

RESEARCH PAPER

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Genera and species of Baetidae in Japan: *Nigrobaetis*, *Alainites*, *Labiobaetis*, and *Tenuibaetis* n. stat. (Ephemeroptera)

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Abstract We describe morphological characters of the genera *Nigrobaetis*, *Alainites*, *Labiobaetis*, and *Tenuibaetis* n. stat. and provide generic situations of six Japanese species: *Nigrobaetis chcoratus* n. comb., *N. sacishimensis* n. comb., *Alainites atagonis*, *A. florens*, *A. yoshinensis*, and *Tenuibaetis pseudofrequentus*. To evaluate the polarities of the morphological characters and the monophyly of *Nigrobaetis*, *Alainites*, *Labiobaetis*, and *Tenuibaetis*, character states of these four genera were compared with the genus *Cloeon* as an outgroup. *Labiobaetis* is considered to be a monophyletic group supported by a wide paraglossa. *Tenuibaetis* is a monophyletic group that is distinguishable from the related genera by robust setae with a medial ridge on the dorsomedian surface of the nymphal femur. We did not find any synapomorphic characters of *Nigrobaetis* or *Alainites*. Although we tentatively treat *Nigrobaetis* and *Alainites* as distinct genera, they are considered to be paraphyletic taxa.

Key words Ephemeroptera · Baetidae · Genera · Taxonomy · Japan

Introduction

The genus *Baetis* Leach (s. lat.) contains a large number of species and is considered polyphyletic. In Palearctic and Oriental species, subdivision of *Baetis* (s. lat.) into genera or

subgenera was initiated by Novikova and Kluge (1987), who erected the subgenera *Nigrobaetis*, *Labiobaetis*, and *Takobia*. Waltz and McCafferty (1987) transferred some *Baetis* (s. lat.) species to the genera *Acentrella* Bengtsson and *Baetiella* Uéno. Waltz et al. (1994) raised *Nigrobaetis* from subgenus to genus and also established the genus *Alainites* Waltz and McCafferty. Subsequently McCafferty and Waltz (1995) raised *Labiobaetis* to the generic rank. Kang et al. (1994) erected five new subgenera: *Acerbaetis* Kang and Yang, *Tenuibaetis* Kang and Yang, *Tatubaetis* Kang and Yang, *Mullerbaetis* Kang and Yang and *Margobaetis* Kang and Yang, based on 13 species occurring in Taiwan. But Waltz and McCafferty (1997) transferred these subgenera to *Alainites*, *Baetiella*, *Baetis* (s. str.), *Labiobaetis*, and *Nigrobaetis*, respectively. A total of 18 *Baetis* (s. lat.) species, including 12 species from Taiwan, two from the Himalayas, two from West Malaysia, one from Algeria, and one from Tajikistan, were also transferred to *Alainites*, *Baetiella*, *Labiobaetis*, *Nigrobaetis*, and *Takobia* by Waltz and McCafferty (1997).

In Japan, 22 *Baetis* (s. lat.) species were recorded by Uéno (1928, 1931a, 1931b, 1969), Matsumura (1931), Imanishi (1937), and Gose (1965, 1980a, 1980b), but currently 17 species are valid. Kobayashi (1987) distinguished 18 *Baetis* species in the nymphal stage, in which he gave alphabetical provisional names to 13 species. Tanida (1991) provided photographs of 14 Japanese *Baetis* (s. lat.) species.

Recently, Japanese *Baetis* (s. lat.) species were also assigned to other subgenera or transferred to other genera, although Ishiwata (2001a) retained their generic situation as *Baetis*. Novikova and Kluge (1994) assigned *B. chcoratus* Gose, *B. florens* Imanishi, and *B. yoshinensis* Gose to the subgenus *Nigrobaetis*. Waltz et al. (1994) transferred *B. sacishimensis* Uéno to the genus *Alainites*. Waltz and McCafferty (1997) transferred *B. atagonis* Imanishi and *A. sacishimensis* to the genus *Nigrobaetis*, and *B. (N.) yoshinensis* to *Alainites*. Herein, we raise the subgenus *Tenuibaetis* to genus. We also provide the present generic situation of the following baetid species that are present in Japan: *Nigrobaetis chcoratus* n. comb., *N. sacishimensis* n. comb., *Alainites atagonis*, *A. florens*, *A. yoshinensis*, and

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Tenuibaetis pseudofrequentus (Müller-Liebenau). The polarity of morphological characters and monophyly are discussed in regard to these genera.

Descriptions

Genus *Nigrobaetis* Novikova and Kluge, 1987
[Japanese name: Tobiiro-Kokagerou-Zoku]

Baetis (*Nigrobaetis*) Kazlauskas, 1972, 337 nom. nud., in Waltz et al., 1994, 34; Novikova and Kluge, 1987, 8 (type species: *Ephemer niger* Linné 1761, by original designation); Novikova and Kluge, 1994, 623 (in part).

Nigrobaetis: Waltz et al., 1994, 34; Waltz and McCafferty, 1997, 138.

Baetis (*Margobaetis*) Kang and Yang, in Kang et al., 1994, 11 (type species: *Baetis mundus* Chang and Yang, 1994, by original designation).

Distribution. Palearctic, Oriental, Ethiopian.

Characters of imagoes. Anterior margin of frons with medial ridge, convex in lateral view (Fig. 1A). Hind wing present or absent; when present, with distinct costal projection and two or three longitudinal veins, with vein II forked (Fig. 2A). Apical segment of forceps elongate (Fig. 3A).

Characters of nymphs. Medial ridge of frons present or absent (Fig. 4A: median ridge present). Distal lobe of an-

tenal scape absent (Fig. 5A). Inner margin of mandible with row of spines (Fig. 6A, B). Right prosthema maniform (Fig. 6A) or spinelike (Fig. 6B). Depression near apex of maxillary palpus absent (Fig. 7A). Glossa with setal patch at subapical region (Fig. 8A). Paraglossa 1.0–1.6 times wider than glossa (Fig. 8A). Labial palpus with segment II not expanded on inner margin, segment III blunt at apex (Fig. 9A). Femur without robust setae on dorsomedian surface (Fig. 10A). Villopore absent (Fig. 11A). Paraproct without projection on inner distal end, patch of notched scales present or absent on the surface (Fig. 12A: notched scales absent).

In nymphs, we found the following characters of *Nigrobaetis* species: lack of robust setae on dorsomedian surface of femur (Fig. 10A) and presence of patch of notched scales on paraproct.

Novikova and Kluge (1987) erected the subgenus *Nigrobaetis*, but they did not provide any diagnostic characters for this subgenus. Waltz et al. (1994) raised *Nigrobaetis* to the generic rank and adopted the combination of the following characters as a diagnosis of *Nigrobaetis*: elongate

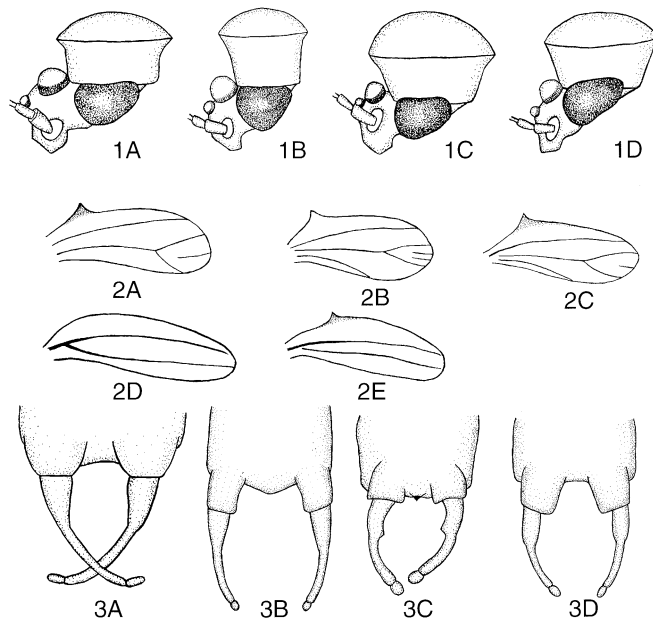


Fig. 1A–D. Imaginal characters of baetid species: male heads in lateral view. **A**, *Nigrobaetis* sp. D; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis* sp. G; **D**, *Tenuibaetis pseudofrequentus*

Fig. 2A–E. Imaginal characters of baetid species: Hind wings. **A**, *Nigrobaetis sachisimensis* [redrawn from Uéno (1969)]; **B**, *Alainites atagonis* [redrawn from Gose (1980b)]; **C**, *A. yoshinensis*; **D**, *Labiobaetis* sp. G; **E**, *Tenuibaetis pseudofrequentus*

Fig. 3A–D. Imaginal characters of baetid species: forceps. **A**, *Nigrobaetis sachisimensis* [redrawn from Uéno (1969)]; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis tricolor* [sclerotized plate, redrawn from Keffermüller (1972)]; **D**, *Tenuibaetis pseudofrequentus*

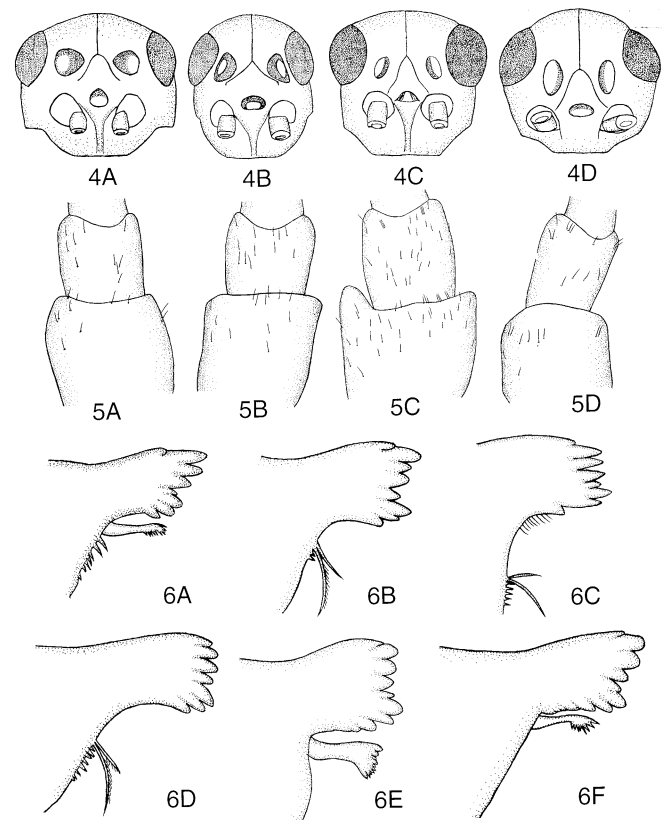


Fig. 4A–D. Nymphal characters of baetid species: heads. **A**, *Nigrobaetis chocoratus*; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis* sp. G; **D**, *Tenuibaetis pseudofrequentus*

Fig. 5A–D. Nymphal characters of baetid species: basal segments of antennae. **A**, *Nigrobaetis chocoratus*; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis* sp. G (a distal lobe on scape); **D**, *Tenuibaetis pseudofrequentus*

Fig. 6A–F. Nymphal characters of baetid species: right mandibles. **A**, *Nigrobaetis* sp. D; **B**, *N. chocoratus*; **C**, *Alainites florens*; **D**, *A. yoshinensis*; **E**, *Labiobaetis* sp. G; **F**, *Tenuibaetis pseudofrequentus*. Figures 6B, C were redrawn from Gose (1980a)

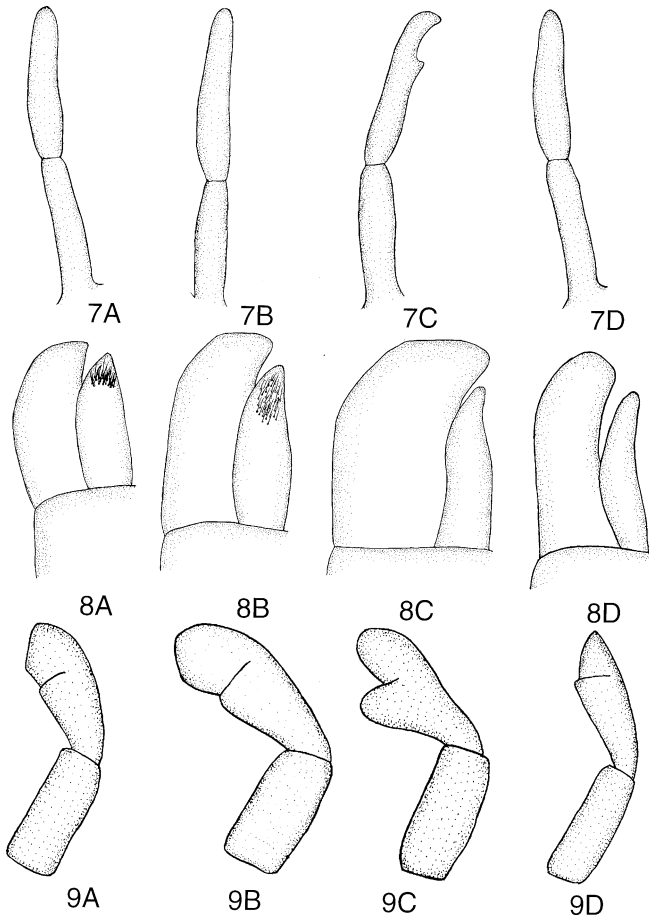


Fig. 7A–D. Nymphal characters of baetid species: maxillary palpi. **A**, *Nigrobaetis chocoratus*; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis* sp. G; **D**, *Tenuibaetis pseudofrequentus*

Fig. 8A–D. Nymphal characters of baetid species: labia (right half, dorsal, marginal setae omitted). **A**, *Nigrobaetis chocoratus*; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis* sp. G; **D**, *Tenuibaetis pseudofrequentus*

Fig. 9A–D. Nymphal characters of baetid species: labial palpi. **A**, *Nigrobaetis chocoratus*; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis morus*; **D**, *Tenuibaetis pseudofrequentus*. Figures 9A, C, D were redrawn from Kang et al. (1994)

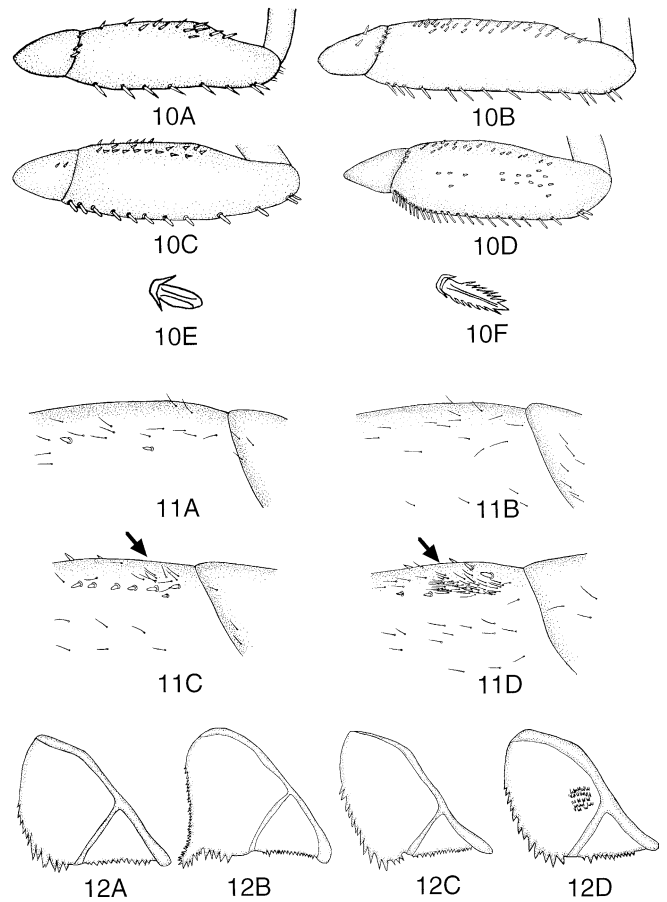


Fig. 10A–F. Nymphal characters of baetid species: femora and robust setae in the dorsomedian surface. **A**, *Nigrobaetis chocoratus*; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis* sp. G; **D**, *Tenuibaetis pseudofrequentus*; **E**, robust seta of *T. pseudofrequentus*; **F**, robust seta of *Cloeon dipterum*

Fig. 11A–D. Nymphal characters of baetid species: proximal ends of anterior margin of femora (ventral). **A**, *Nigrobaetis chocoratus*; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis* sp. G (villopore arrowed); **D**, *Tenuibaetis pseudofrequentus* (villopore arrowed)

Fig. 12A–D. Nymphal characters of baetid species: paraprocts. **A**, *Nigrobaetis chocoratus*; **B**, *Alainites yoshinensis*; **C**, *Labiobaetis* sp. G; **D**, *Tenuibaetis pseudofrequentus*

apical segment of forceps in imago (Fig. 3A), presence of setal patch near apex of glossa (Fig. 8A), and lack of projection on paraproct in nymph (Fig. 12A). At present, we do not know any synapomorphic characters of *Nigrobaetis* (see discussions below). Probably *Nigrobaetis* is a paraphyletic taxon. We, however, tentatively treat *Nigrobaetis* as a distinct genus following the opinion of Waltz et al. (1994).

Nigrobaetis includes the *gracilis* group and a part of the *niger* group of *Baetis* provided by Müller-Liebenau (1969) (Waltz and McCafferty 1997).

Nigrobaetis chocoratus (Gose 1980) n. comb.
 [Japanese name: Tobiiro-Kokagerou]

Baetis chocoratus Gose, 1980a, 79; Gose, 1985, 20; Kobayashi, 1987, 53; Ishiwata, 2001a, 66; Ishiwata, 2001b, 180.

Baetis (*Nigrobaetis*) *chocoratus*: Novikova and Kluge, 1994, 628.

Alainites chocoratus: Waltz and McCafferty, 1997, 135.

Distribution. Japan (Honshu, Shikoku, Kyushu)

Gose (1980a) described this species in the nymphal stage and showed its spinelike right prostheca (Fig. 6B). The nymph of this species lacks a projection at the inner distal margin of the paraproct (Ishiwata 2001b) (Fig. 12A). The imago of this species has not been described. We found that the nymphal glossa possesses a setal patch near the apex (Fig. 8A). Although Waltz and McCafferty (1997) placed this species in *Alainites*, we assign it to *Nigrobaetis* based on the absence of the projection on the paraproct (Fig. 12A).

Nigrobaetis sacishimensis (Uéno 1969) n. comb.

[Japanese name: Ryukyu-Kokagerou]

Baetis sacishimensis Uéno, 1969, 222; Gose, 1980b, 122; Ishiwata, 2001a, 67; Ishiwata and Kobayashi, 2003, 296.

Alainites sacishimensis: Waltz et al., 1994, 34.

Distribution. Japan (Ryukyu Islands)

The male imago of this species was described by Uéno (1969), but the female and nymph are not known. The hind wing of this species has two longitudinal veins, and vein II is forked (Fig. 2A) (Uéno 1969). In the forceps of this species, the apical segment is elongate (Fig. 3A) (Uéno 1969; Gose 1980b). Although Waltz and McCafferty (1997) placed this species in *Alainites*, we assign it to *Nigrobaetis* based on the two longitudinal veins, with vein II forked in the hind wing, and the elongate apical segment of the forceps.

Genus *Alainites* Waltz and McCafferty, 1994

[Japanese generic name: Shirinaga-Kokagerou-Zoku]

Alainites Waltz and McCafferty, in Waltz et al., 1994, 34 (type species: *Baetis muticus* Linné, 1758, by original designation); Waltz and McCafferty, 1997, 135.

Baetis (*Nigrobaetis*) Kazlauskas, 1972, 337 nom. nud., in Waltz et al., 1994, 34; Novikova and Kluge, 1987, 8 (type species: *Ephemera niger* Linné 1761, by original designation); Novikova and Kluge, 1994, 623 (in part).

Baetis (*Acerbaetis*) Kang and Yang, in Kang et al., 1994, 35 (type species: *Baetis clivus* Chang and Yang, 1994, by original designation).

Distribution. Palearctic, Oriental.

Characters of imagoes. Anterior margin of frons with medial ridge, convex in lateral view (Fig. 1B). Hind wing present or absent; when present, with distinct costal projection and three longitudinal veins, with vein II forked (Fig. 2B, C). Apical segment of forceps globular (Fig. 3B) or slightly elongate and curved.

Characters of nymphs. Medial ridge of frons present (Fig. 4B). Distal lobe on antennal scape absent (Fig. 5B). Inner margin of mandible with row of spines (Fig. 6C, D). Right prostheca spinelike (Fig. 6C, D). Maxillary palpus without depression near apex (Fig. 7B). Glossa with setal patch at subapical region (Fig. 8B). Paraglossa 1.3–1.5 times wider than glossa (Fig. 8B). Labial palpus with segment II not expanded on inner margin, segment III blunt at apex (Fig. 9B). Femur without robust setae on dorsomedian surface (Fig. 10B). Villopore absent (Fig. 11B). Paraproct with projection on inner distal end, without a patch of notched scales (Fig. 12B).

Waltz et al. (1994) erected the genus *Alainites*. This genus can be separated from other genera by the combination of the following characters: a globular or slightly elongate apical segment of the forceps in the male imago (Fig. 3B) and a projection on the inner distal end of the paraproct in the nymph (Fig. 12B) (Waltz et al. 1994). We found that the following characters are common to *Alainites* and *Nigrobaetis*: convex anterior margin of frons (Fig. 1B) and forked vein II of hind wing in the imago (if hind wing present) (Fig. 2C); medial ridge of frons (Fig. 4B), a setal patch near apex of glossa (Fig. 8B), and the absence of villopore in nymphs (Fig. 11B) (Table 1). *Alainites* species have three longitudinal veins in the hind wing in the imago and a spinelike prostheca in the nymph, but these character states are known in some *Nigrobaetis* species (Table 1). It is probable that *Alainites* is a paraphyletic taxon, because synapomorphic characters of this genus have not been found (see discussion below). We, however,

tentatively adopt the generic status of *Alainites* provided by Waltz et al. (1994).

The *muticus* group (Müller-Liebenau 1974) and part of the *niger* group (Müller-Liebenau 1969) of *Baetis* are transferred to *Nigrobaetis* (Waltz and McCafferty 1997).

Alainites atagonis (Imanishi 1937)

[Japanese name: Atago-Kokagerou]

Baetis atagonis Imanishi, 1937, 337; Gose, 1980b, 122; Ishiwata, 2001a, 66.

Alainites atagonis: Waltz and McCafferty, 1997, 135.

Distribution. Japan (Honshu: Kyoto Pref.)

Imanishi (1937) described male and female imagoes of this species, but the type specimens are lost (Narita, personal communication). Neither nymphs nor additional imagoes have been collected. This species has three longitudinal veins in the hind wing, with vein II forked (Fig. 2B) (Imanishi 1937; Gose 1980b). The forceps of this species possess a projection on the inner apical margin of the basal segment (Imanishi 1937). Presumably Waltz and McCafferty (1997) assigned this species to *Alainites* based only on the original description. The venation in the hind wing indicates that this species can be assigned to *Alainites* or *Nigrobaetis*, but the projection of the basal segment of the forceps is not known in other *Alainites* species. We cannot determine whether this species belongs to *Nigrobaetis* or *Alainites*, but we tentatively follow the generic assignment of Waltz and McCafferty (1997). Waltz and McCafferty (1997) mistook Gose as the author of this species.

Alainites florens (Imanishi 1937)

[Japanese name: Furorensu-Kokagerou]

Baetis florens Imanishi, 1937, 337; Gose, 1980a, 79; Gose, 1980b, 122; Gose, 1985, 20; Ishiwata, 2001a, 66.

Baetis (*Nigrobaetis*) *florens*: Novikova and Kluge, 1994, 628.

Alainites florens: Waltz and McCafferty, 1997, 135.

Distribution. Japan (Honshu: Kyoto Pref.)

Male and female imagoes were described by Imanishi (1937) and the nymphs by Gose (1980a). As in *A. atagonis*, the type specimens of this species are lost (Narita, personal communication). Imagoes of this species possess hind wings with two simple longitudinal veins (Imanishi 1937) and the apical segment of the forceps is slightly elongate (Gose 1980b). The nymph of this species possesses a spinelike right prostheca (Fig. 6C) (Gose 1980a, 1985). Novikova and Kluge (1987) located this species under the subgenus *Nigrobaetis*, but Waltz and McCafferty (1997) transferred it to the genus *Alainites*. Hind wings without forked veins are not known in *Alainites*, but the shape of the right prostheca in the nymph indicates that this species can be placed in *Alainites* or *Nigrobaetis*. The generic situation is also doubtful in this species, but herein we tentatively follow the generic assignment of Waltz and McCafferty (1997).

Alainites yoshinensis (Gose 1980)

[Japanese name: Yoshino-Kokagerou]

Baetis yoshinensis Gose, 1980a, 79; Gose, 1980b, 122; Gose, 1985, 20; Kobayashi, 1987, 53; Ishiwata, 2001a, 68;

Table 1. Character states of *Alainites*, *Nigrobaetis*, *Labiobaetis*, *Tenuibaetis*, and *Cloeon* as a possible outgroup genus

	Baetinae					Cloeoninae	
	<i>Nigrobaetis</i>	<i>Alainites</i>	<i>Labiobaetis</i>	<i>Tenuibaetis</i>		<i>Cloeon</i>	<i>Cloeon</i>
Imagoes							
Frons	Convex	Convex	Convex/straight	Straight	Straight	Straight	Straight
Hind wing (if present)	+/-	+/-	+/-	+	+	-	-
	Distinct	Distinct	Weak/absent	Distinct	Distinct	-	-
	2/3	3	2	2	2	-	-
	+	+	-	-	-	-	-
Forceps	Elongate	Globular/slightly elongate	Globular	Oval	Oval	Oval	Oval
	-	-	+	-	-	-	-
Nymphs							
Frons	+/-	+	+/-	-	-	-	-
Antennal scape	-	-	+	-	-	-	-
Mandible	+	+	-	-	-	+	+
Right prosthema	Maniform/spinelike	Spinelike	Maniform	Maniform	Maniform	Maniform	Maniform
Maxillary palpus	-	-	+/-	-	-	-	-
Labium	+	+	1.8 <	1.3-1.8	1.3-1.8	-	-
	1.0-1.6	1.3-1.5	Blunt	Pointed	Pointed	About 1.0	About 1.0
	Blunt	Blunt	+/-	-	-	Blunt	Blunt
Labial palpus	-	-	-	+	+	-	-
Femur	-	-	-	+	+	+	+
	-	-	-	(smooth margin)	(smooth margin)	(serrated margin)	(serrated margin)
Villopore	-	-	+ (rudimentary)/absent	+	+	-	-
Paraproct	-	+	-	-	-	-	-
	+/-	-	+/-	+	+	+/-	+/-
	-	-	-	-	-	-	-
Projection at inner distal end	-	+	-	-	-	-	-
Patch of notched scale	+/-	-	+/-	+	+	+/-	+/-

Ishiwata, 2001b, 180; Ishiwata, 2002, 15; Ishiwata and Kobayashi, 2003, 296.

Baetis (Nigrobaetis) yoshinensis: Novikova and Kluge, 1994, 629.

Alainites yoshinoensis [!]: Waltz and McCafferty, 1997, 135.

Distribution: Japan (Hokkaido, Honshu, Shikoku, Kyushu, Ryukyu Islands)

Nymphs and male imagoes of this species were described by Gose (1980a) and Gose (1980b), respectively, but the female imago is unknown. The male imago of this species possesses three longitudinal veins in the hind wing, with vein II forked (Gose 1980b) (Fig. 2C). The apical segment of the forceps is globular (Fig. 3B) (Gose 1980b). The nymph of this species has a spinelike right prosthema (Fig. 6D) (Gose 1980a, 1985; Ishiwata 2001b) and a paraprot with a projection at the inner distal end (Fig. 12B) (Ishiwata 2001b). We found that the nymphal glossa had a subapical setal patch (Fig. 9B). This species can be assigned to *Alainites* based on the diagnoses provided by Waltz et al. (1994). Nymphs of *A. yoshinensis* have six pairs of gills (Kobayashi 1987; Ishiwata 2001b), but Novikova and Kluge (1994) misunderstood that this species had seven pairs of gills in keys for nymphs of *Nigrobaetis* species.

Genus *Labiobaetis* Novikova and Kluge, 1987

[Japanese generic name: Futohige-Kokagerou-Zoku]

Baetis (Labiobaetis) Novikova and Kluge, 1987, 8 (type species: *Baetis atrebatinus* Eaton, 1870, by original designation).

Baetis (Mullerbaetis) Kang and Yang, in Kang et al., 1994, 32 (type species: *Baetis molawiensis* Müller-Liebenau, 1984, by original designation).

Labiobaetis: McCafferty and Waltz, 1995, 19; Gattolliat, 2001, 97, previously synonymized with *Pseudocloeon* Klapálek, 1905 (type species: *Pseudocloeon kraepelini* Klapálek, 1905, by monotypy) by Lugo-Ortiz et al., 1999, 1.

Distribution. Palearctic, Oriental, Ethiopian, Nearctic.

Characters of imagoes. Anterior margin of frons with medial ridge, straight or convex in lateral view (Fig. 1C: convex in lateral view). Hind wing present or absent; when present, costal projection weak or absent, with two simple longitudinal veins (Fig. 2D). Apical segment of forceps globular, with sclerotized plate between basal segments (Fig. 3C).

Characters of nymphs. Medial ridge on frons present or absent (Fig. 4C: medial ridge present). Distal lobe on antennal scape present or absent (Fig. 5C: distal lobe present). Inner margin of mandible without row of spines (Fig. 6E). Right prosthema manifold (Fig. 6E). Depression near apex of maxillary palpus present or absent (Fig. 7C: depression present). Glossa without a setal patch at subapical region (Fig. 8C). Paraglossa at least 1.8 times wider than glossa (Fig. 8C). Labial palpus with segment II distinctly expanded on inner margin or not, segment III blunt at apex (Fig. 9C: expansion present). Femur without robust setae on dorsomedian surface (Fig. 10C). Villopore rudimentary or absent (Fig. 11C: rudimentary). Paraproct without projec-

tion on inner distal end, patch of notched scales present or absent (Fig. 12C: notched scales absent).

In nymphs, we found the following characters in *Labiobaetis*: lack of a setal patch near the apex of the glossa (Fig. 8C), the absence of robust setae on the dorsomedian surface of the femur (Fig. 10C), and the presence of a patch of notched scales on the paraproct.

Novikova and Kluge (1987) erected the subgenus *Labiobaetis* based on the following characters: sclerotization between forceps (Fig. 3C), wide paraglossa (Fig. 8C), and inner expansion on segment II of labial palpus (Fig. 9C). McCafferty and Waltz (1995) raised *Labiobaetis* to the generic rank and adopted the following characters as generic diagnoses: sclerotized plate between forceps (Fig. 3C), distal lobe of antennal scape (Fig. 5C), depression of maxillary palpus (Fig. 7C), and villopore being rudimentary or absent (Fig. 11C: rudimentary villopore).

Lugo-Ortiz and McCafferty (1997) and Gattolliat (2001) described African *Labiobaetis* species that lack the distal lobe of the antennal scape (Fig. 5C) and the depression of the maxillary palpus (Fig. 7C). The inner margin of segment II of the labial palpus is not expanded in a species from North America (Moriyama and McCafferty 1979). Although these characters are not treated as generic diagnoses, the wide paraglossa supports monophyly of *Labiobaetis* (see discussion). Thus, we treat *Labiobaetis* as a distinct genus.

Waltz and McCafferty (1985, 1987) pointed out that the shape of the forceps was similar between *Pseudocloeon* and *Labiobaetis*, and Lugo-Ortiz et al. (1999) synonymized *Labiobaetis* with the genus *Pseudocloeon* Krapálek 1905. But the nymphal stage of *Pseudocloeon* remains unknown, and Waltz and McCafferty (1985, 1987) did not show the presence of a sclerotized plate between the forceps of *Pseudocloeon*. Gattolliat (2001) did not consider *Labiobaetis* as a junior synonym of *Pseudocloeon*, and we approve of his conclusion.

Baetis species of the *atrebatinus* group (Müller-Liebenau 1969), the *molawiensis* group (Müller-Liebenau 1984), and *propinquus* group (Traver 1935) are assigned to *Labiobaetis* (Waltz and McCafferty 1997).

Genus *Tenuibaetis* Kang and Yang, 1994 n. stat.

[Japanese generic name: Higetogari-Kokagerou-Zoku]

Baetis (Tenuibaetis) Kang and Yang, in Kang et al., 1994, 26 (type species: *Baetis pseudofrequentus* Müller-Liebenau, 1985, by original designation); previously synonymized with *Baetiella* Uéno 1931 (type species: *Acentrella japonica* Imanishi, 1930, by monotypy) by Waltz and McCafferty, 1997, 135.

Distribution. Palearctic, Oriental.

Characters of imagoes. Anterior margin of frons with medial ridge, straight in lateral view (Fig. 1D). Hind wing with distinct costal projection and two simple longitudinal veins (Fig. 2E). Apical segment of forceps oval (Fig. 3D).

Characters of nymphs. Medial ridge of frons absent (Fig. 4D). Distal lobe of antennal scape absent (Fig. 5D). Inner margin of mandible smooth, without row of spines (Fig. 6F). Right prosthema manifold (Fig. 6F). Depression near apex of maxillary palpus absent (Fig. 7C). Glossa without setal

patch at subapical region (Fig. 8D). Paraglossa 1.3–1.8 times wider than glossa (Fig. 8D). Labial palpus with segment II not expanded on inner distal margin, segment III pointed at apex (Fig. 9D). Robust setae with medial ridge present on dorso-median surface of femur (Fig. 10D, E). Villopore present (Fig. 11D). Paraproct with patch of notched scales, without projection on inner distal margin (Fig. 12D).

In nymphs of *Tenuibaetis*, we found the following character states: width of paraglossa 1.3–1.8 times wider than glossa (Fig. 8D) and lack of medial ridge of frons (Fig. 4D), distal lobe of antennal scape (Fig. 5D), depression near apex of maxillary palpus (Fig. 7C), setal patch near apex of glossa (Fig. 8D), and projection on inner distal end of paraproct (Fig. 12D).

Kang et al. (1994) erected the subgenus *Tenuibaetis* based on nymphs of three Taiwanese *Baetis* species by combination of the following characters: mandible with smooth inner margin (Fig. 6F), pointed apex of labial palpus (Fig. 9D), femur with villopore (Fig. 11D), and paraproct with a patch of notched scales (Fig. 12D). Waltz and McCafferty (1997) assigned *Tenuibaetis* to the genus *Baetiella* based on the shape of the labial palpus. The genus *Baetiella* is distinguishable from the other genera by the combination of the following characters: absence of hind wing in imago; labial palpus with conical apex and two glabrous cerci in the nymph (Uéno 1931b). In *Tenuibaetis* species, two lateral cerci and a terminal filament are fringed with fine setae (Kang et al. 1994). We found that robust setae with medial ridges on the dorsomedian surface of the nymphal femur (Fig. 10D, E) are useful to separate *Tenuibaetis* from *Baetiella* and its related genera. Thus, we raise *Tenuibaetis* to the generic rank.

Imagoes of *Tenuibaetis* possess a distinct costal projection and two simple longitudinal veins in the hind wing (Fig. 2E) and an oval apical segment of the forceps (Fig. 3D) (Tong and Dudgeon 2000). This genus includes *T. pseudofrequentus*, *T. arduus* n. comb., and *T. inortatus* n. comb.

Tenuibaetis pseudofrequentus (Müller-Liebenau 1985)
[Japanese name: Higetogari-Kokagerou]

Baetis pseudofrequentus Müller-Liebenau, 1985, 38; Kobayashi, 1987, 53; Ishiwata, 2001a, 67; Ishiwata and Kobayashi, 2003, 296.

Baetis (Tenuibaetis) pseudofrequentus: Kang et al., 1994, 26.

Baetiella pseudofrequenta: Waltz and McCafferty, 1997, 135; Tong and Dudgeon, 2000, 143.

Distribution: Japan (Ryukyu Islands), Taiwan.

This is the type species of *Tenuibaetis* designated by Kang et al. (1994). This species was recorded from the Ryukyu Islands by Kobayashi (1987).

Discussion on morphology and monophyly of *Nigrobaetis*, *Alainites*, *Labiobaetis*, and *Tenuibaetis*

In Table 1, we show the following morphological characters of *Nigrobaetis*, *Alainites*, *Labiobaetis*, *Tenuibaetis*, and a

possible outgroup genus *Cloeon*: the frons, hind wing, and forceps of the imago; the frons, antennal scape, mandible, maxillary palpus, labium, labial palpus, femur, villopore, and paraproct of the nymph. To evaluate the polarities and monophyly of the four genera, the table was compiled by our examination of materials and the descriptions by Novikova and Kluge (1987), Kang et al. (1994), Waltz et al. (1994), McCafferty and Waltz (1995), and Lugo-Ortiz and McCafferty (1997).

Imagoes

Frons: The medial ridge of the imaginal frons is convex in the lateral view in *Nigrobaetis*, *Alainites*, and some species of *Labiobaetis* (Figs. 1A–C) (Table 1). This character state cannot be considered as a synapomorphy of *Nigrobaetis*, *Alainites*, or *Labiobaetis*.

Hind wing: The hind wing is lost independently within genera *Nigrobaetis*, *Alainites*, and *Labiobaetis* (Table 1). When the hind wing is present, the number of longitudinal veins is two in *Labiobaetis* and *Tenuibaetis* and three in *Alainites*, but the number is variable between two and three within *Nigrobaetis* (Table 1). Vein II is forked in *Nigrobaetis* and *Alainites* (Figs. 2A–C) (Table 1). The costal projection is weak or absent in *Labiobaetis* species (Fig. 2D) (Table 1), but this character state is also known in *Acentrella* (Novikova and Kluge 1987). Considering the variability of the character states, including its presence, the hind wing is not adequate for distinguishing baetid genera.

Forceps: The shape of the apical segment is variable among *Alainites*, *Nigrobaetis*, *Labiobaetis*, and *Tenuibaetis* (Fig. 3A–D) (Table 1). Based on Kluge and Novikova (1992), we considered the elongate apical segment plesiomorphic and the oval one apomorphic in Cloeoninae. Similarly, it is possible that the elongate apical segment in *Nigrobaetis* (Fig. 3A) is plesiomorphic and that the shorter ones in *Alainites*, *Labiobaetis*, and *Tenuibaetis* (Fig. 3B, C, D) are apomorphic. McCafferty and Waltz (1995) treated a sclerotized plate between the forceps of *Labiobaetis* species (Fig. 3C) as a plesiomorphic character, but they distinguished *Labiobaetis* from other genera by the sclerotized plate. We also consider it as a diagnosis of *Labiobaetis* based on McCafferty and Waltz (1995), but we deduce that it is an apomorphic character from its uniqueness among baetid genera.

Nymphs

Frons: The medial ridge of the nymphal frons is known in *Nigrobaetis*, *Alainites*, and *Labiobaetis* (Fig. 4A–C), but it is absent in some species of *Nigrobaetis* and *Labiobaetis* (Table 1). This character is not a synapomorphic character of *Nigrobaetis*, *Alainites*, or *Labiobaetis*.

Antennal scape: Most species of *Labiobaetis* possess a distal lobe of the antennal scape (Fig. 5C) (Table 1). This character state cannot be treated as a synapomorphy of *Labiobaetis*, but, when the distal lobe is present, we can use

it to distinguish *Labiobaetis* from the related genera because its presence is restricted to the genus.

Mandible: A row of spines exists on the inner margin of the mandible in *Nigrobaetis* and *Alainites* (Fig. 6A–D) (Table 1). This character state is considered plesiomorphic, and the lack of the row of spines in *Labiobaetis* and *Tenuibaetis* is an apomorphic character state. The right prosthema is spinelike in *Alainites* (Fig. 6C, D) and some species of *Nigrobaetis* (Fig. 6A, B) (Table 1). This is an apomorphic state, but it is not considered a synapomorphic character of *Nigrobaetis* or *Alainites*.

Maxillary palpus: A depression near the apex of the maxillary palpus (Fig. 7C) was considered a synapomorphic character of *Labiobaetis* by McCafferty and Waltz (1995), but some *Labiobaetis* species lack the depression (Lugo-Ortiz and McCafferty 1997) (Table 1). This character state is not considered a synapomorphy of *Labiobaetis*. However, its presence is restricted to *Labiobaetis* among the related genera, and we can use the depression to distinguish *Labiobaetis* species.

Labium: A setal patch is present near the apex of the glossa in *Nigrobaetis* and *Alainites* (Fig. 8A, B) (Table 1). This character state is also known in the genus *Takobia* (Waltz et al. 1994), which has not been recorded in Japan. The setal patch is not a synapomorphic character of *Nigrobaetis* or *Alainites*. The width of the paraglossa is almost equal to that of the glossa in Cloeoninae (Novikova and Kluge 1987) (Table 1), but in *Nigrobaetis*, *Alainites*, and *Tenuibaetis*, the paraglossa is 1.0–1.8 times wider than the glossa (Figs. 8A, B, D) and, in *Labiobaetis*, more than 1.8 times wider than the glossa (Fig. 8C) (Table 1). We conclude that the wide paraglossa of *Labiobaetis* is a synapomorphic character.

Labial palpus: The inner margin of segment II of the labial palpus is expanded in *Labiobaetis* (Fig. 9C), but a similar expansion is also known in the *buceratus* group of *Baetis* (Müller-Liebenau 1969). Morihara and McCafferty (1979) described one species from North America in which the expansion is not developed. The expansion is not considered a synapomorphy of *Labiobaetis*. The apex of the labial palpus is pointed in *Tenuibaetis* (Fig. 9D) (Table 1), but this character state is also known in the genus *Baetiella* (Uéno 1931b; Waltz and McCafferty 1987, 1997). Thus, the pointed apex of the labial palpus (Fig. 9D) is not a synapomorphic character of *Tenuibaetis*.

Femur: Robust setae with a median ridge (Fig. 10E) were present on the dorsomedian surface of the nymphal femur of *Tenuibaetis* species (Fig. 10D) (Table 1). Similar setae are present on the femur of *Cloeon* species, but the margin is smooth in *Tenuibaetis* (Fig. 10E), whereas it is deeply serrated in *Cloeon* (Fig. 10F) (Table 1). We concluded that the presence of ridged robust setae in the two genera is a result of parallelism, and that this character can be used to distinguish *Tenuibaetis* from the related genera. On the basis of the presence of a villopore, Waltz and McCafferty (1987) grouped the genera closely related to *Baetis* (s. str.) and provided the *Baetis* complex. It includes *Acentrella*, *Baetiella*, *Baetis*, *Barbaetis* Waltz and McCafferty, *Demoreptus* Lugo-Ortiz and McCafferty,

Gratia Thomas, *Heterocloeon* McDunnough, *Labiobaetis*, *Liebebiella* Waltz and McCafferty, *Platybaetis* Müller-Liebenau, *Plauditus* Lugo-Ortiz and McCafferty, and *Tanzaniella* Gillies (Lugo-Ortiz and McCafferty 1998a,b). *Tenuibaetis* also belongs to the *Baetis* complex because its species possess a developed villopore (Fig. 11D) (Table 1). The villopore is rudimentary (Fig. 11C) or absent in *Labiobaetis* (McCafferty and Waltz 1995) (Table 1). Lugo-Ortiz and McCafferty (1997) considered this character state as a result of secondary loss and assigned *Labiobaetis* to the *Baetis* complex. All species of *Nigrobaetis* and *Alainites* lack a villopore (Figs. 11A, B) (Table 1), and Lugo-Ortiz and McCafferty (1997) assigned them to the *Indobaetis* complex, including *Indobaetis*, *Takobia*, and *Dipheter* Waltz and McCafferty.

Paraproct: A projection exists at the inner distal end of the paraproct in *Alainites* species (Fig. 12B) (Table 1), but it is also present in the genera *Takobia* and *Indobaetis* (Waltz et al. 1994). Kang et al. (1994) used the patch of notched scales of the paraproct to distinguish the subgenus *Tenuibaetis* (Fig. 12D) (Table 1) (Kang et al. 1994), but the scales are also found in some species of *Nigrobaetis* and *Labiobaetis*. Müller-Liebenau (1969) showed that a patch of notched scales is present in *Acentrella*, which she included in the *lapponicus* group of *Baetis*. Thus, the patch of notched scales is not a synapomorphic character of *Tenuibaetis*.

Consequently, we could not find any synapomorphic characters of *Nigrobaetis* and *Alainites*. Although further evaluation on monophyly of these genera is required, we tentatively retain the generic status of *Nigrobaetis* and *Alainites* following Waltz et al. (1994). *Labiobaetis* has a synapomorphic wide paraglossa (Fig. 9C). Herein we did not assign any Japanese species of *Baetis* (s. lat.) to *Labiobaetis*. However, among the species with provisional alphabetical names, *B. sp. G* and *B. sp. Q* possess a distal lobe on the antennal scape (Kobayashi 1987). We found that *B. sp. G* and *B. sp. Q* possess a depression near the apex of the maxillary palpus and a wide paraglossa, and these species are assignable to *Labiobaetis* (Fujitani et al. in press). *Tenuibaetis* is treated as a distinct genus based on the presence of ridged robust setae on the dorsomedian surface of the nymphal femur (Fig. 10E). This character supports the monophyly of *Tenuibaetis*.

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