointed lateral setae (Figs. 9, 13). Mandible incisors as in Figs 8a, b. Tip of maxillary palpus conical with barely visible, small apical spine, surface with numerous fine hairs (Fig. 14). Segment 2 of labial palpus relatively broad with slightly concave inner margin, about twice as broad at apex than at base, distomedial lobe as wide as about 1/

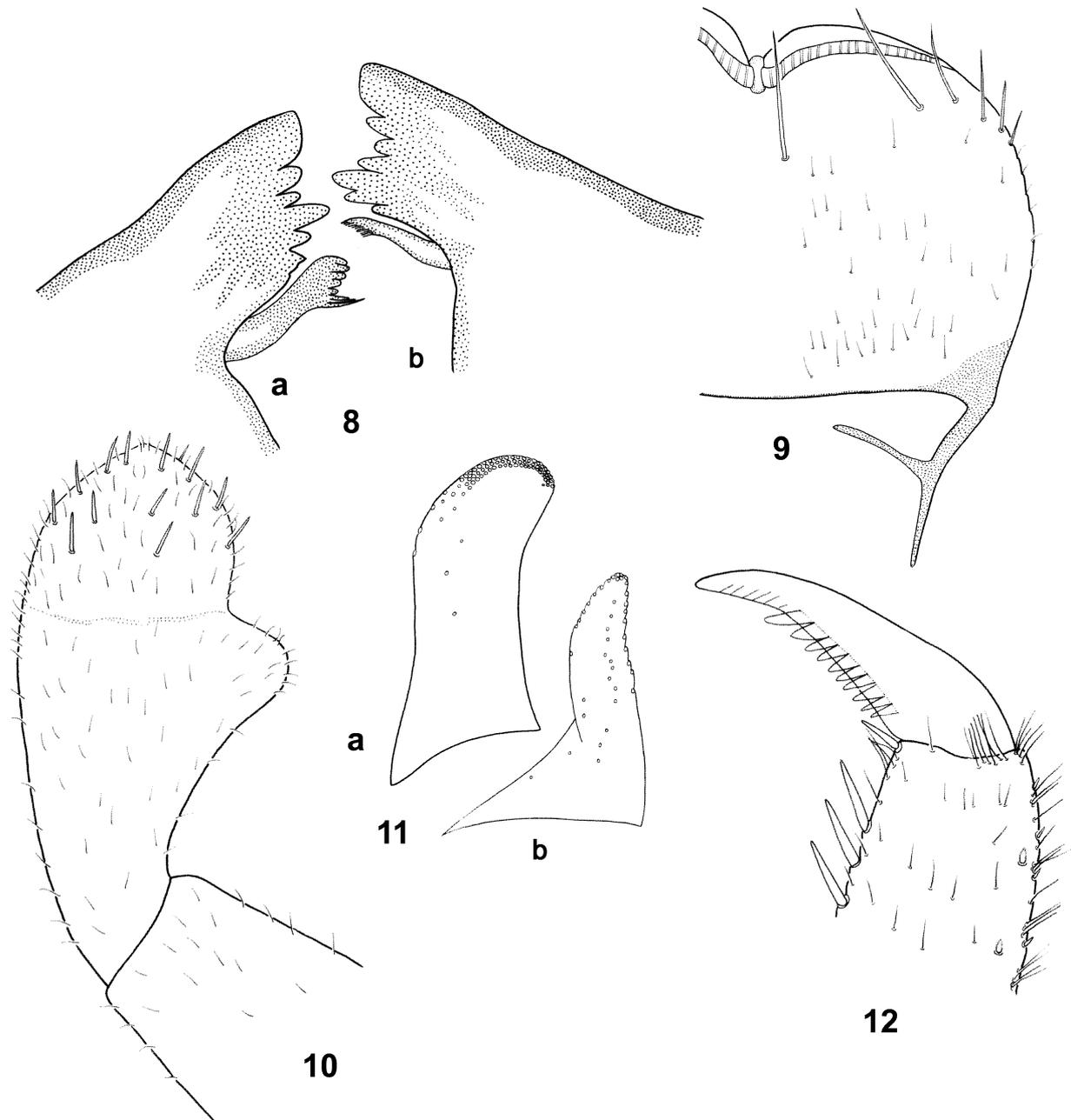
3 of segment 3 at the base. Segment 3 slightly asymmetrical, slightly longer than 1/2 length of segment 2. The length/width ratio of segments 2 and 3 combined is 1.8–2.1 (Fig. 10). Glossae and paraglossae wide, robust. Paraglossae with 3 regular rows of long bristles apically, basal row consisting of at least 16 bristles (Figs. 11 a, b).



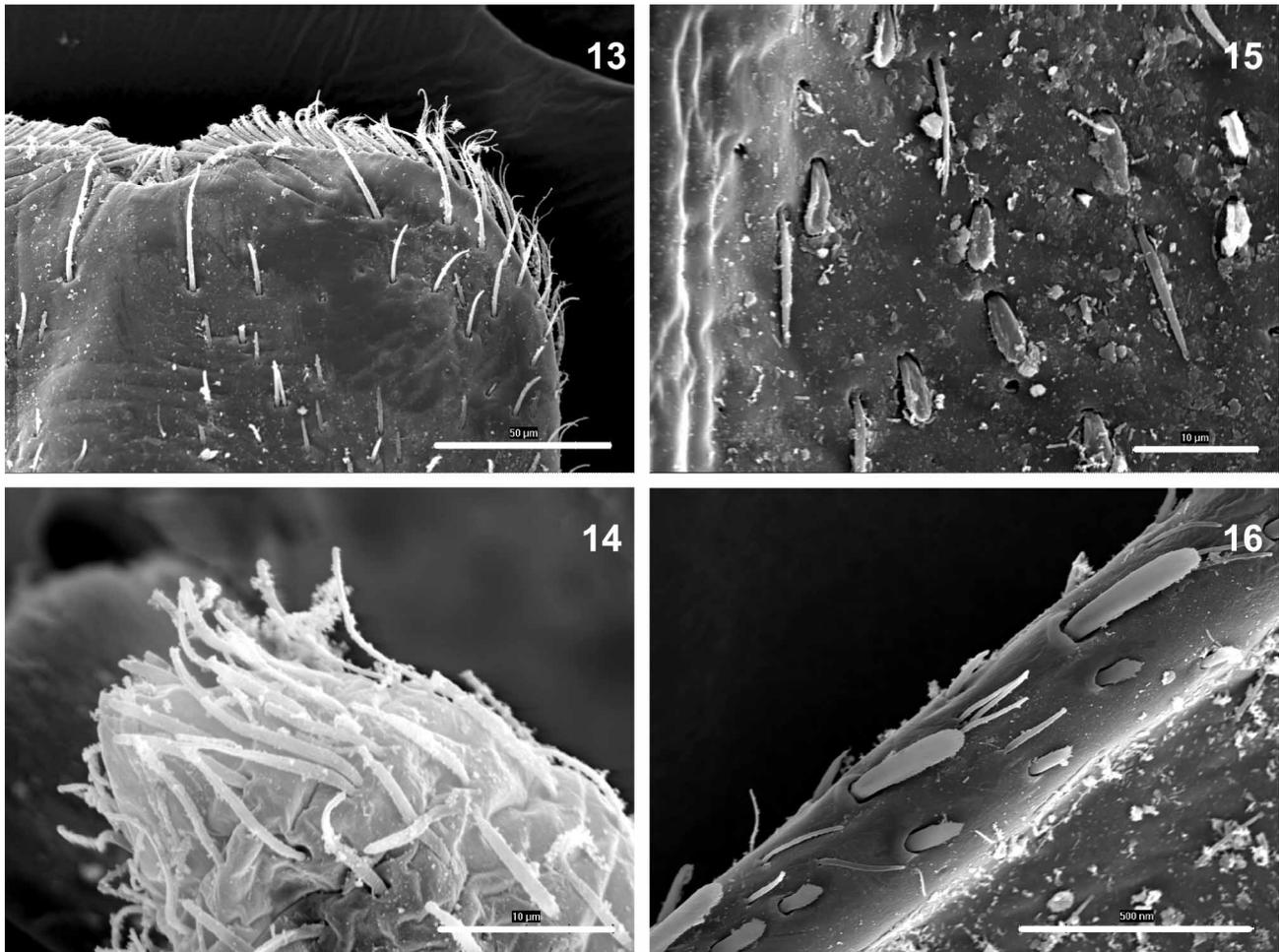
**FIGURES 5–7.** *Baetis zdenkae* sp. nov., male imagoes, paratypes: 5–6, forceps (ventral view); 7, tip of abdomen (lateral view).

Thorax dark, light to dark brown, pronotum with a pair of large pale subtriangular areas laterally, mesonotal color pattern as in Fig. 17. Metanotum brownish with central pale spot. Thorax surface with numerous fine hairs and slender spatulate setae rounded apically (Fig. 15). Sterna pale, yellowish to light brown. Legs yellowish to light brown with distinct large central dark spot on all femora (occasionally with relatively small central spot). Tibiae with brown distal spots (occasionally only with diffuse brownish smudges), tarsi darker distally. Outer margin of femora with a single, sparse row of large spatulate bristles alternating with fine hairs

and small submarginal spatulate setae (Fig. 16). Spatulate bristles relatively short and robust, distinctly rounded at apex, distal portion with shallowly splintered margins (Figs. 18, 19, 21). Femora with (1) slender spatulate setae with convergent margins (Figs. 18–20) and (2) relatively wide and apically rounded spatulate setae with subparallel margins (Fig. 21). Submarginal spatulate setae of distal portion of femora with splintered margins. Inner margin of femora with uniform row of small pointed spines and fine hairs; all surface of femora with spatulate setae and fine hairs (Fig. 22). Outer margins of tibiae with deeply splintered, slender spatulas alternating with fine hairs (Fig. 23). Inner margins with irregular row of spines and fine hairs (Fig. 24). Outer margins of tarsi with small pointed spines and hairs; small submarginal spatulate setae, with distally splintered edges. Inner margins with large pointed spines; splintered submarginal spatulate setae, and fine hairs. Surface of tarsi with numerous hairs and splintered spatulate setae. Tarsal claws elongate, relatively slender with at least 10 teeth, without subapical setae (Figs. 12, 25).



**FIGURES 8–12.** *Baetis zdenkai* sp. nov., mature larvae: 8, left (a) and right (b) mandibular incisors; 9, labrum (dorsal view); 10, labial palpus (ventral view); 11, paraglossa (a) and glossa (b); 12, tarsal claw (hind leg).



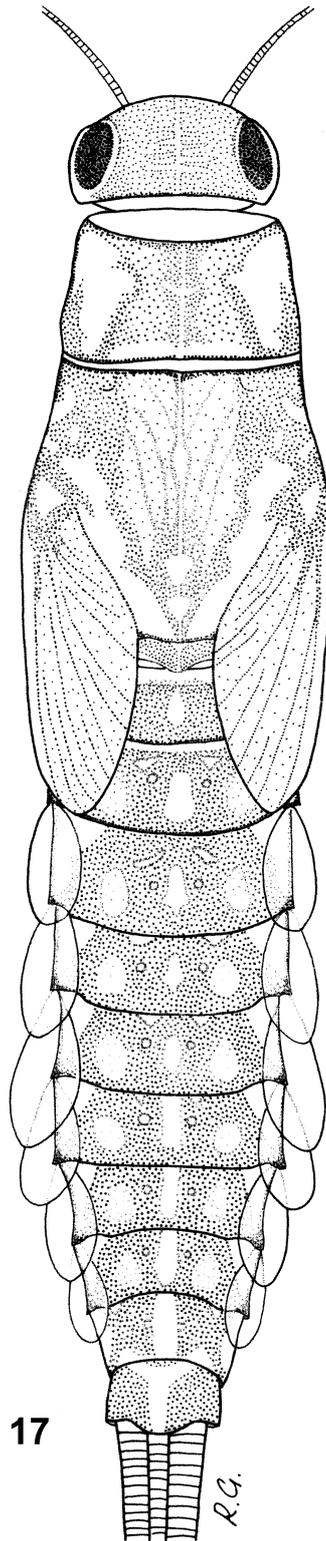
**FIGURES 13–16.** *Baetis zdenkae* sp. nov., mature larvae: 13, labrum (dorsal view); 14, apical portion of the last segment of maxillary palpus; 15, arrangement of spatulate setae on the surface of thorax; 16, outer margin of femur (hind leg). Scale bars: 13 = 500 nm; 14, 15 = 100 nm; 16 = 500 nm.

Abdominal terga dark, yellowish-brown to brown, color pattern as in Fig. 17, muscle insertions pale (cf. Jacob 2003), posterior margins with broad triangular bluntly pointed teeth alternating with setae (Fig. 28), surface with numerous fine hairs, wide bases of hairs and small spatulate setae. Two distinct types of spatulate setae discernible on abdominal tergal surface: (1) elongate narrow ones with lateral convergent margins, and (2) relatively rare ones with subparallel or divergent lateral margins, rounded at apex (Figs. 26, 27). Sterna uniform, yellowish-brown to brown with a pair of short transversal divergent strokes near the anterior margins. Inner margin of paraprocts with a single row of at least 10 (usually 12–15) distinct teeth (Fig. 29), surface with fine hairs and sparse spatulate setae. Gills 1 and 7 slightly asymmetric and subequal in size. Gills 2–6 asymmetric and distally rounded. Both outer and inner gill margins with small teeth alternating with fine hairs. Cerci uniform, yellowish-brown to brown, paracercus shorter by 1/2.

Male and female subimagos unknown.

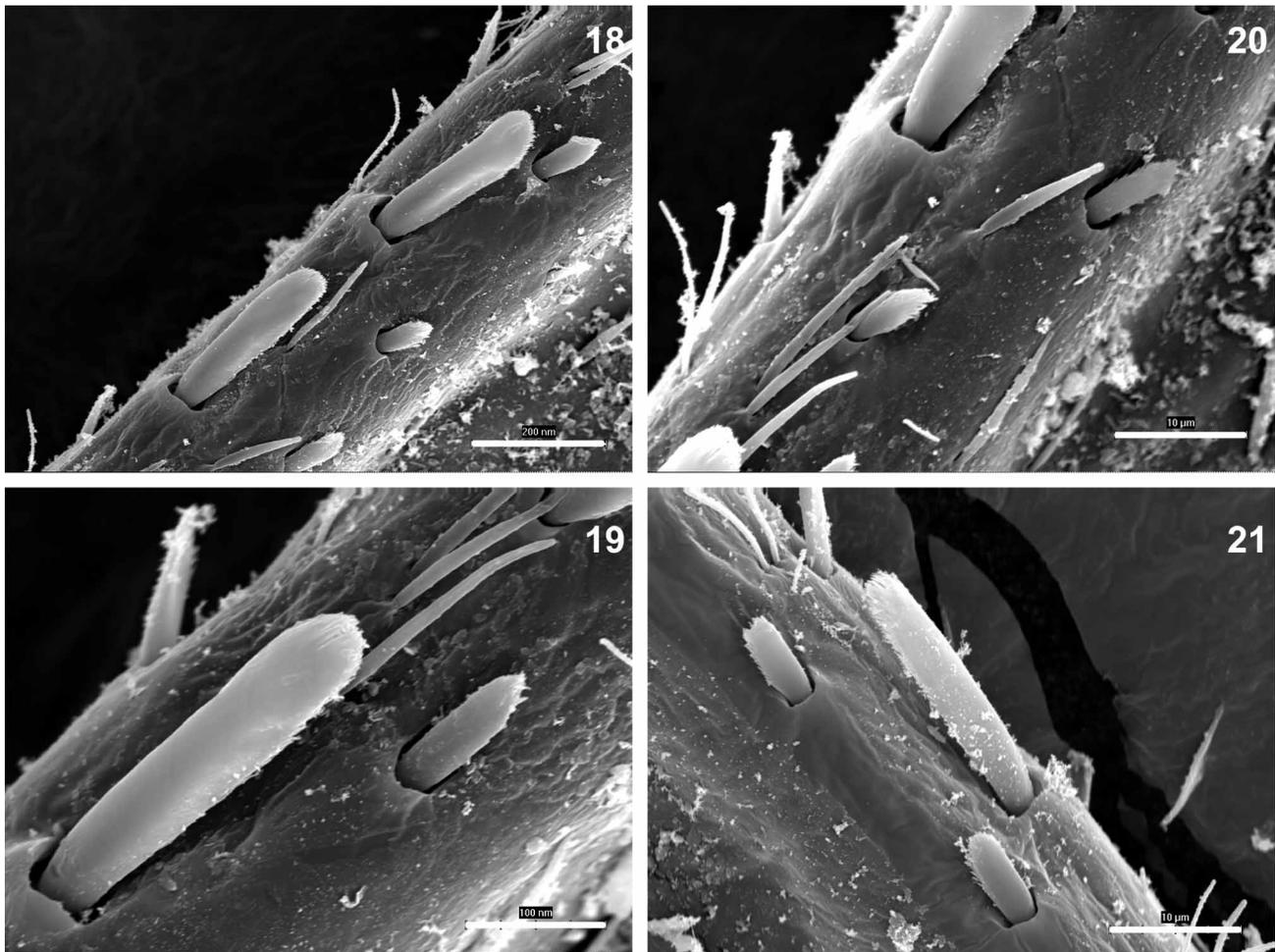
**Etymology.** The species is named for Zdenka, wife of the senior author, to acknowledge her distinguished field assistance during sampling of mayflies on Rhodos.

**Types.** HOLOTYPE: male imago, GREECE, Rhodos (Rodos) Island, stream at the Kremastis Bridge in Kremastí, about 14 km SW of Rhodos City, about 3 km NE of the Diagoras International Airport and about 500 m from its mouth to the Aegean Sea at about 10 m a. s. l., May 28, 2005. PARATYPES: 6 male imagoes, 1 female imago, 275 larvae, same locality and collection date as holotype.



**FIGURE 17.** *Baetis zdenkae* sp. nov., mature larva, general view of body (dorsal view).

**Further material examined (no types).** 256 larvae, GREECE, Rhodos (Rodos) Island, same locality and collection date as holotype; 8 larvae, Greece, Rhodos Island, Argiros Potamos (stream), about 30 km SW of Rhodos City, 1 km NE of Kalavárda and about 1 km from its mouth to the Aegean Sea at about 10 m a. s. l., May 26, 2005.



**FIGURES 18–21.** *Baetis zdenkae* sp. nov., mature larvae, outer margin of femora (hind legs). Scale bars: 18 = 200 nm; 19 = 100 nm; 20, 21 = 100 nm.

All material (preserved in 70% alcohol) was collected by Zdenka and Tomáš Soldán. Genitalia of two male imagoes on slides. Holotype, most paratypes and other material examined deposited in collection of the Biological Centre, Academy of Sciences of the Czech Republic, Institute of Entomology, České Budějovice, Czech Republic; 50 larvae and 1 male imago (all paratypes) deposited in the State Museum of Natural History, National Academy of Sciences of Ukraine, Lviv, Ukraine.

The comparative material of *B. buceratus* was collected in Central Bohemia (the Berounka River basin), Slovakia and Ukraine (the Latorica, Tisza and Dniester River basins) at numerous localities. Larvae and adults of *B. nexus* were collected at several localities of the Dyje (Thaya) River basin in Moravia (Czech Republic), Slovakia and Ukraine (the Latorica and Tisza River basins). For descriptions of some localities see Landa and Soldán (1989), Soldán and Zahrádková (2000), and Horsák (2001). Material of *B. spei* was not studied, morphological characters and other data are based on the original description by Thomas and Dia (1985, 2007).

**Differential diagnosis and affinities.** *B. zdenkae* sp. nov. can be easily distinguished from the other three representatives of the *B. buceratus* species-group (*B. (B.) buceratus* Eaton, 1870, *B. (B.) nexus* Navás, 1918, and *B. (B.) spei* Thomas & Dia, 1985) by the following combination of morphological characters: *in male imago*: (1) faceted surface of turbinate eyes yellowish-brown to light brown (yellowish brown to orange brown in *B. buceratus*, dark brownish in *B. nexus* and flesh-colored in *B. spei*), (2) tricolor combination of stalk of turbinate eyes (stalk paler, light orange in *B. buceratus*, eyes unicolorous in *B. nexus*, stalk flesh-colored in *B. spei* with diffuse and intermittent basal ring), (3) third vein of hind wings relatively short, about

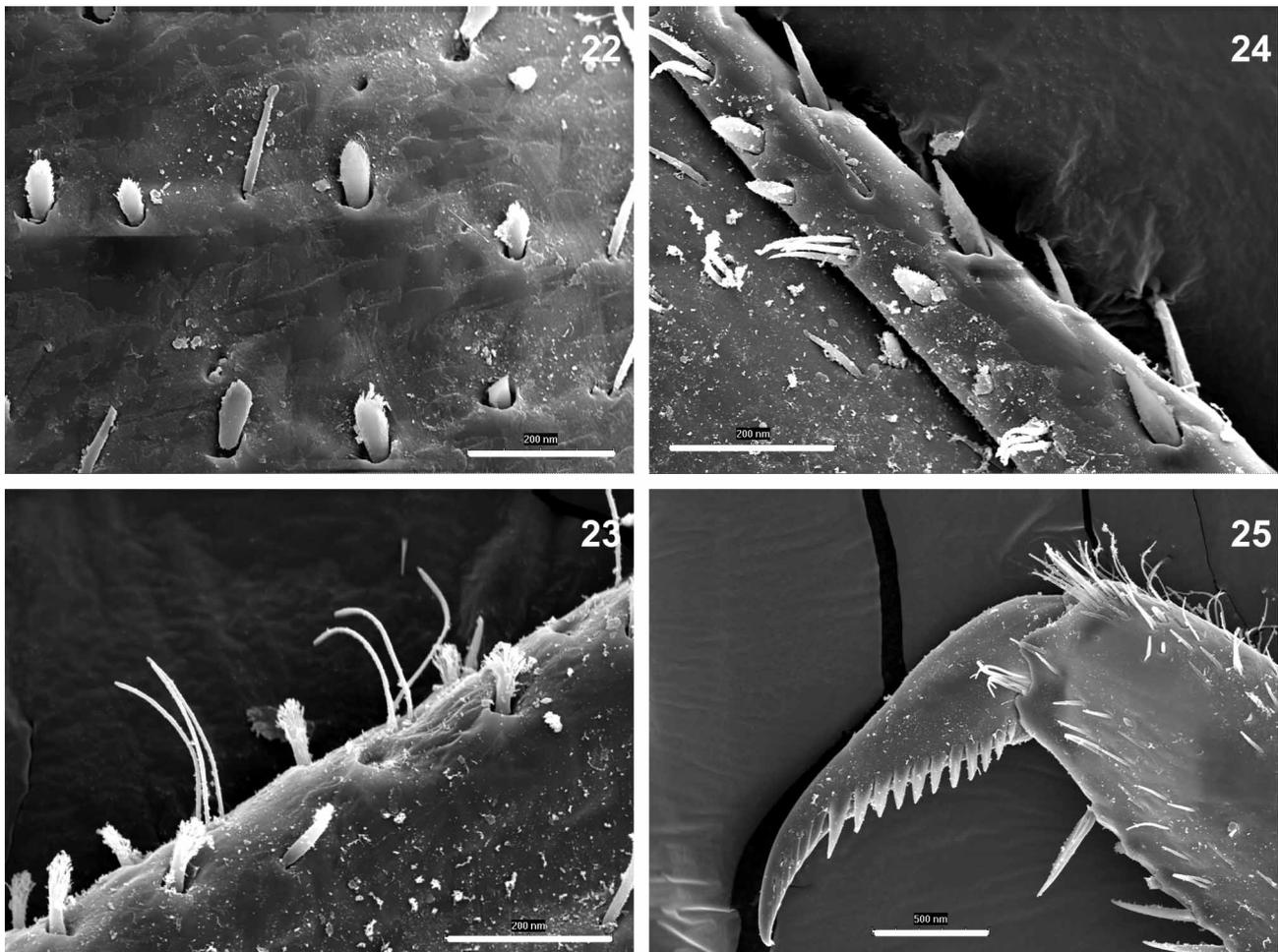
0.38–0.40 wing length (about half of wing length in *B. buceratus*, 1/2 length to longer in *B. nexus*), (4) forceps conspicuously bent up in lateral view (as in *B. buceratus*, nearly straight in *B. nexus* and *B. spei*), (5) basal segment of forceps without posteromedial projection (posteromedially produced into lobe-like projection in *B. buceratus*, *B. nexus* and *B. spei*), and (6) segment 1 of forceps elongate conical (conical in *B. buceratus* and *B. spei*, oval, bulbous with apparently convex inner and outer lateral margins in *B. nexus*); *in larva*: (7) structure of segments 2 and 3 of labial palpi (segment 3 shorter than or equal to 1/2 of segment 2 in *B. nexus*), (8) structure of mandible incisors (cf. e.g., our Figs. 8a, b with Fig. 3g, d by Thomas and Dia 1985: 242 showing *B. spei*), (9) paraglossae with basal row of apical bristles consisting of at least 16 bristles (about 10–12 bristles in *B. spei*), (10) outer margins of femora with single sparse row of spatulate bristles, alternating with fine hairs and submarginal small spatulate setae (as in *B. spei*), (11) structure of small spatulate setae of femora (some of them conspicuously splintered as in *B. spei*), (12) arrangement of small spatulate setae on dorsal surface of femora, (13) posterior margins of abdominal terga with broad bluntly pointed triangular teeth, alternating with setae (teeth rounded, semicircular in *B. spei*, narrow triangular blunt pointed teeth in *B. buceratus*), (14) surface of terga with numerous fine hairs, spatulate setae, and wide bases of hairs and spatulate setae (without spatulate setae in *B. spei*), (15) inner margin of paraproct with 10–15 distinct teeth (about 20–25 teeth of different shape in *B. spei*; about 20 teeth in *B. buceratus* and Thomas and Dia 1985: 243, Fig. 12; about 25 teeth in *B. nexus*, Müller-Liebenau 1969: 149, Abb. 109), (16) paracercus shorter than cerci by 1/2 (subequal in *B. buceratus* and *B. nexus*, about 2/3 of cerci in *B. spei*), and (17) specific color pattern of thorax and abdomen in dorsal view (e.g., a single, conspicuous pale band in the middle of pronotum in *B. spei*, in Thomas and Dia 1985: 243, Fig. 7).

The male genitalia of *B. zdenkae* **sp. nov.** are similar to *B. buceratus*, in the structure and proportions of segments 1–3, and conspicuously bent up forceps (see Müller-Liebenau 1969: 140, Abb. 99–100 or Jacob 2003: 96, Abb. 17a–b). On the other hand, the male imago of the new species differs markedly from *B. buceratus* in color pattern of the faceted surface of the turbinate eyes and their stalks and in hind wing venation (cf. characters 1–3, see also Müller-Liebenau 1969: 139–140, Abb. 104j or Jacob 2003: 97). On the other hand, *B. zdenkae* **sp. nov.** can be easily distinguished from *B. nexus* by the different arrangement of all critical imaginal characters (1–6, see above and cf. Müller-Liebenau 1969: 146–147, Abb. 101, 107, and 108, or Jacob 2003: 98, Abb. 17c).

Larvae of *B. zdenkae* **sp. nov.** can be distinguished from all remaining representatives of the *B. buceratus* species-group by the combination of characters (9 and 14), and, particularly really the critical characters (8 and 16) separate this species from *B. buceratus* and *B. nexus*. Additionally, *B. zdenkae* **sp. nov.** differs from *B. nexus* by the structure of outer margin of femora and paraproct (characters 10 and 15). The latter two characters and the arrangement of triangular teeth on the posterior margin of abdominal terga (character 13), distinguish the new species from *B. spei* with small rounded, nearly semicircular teeth, cf. Thomas and Dia (1985: 243; Fig. 11). Contrary to *B. spei* (muscle insertions on head well visible and contrasting), the head of *B. zdenkae* **sp. nov.**, is rather unicolorous. Labrum of *B. zdenkae* **sp. nov.**, provided with 1 + 4–7 bristles is relatively wider (width/length ratio 1.52–1.55) vs. 1 + 6–8 bristles and width/length ratio 1.35–1.50 in *B. spei*. Further differences between *B. zdenkae* **sp. nov.**, *B. buceratus* and *B. spei* can be found also in thoracic and abdominal terga color patterns (see Müller-Liebenau 1969: 141–145 and 147–150, Abb. 102–103, 109 or Jacob 2003: 96–98, Abb. 31, 18, 19, and Thomas and Dia 1985 for details).

**Biology.** Larvae of *B. zdenkae* **sp. nov.** evidently prefer stream run places of the “lowland” biotopes within the island. These localities (mostly at elevations of 100–250 m a. s. l.) were inhabited by other baetid species, e.g., by apparently dominant *Baetis (Nigrobaetis) digitatus* (Bengtsson, 1912) which is the first faunistic record from Rhodos and *P. fascicaudale*, but no larvae of *B. zdenkae* **sp. nov.** have been collected. Larvae of this new species were found in two streams with permanent water of about 1–3 m across and an average depth of 10–30 cm, moderate to fast current velocity and stony bottom overgrown, in some places, with submerged aquatic vegetation. The current velocity was about 20–50 cm.s<sup>-1</sup> at the most densely inhabited

places, the density of larvae, roughly estimated at about 100–300 ind.m<sup>-1</sup>, decreased rapidly with decreasing current velocity, places with slower current were inhabited rather sparsely. Water temperature ranged from 17 °C early in the morning to 23–26.5 °C in the afternoon at sun-exposed, densely inhabited places (type locality, up to 28.5 °C in pools with very rare occurrence of larvae). As to substrate roughness, larvae preferred gravel places (lithal) covered with cobble and pebble. Their densities in places covered with granules (2.0 mm in diameter) and very coarse (1.0 mm) or coarse (0.5 mm) sand were very low showing rather incidental occurrence. Larvae were not found on fine substrates like medium to very fine sand or silt. If submerged aquatic plants occurred at the places preferred, larval densities among vegetation were comparable with those of stony habitats. However, substrate requirements of larvae do not seem to be pronounced. Stream banks are regulated at numerous places in both biotopes inhabited. For instance, the Argiros Potamos near Kalávarda is a very shallow stream with an artificial concrete streambed in some places.

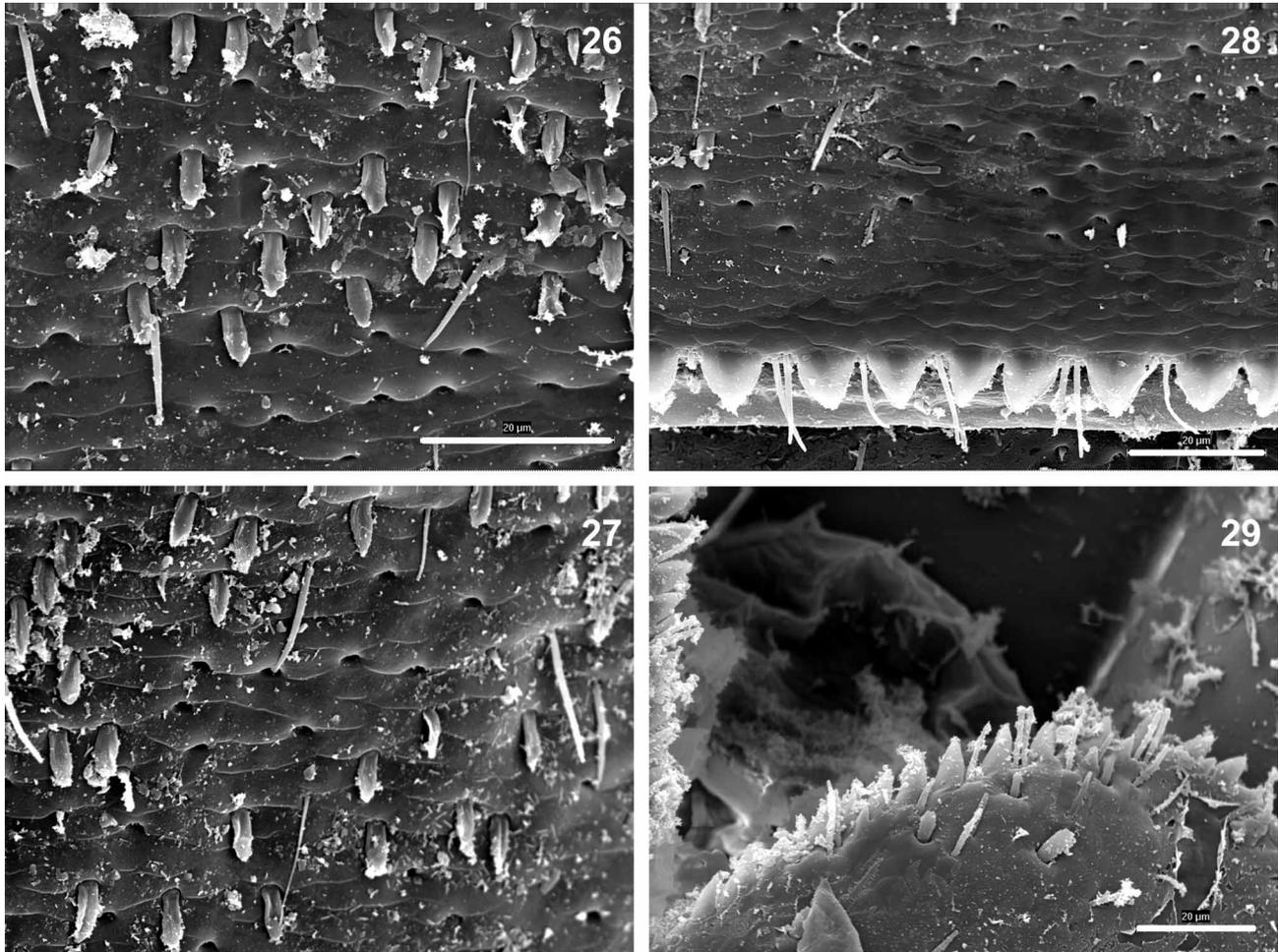


**FIGURES 22–25.** *Baetis zdenkae* **sp. nov.**, mature larvae: 22, surface of femur; 23, outer margin of tibia; 24, inner margin of tibia; 25, tarsal claw (hind legs). Scale bars: 22–24 = 200 nm; 25 = 500 nm.

At the type locality, larvae of *B. zdenkae* **sp. nov.** are clearly dominant forming at least 75% of the mayfly standing crop, they seem to be very rare at the locality of the Argiros Potamos (at most 10% of the mayfly standing crop in May, *Caenis luctuosa* (Burmeister, 1839) and a new species of the *B. lutheri* species-group were dominant). At the type locality, the larvae were collected together with those of *C. luctuosa*, *P. fascicaudale* and *B. (Rhodobaetis) cf. rhodani* (Pictet, 1843).

The life cycle of *B. zdenkae* **sp. nov.** remains unknown in detail. However, judging from the size of larvae in May 2005 and timing of mating flight we might suppose a seasonal, bivoltine winter life cycle, the MBws

type according to the classification by Clifford (1982). Adult emergence by mid May indicates a possibility of two generations a year (second generation might fly from late August to early October). Owing to favorable conditions (generally mild climate, relatively high water temperatures) there is a chance to complete development of larvae originating from the eggs laid in May of the same year. Taking into account approximately linear growth of larvae during winter followed by its acceleration after spring warming of water, and the different size categories of larvae collected at the same time in May, several egg cohorts are likely, as in numerous other mild climate *Baetis* species (cf. Sowa 1975 or Clifford 1982)



**FIGURES 26–29.** *Baetis zdenkae* **sp. nov.**, mature larvae: 26, surface of abdominal tergum IV; 27, surface of abdominal tergum VI; 28, posterior margin of abdominal tergum IV; 29, outer margin of paraproct plate. Scale bars: 26–29 = 20µm.

Subimagines emerge from the water surface and places overgrown with submerged vegetation during daylight hours, from about 10.00 a.m.–16.00 p.m. local time. *Baetis zdenkae* **sp. nov.** showed early morning mating flight activity with the mating flight generally occurring from about 6.30–8.30 a.m. local time. First males started to appear approximately a half hour before sunrise, and showed a typical “pendular” flight pattern usually in groups of about 3–10 individuals, females were observed about 0.5–1 hour later. Although only a few females were observed flying upstream, their flight activity seemed to last at least one hour after males had disappeared. A single female was observed ovipositing on a submerged stone, hence the way of oviposition seems to be similar to other species of the genus *Baetis*.

Generally, the biology of *B. zdenkae* **sp. nov.** resembles that of *B. spei* which was characterized as a rhithro-potamal species by Thomas and Dia (1985), while the remaining representatives of *B. buceratus* species-group occur at rather different (mostly potamal) habitats. However, larvae of *B. spei* showed a wider

range of vertical distribution than those of *B. zdenkae* **sp. nov.** being collected at altitudes of 5–950 m a. s. l. at places 2–48 km from source in well oxygenated water. They were moderately abundant to abundant at streams about 3–10m across, including also a temporary stream. The larvae were characterized as thermophilous (in contrast to those of *B. bisri* Thomas & Dia, 1983 and *B. baroukianus* Thomas & Dia, 1984 living at the same area (Thomas & Dia 1983, 1984), maximal water temperature ranged from 17–29 °C (pH 7.4–8.25), conductivity 290–440  $\mu\text{S}\cdot\text{cm}^{-1}$ . The life cycle of *B. spei* is not fully known, mature larvae were collected from May to August (Thomas & Dia 1985), were collected from May to August (Thomas & Dia 1985), and adults were collected at the same time (Thomas & Dia 2007).

Larvae of *B. buceratus* have been found mostly at the localities of large lowland rivers (epipotamal). They apparently can tolerate a certain degree of pollution being sometimes dominant at these biotopes. Larvae prefer medium to high current speed and stony substrata (gravel and larger stones) but often occur also among submerged plants. Such habitats are described as typical for this species (Buffagni & Desio 1994; Gonzáles del Tánago 1984). *B. buceratus* shows a typical bivoltine winter life cycle (MBws) with overwintering larvae of the first generation. However, there are some data indicating plasticity of the cycle. In Switzerland, larvae live also in epirhithral stream segments although they prefer lower elevations and places with lower current velocity at this area (Sartori & Landolt 1999). According to Landa (1968) older larvae of the first generation appear from March to May – this may indicate ceasing of larval development during winter months rarely found in species with the MBws life cycle type. According to Haybach (1998, 2006) there is one overwintering generation with flight period in spring and two generations following late summer and autumn. Since the adults apparently fly from July to October (Landa 1968; Langford 1971; Sowa 1975), two “summer” generations and, consequently, some type of polyvoltinism (MP) cannot be excluded.

Larvae of *B. nexus* live in lowland waters of different size, being mostly found in rivers, their backwaters and artificial freshwater biotopes (e.g., in the “roach zone”), at places with very low current velocity. They evidently prefer places rich in submerged aquatic vegetation. Azonal species according to Haybach (1998, 2006), habitat preference cannot be evaluated from the rhithron-potamon concept. However, in south Moravia (Czech Republic), the larvae are usually found in a typical epipotamal river, moreover influenced by the upstream impoundment (Horsák 2001) like they do in southern France (Cammouseight & Fontaine 1990, see this paper also for further details on ecological requirements of larvae and their quantitative presentation). Seasonal bivoltine winter life cycles (MBws) have been observed in France (Cammouseight & Fontaine 1990), with two flight periods in May and August, and also in Hungary (Ujhelyi 1966), Germany (Haybach 1998, 2006) and Poland (Keffermüller 1972).

**Distribution.** Since *B. zdenkae* **sp. nov.** is so far known only from Rhodos Island it might be considered endemic to this island. However, the true distribution of *B. zdenkae* **sp. nov.** still remains poorly known so that its classification is preliminary since these possible “endemics” might inhabit a much larger area as shown, for example, by our finding of presumably “endemic” species *B. mirkae* group described from Cyprus also on Rhodos (Soldán & Godunko, 2008). That is why we prefer to wait until further collection records are published. The distribution of *B. zdenkae* **sp. nov.** can be compared to that of *B. spei*, the species known only from Lebanon, only from two river basins (Nahr el Aouali and Nahr ed Damour) as well, so far altogether from 9 localities (Thomas & Dia 1985).

On the other hand the distribution of *B. zdenkae* **sp. nov.** seems to be quite different from the distributions of *B. buceratus* and *B. nexus*. The former species (type locality the Kenneth and Holybrook near Reading, Berkshire, England) belongs to widely distributed Westpalaearctic species. It is known from Europe including the British Islands and some Mediterranean islands, e.g., Sardinia (Belfiore & Gaino 1988) but probably missing in North Africa. Northern limits are situated in Scandinavia – Sweden and Denmark (Bengtsson 1917; Jensen 1969), southeastern ones in Asia Minor, Turkey and Iraq (Koch 1988; Kazanci 1984; Al-Zubaidi *et al.* 1987), eastern limits probably in southern Ural, Caucasus and Central Asia (cf. Kluge 1997). *B. buceratus* is

classified either as a Holomediterranean faunistic element of the expansive type according to Jacob (1972), or a Pontokaspian element according to Haybach (1998) and its area is sympatric to that of *B. zdenkae* **sp. nov.**

*Baetis nexus* belongs to widely distributed Westpalaeartic species as well, however its area is restricted to about 50° N. Northern limits are situated in Germany and Poland. This species is known from Europe except for the British Islands, Fennoscandia and most of the Mediterranean, and is missing in North Africa (see Sartori & Soldán (2006) for complete list of distributional records). Eastern limits are uncertain, the species has been found easternmost in the Asian part of Turkey (Kazanci 1984). The species is considered a typical Pontic faunistic element according to Haybach (1998, 2003).

### Notes to grouping of the subgenus *Baetis* Leach, 1815 s. str.

Three species, namely *B. buceratus*, *B. nexus* and *B. spei* are currently included within the *B. buceratus* species group (cf. e.g., Müller-Liebenau 1969 or Jacob 2003, see also Thomas & Dia 1985), the taxonomy of which seems to be clear and all three species well defined.

Taking into account the arrangement of critical diagnostic characters, *B. zdenkae* **sp. nov.** undoubtedly belongs to the subgenus *Baetis* Leach, 1815 s. str. and the *B. buceratus* species group. This represents one of the 6 “groups” of about 30 European or Westpalaeartic species as defined by Müller-Liebenau (1969) and revised, e.g., by Jacob (2003), now constituting the subgenus *Baetis* s. str. Of the 4 remaining original European species groups (altogether about 35 European or Westpalaeartic species), the former *B. lapponicus* species group by Müller-Liebenau (1969) is now generally classified within the genus *Acentrella* Bengtsson, 1912 having been removed from synonymy with *Baetis* Leach, 1815 by Müller-Liebenau (1981), and 4 further groups (namely *B. atrebatinus*, *B. rhodani*, and *B. niger* + *B. gracilis* species groups) are now currently classified as subgenera *Labiobaetis* Novikova and Kluge, 1987 (6 Westpalaeartic species), *RhodoBaetis* Jacob, 2003 (14 Westpalaeartic species), and *NigroBaetis* *NigroBaetis* (10 Westpalaeartic species) of the genus *Baetis* s. lat., respectively (Novikova & Kluge 1987; Jacob 2003). The latter subgenus is often considered to include also original genera/subgenera *Alainites* Waltz & McCafferty, 1994 (identical with “Die muticus-Kleingruppe” by Jacob 2003: 116), and extralimital *Dipheter* Waltz and McCafferty, 1987, *Takobia* Novikova and Kluge, 1987, *Margobaetis* Kang and Yang, 1994, and *Acerbaetis* Kang and Yang, 1994 (Kang *et al.* 1994; Waltz & McCafferty, 1987; Waltz *et al.* 1994).

Apart from the aforementioned 4 taxa (genera/subgenera or species groups), which are not discussed here in detail (for their definition, re-definition and detailed synonymy see Kang *et al.* 1994: 11, 34; Novikova & Kluge 1994: 625; Waltz *et al.* 1994: 34; Waltz & McCafferty 1997: 135; Bae *et al.* 1998: 90; Jacob 2003: 119), there are, as noted above, 6 further species assemblages, namely the *B. alpinus*, *B. lutheri*, *B. pavidus*, *B. buceratus*, *B. fuscatus*, and *B. vernus* species groups containing 10, 6 (including *B. mirkae* from Cyprus), 1, 4 (including *B. zdenkae* sp. nov), 7, and 3 Westpalaeartic species, respectively. As it has become evident, the excellent “species grouping philosophy” originally suggested by Müller-Liebenau (1969) could be applied to extralimital *Baetis* species as well (see, e.g. *B. transiliensis* or *B. molawinensis* species groups by Novikova 1987 or Müller-Liebenau 1984). Most of them fit very well within the existing 6 “European” species groups and there are some other species groups at least in the East Palaeartic, Oriental and Nearctic Regions as shown and discussed by e.g., Novikova (1987), Müller-Liebenau (1984), and Morihara and McCafferty (1979), respectively.

On the other hand, individual species groups within the subgenus *Baetis* s. str. seem to be rather weakly defined in some respects, especially as far as the imaginal characters are concerned. In order to contribute to the question of grouping, we have attempted to evaluate and review respective group-specific characters some of them already suggested by Müller-Liebenau (1969) and Jacob (2003). There are at least 22 characters (however only 6 of them in imagines) more or less supporting species grouping as generally suggested for a

long time. Taking into consideration *B. zdenkae* **sp. nov.** for example, the principal characters shared with or different from other representatives of the *B. buceratus* species group and other species groups can be specified, as follows:

*In larva:* (i) segments of antennal flagellum shortened in distal portion (two thirds), as in *B. zdenkae* **sp. nov.** (not shortened in the *B. alpinus*, *B. lutheri* and *B. pavidus* species groups), (ii) labrum usually with not more than 1 + 6 long bristles (usually 1 + 3–5; 1 + 6–8 in *B. spei*; many more bristles usually in the *B. alpinus* species group) (+, present in *B. zdenkae* **sp. nov.**), (iii) outer mandibular incisors not divided (as in *B. buceratus* and *B. spei*) or slightly emarginated in the middle (+, as in *B. nexus*, deeply emarginated or divided, e.g. in some representatives of the *B. vernus* species group), (iv) first (outer) mandibular incisor cut or bluntly pointed at apex (+, as in *B. buceratus* and *B. spei*), (v) small subapical tooth or projection on the outer margin of incisors absent (present but hardly distinguishable in *B. zdenkae* **sp. nov.** as in *B. spei*, but well developed, e.g. in some representatives of the *B. vernus* species group), (vi) apex of distal segment of maxillary palpus with conical protuberance (+, very reduced spine present as in *B. spei*, well developed and sometimes numerous spines, e.g. in some representatives of the *B. alpinus* and *B. lutheri* species groups), (vii) apex of relatively short distal segment of labial palpus rounded without any short and flat spine-like bristles (scarce subapical but not considerably flattened or spine-like bristles present in *B. zdenkae* **sp. nov.**), (viii) thoracic nota and abdomen with bordered color patterns (+), i.e. with pronounced muscle insertions that are pale (dark, e.g., in related *B. vernus* species group). cf. Jacob (2003), (ix) anterior (outer) margin of femora with sparse, relatively short and flat bristles (+, long, pointed and numerous bristles in most representatives of the *B. lutheri* and *B. alpinus* species groups as well as in *B. pavidus*), (x) tarsal claws without a pair of subapical bristles (+, present only in the *B. alpinus* and *B. lutheri* species groups), (xi) abdominal terga pale anterolaterally, with two pairs of small darker spots or strokes (+), (xii) posterior (inner) margins of femora with spatulate setae rounded at apex (+, some types of spatulate setae with conspicuously splintered margins in *B. zdenkae* **sp. nov.**, similar but usually less splintered spatulate setae in remaining *B. buceratus* species group representatives but usually missing in other groups), (xiii) posterior margins of terga with a row of triangular spines (+, also in *B. alpinus* and *B. vernus* species groups), (xiv) surface of abdominal terga with numerous spatulate setae bases (+, also in *B. alpinus*), (xv) paracercus subequal in length to cerci in *B. buceratus* and *B. nexus* (as in related *B. vernus* and *B. fuscatus* species groups), shorter by 1/2 in *B. zdenkae* **sp. nov.** or shorter than 2/3 of cerci in *B. spei* (as in the *B. lutheri* and *B. pavidus* species groups), while paracercus is strongly reduced in the *B. alpinus* species group, and (xvi) cerci and paracercus unicolorous (+, as in remaining *B. buceratus* species group representatives, but with transverse dark band, e.g. in related *B. fuscatus* species group).

*In male imago:* (xvii) hind wings with 3 longitudinal veins (+), intercalaries and/or cross veins well developed (cross veins missing in *B. zdenkae* **sp. nov.**, but intercalaries well developed, as in *B. buceratus*), (xviii) forceps base without medial projection, straight or slightly convex (+, convex or emarginated e.g. in related *B. fuscatus* species group), (xix) forceps dark ochre to brownish in basal portion (+, pale, e.g. in related *B. fuscatus* species group), (xx) basal segment cylindrical or subcylindrical posteromedially produced into lobe-like, low projection (projection indistinct in *B. zdenkae* **sp. nov.**, conspicuous apicomedial projection e.g. in the *B. alpinus* species group), (xxi) segment 2 distinctly narrowed in about 1/3 of its length, basal portion conical (+, as in *B. buceratus*) or bulbous (in *B. nexus*), distal part with convex outer and straight inner margin (inner margin slightly convex in *B. zdenkae* **sp. nov.**), (xxii) segment 3 oval, about twice as long as wide (+, as in remaining representatives of the *B. buceratus* species group, in contrast to the nearly spherical shape in *B. fuscatus* species group, or cylindrical, and nearly 3 times longer than wide in some representatives of the *B. alpinus* and *B. lutheri* species groups).

If evaluating the classification of *B. zdenkae* **sp. nov.** within the *B. buceratus* species group, it shares at least partially (+) 17 characters (i–iv, vi, viii–xiv, xvi, xix–xxii) specific just for this species group. The whole *B. buceratus* species group shares at least 12 characters (i, ii, vi, ix–xi, xiii, xiv, xvi, xx, xxii) with the *B. vernus* species group, hence these two groups seem to be most closely related. At least 10 characters (i–iii, v, x,

xi, xiii, xiv, xx, xxii) are shared with the *B. fuscatus* species group while the relationship to other species groups seem to be more remote. For example, only 7 characters (iii, v, vi, xiii, xvi, xviii, xx) seem to be surely shared with the *B. alpinus* species group.

The number of shared characters seems to be relatively high since we have selected only characters occurring in two or more species groups. Naturally, the above differences are much more pronounced when considering characters specific only for the species group (or even for some species of the respective group). For instance, there are the conspicuously bent up forceps in the *B. buceratus* species group or some prominent apomorphies such as the occurrence of “Rosettenbildung im Chagrin” (Müller-Liebenau 1974: 25) in the *B. lutheri* species group, or the quite unique arrangement of posterior margins of abdominal terga in *B. pavidus*. On the other hand, overestimating of unique apomorphies tends to further fragmentation to “subgroups” (Kleingruppen by Jacob 2003) that rather complicate the practical use of “species grouping”, e.g. during routine identification or determination of species. This can be well documented, for instance, with the subgenus *Nigrobaetis* (originally *B. niger* and *B. gracilis* species groups), that has been split, according to the arrangement of the protheca of the right mandible and other characters to at least 4–5 subgroups (see also “super-groups” by Novikova & Kluge 1994).

However, our choice of characters is far from being a complete and definitive enumeration of species group specific ones in the subgenus *Baetis* s. str. which undoubtedly urgently needs further more detailed study, especially as far as the characters of at least the male imago (preferably also females and subimagines) are concerned. For instance, further morphological characters will be undoubtedly found in musculature and muscle insertion in connection with color patterns, e.g. on the head (shape of the epicranial suture), head sense organs (e.g. flat-tipped sensillum and its occurrence within *Baetis*, see Gaino & Rebora 1999, 2003), or prothorax in larvae for distinctly different pronotum color pattern within the individual species (see, e.g. Jacob 2003: 63, Abb. 3). Further, the adult pterothorax apparently shows differences in the arrangement of sutures recently used in differential diagnoses of genera and higher taxa (see Kluge 1994, 2000, 2004 for details), but still very rarely applied in distinguishing species or species groups.

Additionally, the application of ootaxonomy considered of great importance within the Ephemeroptera in general, might help to elucidate *Baetis* species group interrelationships and probably serve as one of (if not the only) reliable characters to classify females and female subimagines. The chorionic structures of a relatively high number of representatives of all 6 European species groups have been described in detail (Kopelke & Müller-Liebenau 1981a, 1981b, 1982) but species group specific characters are hard to define and ootaxonomic study still has not yielded satisfactory results (see discussion by Kopelke & Müller-Liebenau 1982: 22 for details).

Evaluating only the above rather arbitrarily selected 22 characters, there are apparently two “groups of groups”. On one hand, there are the *B. alpinus* and *B. lutheri* species groups and on the other hand the *B. vernus*, *B. buceratus* and *B. fuscatus* species groups with quite different arrangement of at least 6, mainly larval characters (i, ii, iv, vi, ix, and xxii). As to at least the European species, the former “super-group” shows apparent relationships to the subgenus *Rhodobaetis* (shared or very similar character state in: ii, iii, vi, ix, x, xv, xix, xx, xxii), the latter seems to be related to *Labiobaetis* (shared or very similar character state in: i, ii, iv, vi, ix, x, xiii, xx) while the relationships of both “super-groups” to the subgenus *Nigrobaetis* are more remote as documented, e.g., by general body shape, mouthparts and the absence of a femoral villopore (see McCafferty & Waltz 1990 for definition, and Novikova & Kluge 1994, Waltz *et al.* 1994 or Waltz & McCafferty 1997 for details). The *B. pavidus* species group so far comprising only one species represents a “transitory” group, related rather to *B. alpinus* + *B. lutheri* species groups (shared or very similar character state in: i, ii, vii, ix, xii, xv, xxii), but characterized by the quite unique arrangement of some characters (e.g., xiii, xiv, xx and xxi, see Müller-Liebenau 1969: 32 or Jacob 2003: 81 for details).

Concerning biology of the subgenus *Baetis* s. str. in general, very similar relationships can be found as well. Larvae of *B. alpinus* + *B. lutheri* species groups (and also those of *B. pavidus* and most species of the

subgenus *Rhodobaetis*) inhabit stony habitats and often stream run places exposed to maximal current velocity and generally preferring rhithral biotopes at higher altitudes. Larvae of *B. vernus* + *B. buceratus* + *B. fuscatus* (and also those of the subgenus *Labiobaetis*) live, besides stony habitats at places usually with moderate to slow current velocity, very often (sometimes nearly exclusively) also among vascular submerged aquatic plants preferring potamal biotopes at usually lower elevations, including very large rivers.

Obviously, the species groups of *Baetis* s. str. follows in a great extent of the phylogenetic relationships within the subgenus, if we try to evaluate them according to most of apomorphies. However, the character-state of numerous characters is disputable, others may be extremely variable. For instance, the pattern of coloration varies greatly and usually agrees with internal muscle insertions (Müller-Liebenau 1969, 1974, Morihara & McCafferty 1979) and more than one species may express the same pattern. Grouping of most *Baetis* s. str. species (however extralimital) remain unknown and the whole subgenus requires a detailed revision at the species level. No general consensus in taxonomic consequences of species grouping of *Baetis* s. str. have been achieved, most authors recommend to wait until the revision is done. However, not available names (cf. Hubbard 1979 and ICZN art. 13.3) *Holobaetis* Sukatskene, 1962, *Montobaetis* Kazlauskas, 1972 and *Vernobaetis* Kazlauskas, 1972 have been applied to treat probably the *B. alpinus*, *B. vernus* and *B. fuscatus* species groups (cf. Sukatskene 1962, Kazlauskas 1972) and at least some Oriental species have been treated under the name *Tatubaetis* Kang & Yang, 1994 (in Kang *et al.* 1994: 23) now considered a subjective junior synonym of *Baetis* s. str. (Waltz & McCafferty 1997: 137). Recently, the subgenus *Patites* Thomas & Dia, 2000, has been erected to include *B. melanonyx* (Pictet, 1843) and *B. baroukianus* (type species) described from Lebanon, both species previously belonging to the *B. alpinus* species-group.

## Acknowledgements

Our sincere thanks are due to unknown reviewers for valuable comments to improve the manuscript. This study was supported by the Grant Agency of the Czech Republic (Project No. 206/08/1389 and No. 206/06/1133), and of the Grant Agency of the Academy of Sciences of the Czech Republic (Project No. QS500070505).

## References

- Alba-Tercedor, J. (1984) A revision of the European species of the genus *Baetis* LEACH, 1815 described by Reverend Longinos NAVÁS (Baetidae). In: Landa, V., Soldán, T. & Tonner, M. (Eds), *Proceedings of the IVth International Conference on Ephemeroptera*, Institute of Entomology, Academy of Sciences of the Czech Republic, Bechyne (Czech Republic), pp. 53–59.
- Alba-Tercedor, J. (2002) A new synonymy in *Baetis*: *Baetis nexus* Navás, 1918 is the valid name of *Baetis pentaphlebodes* Ujhelyi, 1966 (Ephemeroptera: Baetidae). *Aquatic Insects*, 24, 77–79.
- Alba-Tercedor, J. & Jáimez-Cuéllar, P. (2003) Checklist and historical evolution of the knowledge of Ephemeroptera in the Iberian Peninsula, Balearic and Canary Islands. In: Gaino, E (Ed.), *Research Update on Ephemeroptera and Plecoptera*, Università di Perugia, Perugia (Italy), pp. 91–97.
- Alba-Tercedor, J. & Peters, W.L. (1985) Types and additional specimens of Ephemeroptera studied by Longinos Navás in the Museo de Zoología del Ayuntamiento, Barcelona, Spain. *Aquatic Insects*, 7, 215–227.
- Al-Zubaidi, F., Braasch, D. & Al-Kayatt, A. (1987) Mayflies from Iraq (Insecta, Ephemeroptera). *Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden*, 14, 179–184.
- Bae, Y. J., Kluge, N. J. & Chun, D.J. (1998) New synonymy and new data on the distribution of the mayflies from Korea and the Russian Far East (Ephemeroptera). *Zoosystematica Rossica*, 7, 89–94.
- Belfiore, C. & D'Antonio, C. (1990) *Pseudocentropilum calabrum* sp. n. (Ephemeroptera, Baetidae), a new species of mayfly from Southern Italy. *Acta Entomologica Bohemoslovaca*, 87, 117–121.
- Belfiore, C. & Gaino, E. (1988) Il popolamento a Efemerotteri della Sardegna (Ephemeroptera). *Bollettino della Società Entomologica Italiana*, 20 (2), 75–83.

- Bengtsson, S. (1912) Neue Ephemeriden aus Schweden. *Entomologisk Tidskrift*, 33, 107–117.
- Bengtsson, S. (1917) Weitere Beiträge zur Kenntnis der nordischen Eintagsfliegen. *Entomologisk Tidskrift*, 38, 174–194.
- Bogoescu, C.D. (1947) Un genre nouveau d'Ephéméroptère trouvé en Roumanie. *Bulletin de la Section Scientifique de l'Académie Roumaine*, 29, 602–606.
- Buffagni, A. & Desio, F. (1994) Le specie del genere *Baetis* LEACH (Ephemeroptera: Baetidae) nell'Italia settentrionale: sintesi ecologica. In: *Atti XVII Congresso Ital. entomologia, Undine*, pp. 413–416.
- Burmeister, H. (1839) Ephemerina. *Handbuch der Entomologie*, 2 (2), 788–804.
- Camousseight, A. & Fontaine, J. (1990) The biological cycle of *Baetis pentaplebedes* Ujhelyi 1966, in an old meander of the Rhône River, France (Ephemeroptera: Baetidae). In: Campbell, I.C. (Ed.), *Mayflies and Stoneflies: Life Histories and Biology*, Kluwer Academic Publishers, Dordrecht (Netherlands), pp. 27–34.
- Clifford, H.F. (1982) Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. *Quaestiones Entomologicae*, 18, 15–90.
- Eaton, A.E. (1869) On *Centroptilum*, a new genus of the Ephemeridae. *Entomologist's Monthly Magazine*, 6, 131–132.
- Eaton, A.E. (1870) On some new British species of Ephemeridae. *Transactions of the Entomological Society of London*, 1870 (1), 1–8.
- Gaino, E. & Reborá, M. (1999) Flat-tipped sensillum in Baetidae (Ephemeroptera): a microcharacter for taxonomic and phylogenetic considerations. *Journal of Invertebrate Biology*, 118, 63–67.
- Gaino, E. & Reborá, M. (2003) The sensilla on the labial and maxillary palps of the nymph of *Baetis rhodani* (Ephemeroptera: Baetidae). In: Gaino, E. (Ed.), *Research Update on Ephemeroptera & Plecoptera*, Università di Perugia, Perugia (Italy), pp. 445–451.
- González del Tánago, M. (1984) Distribución y biología de la familia Baetidae (Ephem.) en la Cuenca del Duero. *Boletín de la Asociación de español Entomología*, 8, 73–94.
- Haybach, A. (1998) Die Eintagsfliegen (Insecta: Ephemeroptera) von Rheinland – Pfalz – Zoogeographie, Faunistik, Ökologie, Taxonomie und Nomenklatur – Unter besonderer Berücksichtigung der Familie Heptageniidae und unter Einbeziehung die übrigen aus Deutschland bekannten Arten. Dissertation am Fachbereich Biologie der Johannes Gutenberg-Universität Mainz, 417 pp.
- Haybach, A. (2003) Zoogeographische Aspekte der Eintagsfliegenbesiedlung Deutschlands (Insecta, Ephemeroptera). *Verhandlungen der westdeutschen Entomologentagung*, 2002, 187–209.
- Haybach, A. (2006) Die Eintagsfliegen von Rheinland-Pfalz (Insecta Ephemeroptera). *Mainzer Naturwissenschaftliches Archiv, Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz*, 29, 121 pp.
- Horsák, M. (2001) Contribution to the knowledge of macroinvertebrate fauna of the Dyje River downstream of the Nové Mlýny Reservoirs (Czech Republic). *Scripta Facultatis scientiarum naturalium Universitatis Masarykianae brunensis, Biologia, Supplementum*, 27, 41–62.
- Hubbard, M.D. (1979) Genera and subgenera of Recent Ephemeroptera. *Eatonia, Supplement 2*, 1–8.
- Jacob, U. (1972) Beitrag zur autochthonen Ephemeropterenfauna in der Deutschen Demokratischen Republik. Dissertation Universität Leipzig, Leipzig, 158 pp.
- Jacob, U. (1991) Ephemeroptera: Zur Systematik der europäischen Baetidae auf Gattungsebene. *Verhandlungen der Westdeutschen Entomologentagung*, 1990, 271–290.
- Jacob, U. (2003) *Baetis* Leach, 1815 sensu stricto oder sensu lato. Ein Beitrag zum Gattungskonzept auf der Grundlage von Artengruppen mit Bestimmungslüsseln. *Lauterbornia*, 47, 59–129.
- Jensen, C.F. (1969) *Baetis buceratus* EAT. og *Metretopus borealis* EAT. nye for Danmark Ephemeroptera-Døgnfluer). *Flora og Fauna*, 75, 129–134.
- Leach, W.E. (1815) *Entomology*. Brewster's Edinburgh Encyclopaedia, 9, 57–172.
- Kang, S.C., Chang, H.C. & Yang, C.T. (1994) A revision of the genus *Baetis* in Taiwan (Ephemeroptera, Baetidae). *Journal of the Taiwan Museum*, 47 (2), 9–44.
- Kazanci, N. (1984) New Ephemeroptera (Insecta) from Turkey. *Aquatic Insects*, 6, 253–258.
- Kazlauskas, R.S. (1972) Neues über das System der Eintagsfliegen der Familie Baetidae (Ephemeroptera). *Proceedings of the 13th International Congress of Entomology, Moscow, 1968*, 3, 337–338.
- Keffermüller, M. (1972) Investigations on the mayflies (Ephemeroptera) fauna in Great Poland. V. *Polskie Pismo Entomologiczne*, 43, 527–533. (in Polish, Engl. sum.)
- Kluge, N.J. (1994) Pterothorax structure of mayflies (Ephemeroptera) and its use in systematics. *Bulletin de la Société entomologique de France*, 99 (1), 41–61.
- Kluge, N.J. (1997). *Order Ephemeroptera*. In: Tsalolikhin, S.J. (Ed.). *Key to Freshwater Invertebrates of Russia and adjacent lands*, Vol. 3, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, pp. 175–220, Tab. 8–20 (304–329). (in Russian)
- Kluge, N.J. (2000). *Modern systematics of insects. Part I. Principles of systematics of living organisms and general system of insects with classification of primary wingless and palepterous insects*. LAN' Publishers, St. Petersburg, 336 pp. (in Russian)
- Kluge, N.J. (2004) *The Phylogenetic System of Ephemeroptera (the first experience in consistently non-ranking taxon-*

- omy) Volume 1. *Ephemeroptera except for Turbanoculata and Leptophlebia/fg1*. Kluwer Academic Publishers, Dordrecht, 456 pp.
- Koch, S. (1988) Mayflies of the northern Levant (Insecta: Ephemeroptera). *Zoology in the Middle East*, 2, 89–112.
- Kopelke, J.-P. & Müller-Liebenau, I. (1981a) Eistrukturen bei Ephemeroptera und deren Bedeutung für die Aufstellung von Artengruppen am Beispiel der europäischen Arten der Gattung *Baetis* Leach, 1815. Teil II: *rhodani*-, *vernus*- und *fuscatus*-Gruppe. *Spixiana*, 4, 39–54.
- Kopelke, J.-P. & Müller-Liebenau, I. (1981b) Eistrukturen bei Ephemeroptera und deren Bedeutung für die Aufstellung von Artengruppen am Beispiel der europäischen Arten der Gattung *Baetis* Leach, 1815. Teil III: *buceratus*-, *atrebatinus*-, *niger*-, *gracilis*- und *muticus*-Gruppe (Ephemeroptera, Baetidae). *Deutsche Entomologische Zeitschrift*, 28, 1–6.
- Kopelke, J.-P. & Müller-Liebenau, I. (1982) Eistrukturen bei Ephemeroptera und deren Bedeutung für die Aufstellung von Artengruppen am Beispiel der europäischen Arten der Gattung *Baetis* Leach, 1815, (Insecta: Baetidae). Teil I: *alpinus*-, *lutheri*-, *pavidus*- und *lapponicus*-Gruppe. *Gewässer und Abwässer*, 68/69, 7–25.
- Landa, V. (1968) Developmental cycles of Central European Ephemeroptera and their interrelations. *Acta Entomologica Bohemoslovaca*, 65, 276–284.
- Landa, V. & Soldán, T. (1989) *Distribution of Mayflies (Ephemeroptera) and its changes in the Labe Basin of Czechoslovakia in Connection with Changes of Water Quality*. Academia, Praha, Studie CSAV, 17, 171 pp. (in Czech, Engl. sum.)
- Langford, T.E. (1971) The distribution, abundance and life histories of stoneflies (Plecoptera) and mayflies (Ephemeroptera) in a British river, warmed by cooling-water from a power station. *Hydrobiologia*, 38 (2), 339–377.
- McCafferty, W.P. & Waltz, R.D. (1990) Revisionary synopsis of the Baetidae (Ephemeroptera) of North and Middle America. *Transactions of the American Entomological Society*, 116, 769–799.
- Morihara, D.K. McCafferty, W.P. (1979) The *Baetis* larvae of North America (Ephemeroptera: Baetidae). *Transactions of the American Entomological Society*, 105, 139–221.
- Müller-Liebenau, I. (1969) Revision der europäischen Arten der Gattung *Baetis* Leach, 1815 (Insecta, Ephemeroptera). *Gewässer und Abwässer*, 48/49, 1–214.
- Müller-Liebenau, I. (1974) Baetidae aus Südfrankreich, Spanien und Portugal (Insecta, Ephemeroptera). *Gewässer und Abwässer*, 53/54, 7–42.
- Müller-Liebenau, I. (1981) Review of the original material of the baetid genera *Baetis* and *Pseudocloeon* from the Sunda Islands and Philippines described by G. Ulmer, with some general remarks (Insecta: Ephemeroptera). *Mitteilungen Hamburg Zoologisches Museum und Institute*, 78, 197–208.
- Müller-Liebenau, I. (1984) New genera and species of the family Baetidae from West Malaysia (River Gombak) (Insecta: Ephemeroptera). *Spixiana*, 7, 253–284.
- Navás, L. (1918) Excursiones entomológicas por el Norte de la provincia de Lérida (6–24 de Julio de 1917). *Butlletí de la Institució catalana d'Historia Natural*, 1918, 36–49.
- Newman, E. (1853) *Proposed division of Neuroptera into two classes*. *Zoologist*. Volume 11, John von Voorst Paternoster Row., London, 181–204.
- Novikova, E.A. (1987) Mayflies of the group *Baetis transiliensis* Brod. (Ephemeroptera, Baetidae) in Middle Asia. *Entomologicheskoe Obozrenie*, 66 (3), 572–576. (in Russian, Engl. sum.)
- Novikova, E.A. & Kluge, N.J. (1987). Systematics of the genus *Baetis* (Ephemeroptera, Baetidae), with description of new species from Middle Asia. *Vestnik Zoologii*, 1987 (4), 8–19.
- Novikova, E.A. & Kluge, N.J. (1994) Mayflies of the subgenus *Nigrobaetis* (Ephemeroptera, Baetidae, Baetis). *Entomologicheskoe Obozrenie*, 73 (3), 623–644. (in Russian, Engl. sum.)
- Pictet, F.J. (1843-1845) *Histoire naturelle générale et particulière des insectes névroptères. Famille des éphémérides*. Chez Kessmann, J. & Cherbuliz, Ab., Genève, 1–300.
- Sartori, M. & Landolt, P. (1999) Atlas de distribution des Ephémères de Suisse (Insecta, Ephemeroptera). *Fauna helvetica*, 3, SEG–CSCF ed., Neuchâtel, 214 pp.
- Sartori, M. & Soldán, T. (2006) Case 3322. *Baetis pentaplebedes* Ujhelyi, 1966 (Insecta, Ephemeroptera) proposed precedence over *Baetis nexus* Navás, 1918. *Bulletin of Zoological Nomenclature*, 63 (1), 23–27.
- Soldán, T. & Godunko, R.J. (2008) Two new species of the genus *Baetis* Laech, 1815 (Ephemeroptera: Baetidae) from Cyprus. *Annales Zoologici*, 58 (1): 79–104.
- Soldán, T. & Zahrádková, S. (2000) Ephemeroptera of the Czech Republic: Atlas of Distribution. In: Helešic, J. & Zahrádková, S. (Eds). *Fauna Aquatica Europae Centralis I*. Masaryk University, Brno (Czech Republic), 401 pp.
- Sowa, R. (1975) Ecology and biogeography of mayflies (Ephemeroptera) of running waters in the Polish part of the Carpathians. 2. Life cycles. *Acta Hydrobiologica*, 17, 319–353.
- Sowa, R. (1985) *Pseudocentropilum fascicaudale* n. sp. (Ephemeroptera, Baetidae) from Greece. *Acta Hydrobiologica*, 27, 75–80.
- Stephens, J.F. (1836) Family III. – *Ephemeridae*, Leach. Illustrations of British Entomology, Mandibulata, London, 6, 54–70.

- Sukatskene, I.K. (1962) Mayflies (Ephemeroptera) of the Angara River and its tributaries in the area of the Bratsk Hydro-electric Station Reservoir. *Lietuvos TSR Mokslu Akad. Darbai, Ser. C, 2*, 107–122. (in Russian)
- Thomas, A.G.B. & Dia, A. (1983) *Baetis bisri* n. sp., Ephéméroptère nouveau du Liban (Baetidae). *Annales de Limnologie*, 19 (3), 213–217.
- Thomas, A.G.B. & Dia, A. (1984) *Baetis baroukianus* n. sp., Ephéméroptère nouveau du Liban (Baetidae). *Bulletin de la Société de Histoire Naturelle Toulouse*, 120, 7–11.
- Thomas, A.G.B. & Dia, A. (1985) *Baetis spei* n. sp., Ephéméroptère nouveau du Liban: description et écologie (Baetidae). *Annales de Limnologie*, 21 (3), 241–245.
- Thomas, A. & Dia, A. (2000) Compléments et corrections à la faune des Ephéméroptères du Proche-Orient. 4. Description de l'imago mâle de *Baetis baroukianus* Thomas & Dia, 1984 et érection de *Patites* n. subgen. [Ephemeroptera, Baetidae]. *Ephemera* (1999), 1 (2), 105–109.
- Thomas, A. & Dia, A. (2007) Compléments et corrections à la faune des Éphéméroptères du Proche-Orient. 7. Description de l'imago mâle de *Baetis spei* Thomas, 1985 [Ephemeroptera, Baetidae]. *Ephemera*, 8 (2): 75–78.
- Ujhelyi, S. (1966) The mayflies of Hungary, with the description of a new species, *Baëtis pentaplebedes* sp. n. (Ephemeroptera). *Acta Zoologica Academiae Scientiarum Hungaricae*, 12 (1–2), 203–210.
- Waltz, R.D. & McCafferty, W.P. (1987) New genera of Baetidae for some Nearctic species previously in *Baetis* Leach (Ephemeroptera). *Annals of the Entomological Society of America*, 80 (5), 667–670.
- Waltz, R.D. & McCafferty, W.P. (1997) New generic synonymies in Baetidae (Ephemeroptera). *Entomological News*, 108, 134–140.
- Waltz, R.D., McCafferty, W.P. & Thomas, A. (1994) Systematics of *Alainites* n. gen., *Dipheter*, *Indobaetis*, *Nigrobaetis* n. stat., and *Takobia* n. stat. (Ephemeroptera, Baetidae). *Bulletin de la Société de Histoire Naturelle Toulouse*, 130, 33–36.