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Description of the larvae of four Japanese *Platambus* Thomson, 1859 (Coleoptera: Dytiscidae: Agabinae) with phylogenetic considerations

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Abstract

The larvae of four species of *Platambus* Thomson, 1859 from Japan, *P. pictipennis* (Sharp, 1873), *P. convexus* Okada, 2011, *P. fimbriatus* (Sharp, 1884) and *P. sawadai* (Kamiya, 1932) are described for the first time including a detailed chaetotaxy analysis of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphi. A provisional parsimony analysis based on 39 informative larval characteristics of 15 species in seven genera of the subfamily Agabinae was conducted using the program TNT. Larvae of the *Platambus* species studied stand out from those of other genera of Agabinae by the unique presence of a subquadrate last abdominal segment not protruding posteriorly into siphon and the much shorter length of the primary urogomphal seta UR5 compared to seta UR7 in first instar larva.

Key words: Coleoptera, Dytiscidae, Agabinae, *Platambus*, chaetotaxy, larvae, Palearctic

Introduction

The dytiscid genus *Platambus* Thomson, 1859 contains 67 species distributed in the Nearctic, Neotropical, Oriental and Palearctic regions (Bian & Ji 2008; Hendrich & Przewoźny 2015; Hájek & Zhang 2019; Nilsson & Hájek 2019). These beetles generally occur in lotic environments although some species may be found in small ponds or ditches (Brancucci 1988; Miller & Bergsten 2016).

In term of classification, *Platambus* is placed within the subfamily Agabinae, which comprises three tribes; Agabini (*Platambus*, *Agabinus* Crotch, 1873, *Agabus* Leach, 1817, *Hydronebrius* Jakovlev, 1897, *Ilybiosoma* Crotch, 1873 and *Ilybius* Erichson, 1832), Hydrotrupini (*Hydrotrupes* Sharp, 1882) and Platynectini (*Andonectes* Guéorguiev, 1971 and *Platynectes* Régimbart, 1879) (Miller 2001; Miller & Bergsten 2014, 2016, Toussaint *et al*. 2017). As with other genera in the tribe Agabini, *Platambus* has experienced some rearrangements over the past several years. Nilsson (2000) expanded the concept of *Platambus* as defined by Brancucci (1988) to include the bitypic Nearctic genus *Agabinus* and members of the following *Platambus* species-groups: *americanus*, *confusus*, *optatus*, *semivittatus* and *spinipes*. More recently Nilsson (2015) resurrected the genus *Agabinus* in accordance with Alarie & Larson (1998) and Ribera *et al*. (2008). As so defined, however, *Platambus* and *Agabus* appear to be paraphyletic and need further reclassification (Ribera *et al*. 2004).

Larval morphology is important in the study of phylogenetic relationships amongst Holometabola. As different expressions of the same genotype, larval characters help to complement adult characters that have been traditionally the primary basis for classification. As demonstrated recently larval chaetotaxy is a particularly significant source of characters both for diagnosis of the genera and species and for the study of the phylogenetic relationships within the Dytiscidae (Michat *et al*. 2017). There is an overall pattern of setae and pores, which is widespread among taxa, though it is modified in a variety of groups. This generalized pattern is consistent enough to be used for phylogenetic analysis and yet sufficiently variable to allow for taxonomic distinction.

Larval morphology of most *Platambus* species is still poorly known. Larvae of *P. maculatus* (Linnaeus, 1758)

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(*maculatus*-group), *P. flavovittatus* (Larson & Wolfe, 1998), *P. semivittatus* (LeConte, 1852), and *P. stagninus* (Say, 1823) (*semivittatus*-group) and *P. koreanus* (Nilsson, 1996) (*optatus*-group) have been previously described (Matta 1986; Galewski 1990; Nilsson 1996; Barman *et al*. 1999; Wilkes *et al*. 2013). More recently Mitamura *et al*. (2017) provided pictures of *Platambus* species from Japan. All those descriptions, however, are rather superficial and none used chaetotaxy, which has been recognized as a source of useful characters both from a phylogenetic and diagnostic perspective (Alarie & Michat 2014; Michat *et al*. 2017).

The recent discovery of larvae of four species of *Platambus* from Japan provided the impetus for this study, which has the following goals: (1) to describe for the first time the larvae of *P. pictipennis* (Sharp, 1873), *P. convexus* Okada, 2011, *P. fimbriatus* (Sharp, 1884) (*maculatus*-group) and *P. sawadai* (Kamiya, 1932) (*sawadai*-group), including detailed morphometric and chaetotaxic analysis of the head capsule and appendages, legs, last abdominal segment and urogomphi and (2) to compare in a phylogenetic context the ground plan of larval features of *Platambus* with those of other genera of Agabinae, which have been described in much detail.

Material and methods

Source of material. Descriptions of larvae are based on several specimens found either in association with adults or reared *ex ovo* (Alarie *et al*. 1989). The localities from which the specimens were obtained are provided under the individual species descriptions.

Methods. Specimens were fixed in boiling water and then transferred to 75% ethanol in glass vials with a tight-fitting cap. Microscopic examination at magnifications up to 1000X was done using on Olympus BHT and Carton DSZ44 compound microscope equipped with Nomarsky microscopy. Photographs of dorsal habitus of selected larvae were taken under RICOH TG-4. Voucher specimens are stored in the larval collections of Ryohei Okada (Tokyo, Japan) and Yves Alarie (Department of Biology, Laurentian University, Sudbury, Ontario, Canada).

Morphometric analysis. All measurements were made with a compound microscope equipped with a micrometer eyepiece. Each part to be measured was adjusted so that it was, as nearly as possible, parallel to the plane of the objectives. The following measurements were taken (with abbreviations shown in parentheses): Head length (HL): total head length including the frontoclypeus, measured medially along epicranial stem. Head width (HW): maximum head width. Length of frontoclypeus (FRL): from apex of nasale to posterior margin of ecdysial suture. Occipital foramen width (OCW): maximum width measured along dorsal margin of occipital foramen. Length of mandible (MN): measured from laterobasal angle to apex. Width of MN: maximum width measured at base. Length of antenna (A), maxillary (MP) and labial (LP) palpi were derived by adding the lengths of the individual segments; each segment is denoted by the corresponding letter(s) followed by a number (e.g. A1: antennomere 1; MP1: maxillary palpomere 1; LP1: labial palpomere 1). A3' is used as an abbreviation for the apical lateroventral process of third antennomere. Length of leg (L1–L3), including the longest claw (CL), was derived by adding the lengths of the individual segments; each leg is denoted by the letter L followed by a number (e.g. L1: prothoracic leg). The length of trochanter includes only the proximal portion, and the length of distal portion is included in the femoral length. Dorsal length of last abdominal segment (LLAS): measured along the midline from anterior to posterior margin. Length of urogomphi (U): total length from base to apex. These measurements were used to calculate several ratios that characterize the body shape.

Chaetotaxic analysis. Primary (present in first-instar larvae) and secondary (added in later instars) setae and pores were distinguished on the head capsule, head appendages, legs, last abdominal segment, and urogomphi. Sensilla were coded by two capital letters and a number (setae) or a lowercase letter (pores). The following abbreviations were used: AB: last abdominal segment; AN: antenna; CO: coxa; FE: femur; FR: frontoclypeus; LA: labium; MN: mandible; MX: maxilla; PA: parietale; PT: pretarsus; TA: tarsus; TI: tibia; TR: trochanter; UR: urogomphi. Setae and pores present in first-instar larvae were coded by comparison with the ground plan of chaetotaxy of the subfamilies Agabinae and Colymbetinae (Alarie 1995, 1998; Michat *et al*. 2017). Setae located at the apices of the maxillary and labial palpi were extremely difficult to distinguish due to their position and small size. Thus, they are not well represented in the drawings. The number of secondary setae present on the ventral margin of femur was more difficult to assess owing to the presence of a variable number of additional primary setae (Table 1). To solve that problem, they were included in the count of secondary setae.

Phylogenetic analysis. The phylogenetic relationships of the genus *Platambus* and other genera of the subfamily Agabinae which have been described in much detail as larvae were analyzed cladistically using the program TNT (Goloboff *et al*. 2008). A total of 15 Agabinae species in seven genera (*Agabus*, *Agabinus*, *Hydrotrupes*, *Ilybius*, *Ilybiosoma*, *Platynectes*, and *Platambus*) were included. The remaining two genera of the subfamily (*Andonectes* and *Hydronebrius*) were not included because their larvae are either unknown or imperfectly described. Members of two other dytiscid subfamilies (Colymbetinae and Matinae) were used as outgroups. All characters were treated as equally weighted. Multistate characters were treated as non-additive. An exact solution algorithm (implicit enumeration) was implemented to find the most parsimonious trees. Bremer support values were calculated using the commands 'hold 20000', 'sub n' and 'bsupport', where 'n' is the number of extra steps allowed. The process was repeated increasing the length of the suboptimal cladograms by one step, until all Bremer values were obtained (Kitching *et al*. 1998). Bootstrap values were calculated using the following parameters: 'standard (sample with replacement)'; 2000 replicates.

Results

Description of the larvae of *Platambus* Thomson, 1859

Diagnosis. Larvae of *Platambus* are characterized by the following combination of characters: cephalic capsule with neck constriction (Figs 1, 2, 15, 16, 29, 30, 43, 44, 57–60); occipital suture absent; pore FRe absent (Figs 1, 15, 29, 43); A3 lacking a ventroapical spinula, A3' protruding, bulge-like to finger-like (Figs 4, 18, 32, 46); galea present, stipes with additional setae present or absent (Figs 5–6, 19–20, 33–34, 47–48); prementum broader than long (Figs 7–8, 21–22, 35–36,49–50); legs lacking natatory setae (Figs 61–68); femur with several additional setae (Figs 10–11, 24–25, 38–39, 52–53); setae FE5, TI6 and TI7 short, spine-like (Figs 11, 25, 39, 53); LAS subquadrate, siphon lacking (Figs 12–13, 26–27, 40–41, 54–55, 69–72); urogomphi composed of one urogomphomere, lacking secondary setae, with primary seta UR5 much shorter than seta UR7 in instar I larva (Figs 14, 28, 42, 56).

Instar I(Figs 1–56, 73–75). Body. Subcylindrical, narrowing towards abdominal apex. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule (Figs 1–2, 15–16, 29–30, 43–44). HL = 0.64–0.92 mm; HW = 0.59–0.75 mm; FRL = 0.22–0.41 mm. Flattened, rounded or subovate, about as broad as long (HL/HW = 1.04–1.27), maximum width at level of stemmata, sides subparallel or slightly diverging posteriorly; neck constriction present; occipital suture absent; ecdysial line well marked, coronal line long, 0.45–0.65 times HL; occipital foramen broadly emarginate ventrally, HW/OCW = 1.74–2.47; frontoclypeus subtriangular, rounded mesally, extending medially beyond level of anterolateral lobes of frontoclypeus [= adnasalia of Beutel (1994)]; dorsal surface with two spine-like egg bursters [= ruptor ovi of Bertrand (1972)] posteriorly, less than half as broad basally than maximum width of antennomere 1; anterior margin with 10–16 spatulate setae [= lamellae clypeales of Bertrand (1972)] variable in size; gular suture not visible; ocularium present, with six stemmata, four visible dorsally and two ventrally, arranged into two curved vertical rows; tentorial pits visible ventrally on each side at about mid-length. Antenna (Figs 3–4, 17–18, 31–32, 45–46). Slender, shorter than HW (A/HW = 0.60–0.83), composed of four antennomeres; A1 and A4 the shortest (A4/A1 = 0.83–1.37); A3 the longest (A4/A3 = 0.58–0.94); A3' protruding, bulge- or finger-like. Mandible (Figs 9, 23, 37, 51). Prominent, broad basally, distal half projected inwards, sharp apically, 0.44–0.53 times as long as HL; mandibular channel present. Maxilla (Figs 5–6, 19–20, 33–34, 47–48). Cardo small, subovate; stipes short, broad, with minute spinulae proximad to galea; galea well developed, subconical, lacinia absent; palpifer short, palpomere-like, with dorsodistal spinulae; palpus 3-segmented, shorter than antenna (A/MP = 1.13–1.37), MP1 and MP2 the shortest, subequal, MP3 the longest (MP3/MP2 = 1.51–2.06). Labium (Figs 7–8, 21–22, 35–36, 49–50). Prementum subrectangular, broader than long, with minute spinulae on dorsal and ventral surfaces; palpus elongate, 2-segmented, subequal to shorter than maxillary palpus (MP/LP = 1.08–1.47); LP2 longer than LP1 (LP2/LP1 = 1.17–2.00).

Thorax. Terga convex, pronotum slightly shorter than meso- and metanotum combined, meso- and metanotum subequal, wider than pronotum; protergite subrectangular, margins rounded, more developed than meso- and metatergites; meso- and metatergites transverse, with anterotransverse carina; sagittal line visible on the three tergites; thoracic sterna membranous, spiracles absent. Legs (Figs 10–11, 24–25, 38–39, 52–53). Long, well developed, composed of six segments (including pretarsus), L1 the shortest, L3 the longest; L3 = 1.61–2.37 mm, L3/HW

= 2.66–3.48; CO robust, elongate, TR divided into two parts, FE, TI and TA slender, subcylindrical; pretarsus with two long, slender, slightly curved claws, posterior claw shorter than anterior one on L1 and L2, claws subequal in length on L3; claws lacking basoventral spinulae; TI and TA with marginal spinulae variably developed.

Abdomen. 8-segmented; segments I–VII sclerotized dorsally, membranous ventrally; tergites I–VII narrow, transverse, rounded laterally, with sagittal line, with anterotransverse carina, covered with minute spinulae in transverse rows; spiracles absent on segments I–VII; LAS (Figs 12–13, 26–27, 40–41, 54–55). Short, subquadrate, completely sclerotized, ring-like, with anterotransverse carina dorsally and laterally (LAS = 0.16–0.27 mm, LAS/HW = 0.25–0.37), covered with minute spinulae in transverse rows; siphon reduced to almost lacking. Urogomphi. (Figs 14, 28, 42, 56). U = 0.70–1.17 mm, U/HW = 1.18–1.68, one-segmented, longer than LAS (U/LAS = 4.11–6.00), without or with microspinulae.

Chaetotaxy (Figs 1–56). Similar to that of generalized Agabinae larva (Alarie 1995, 1998; Alarie & Larson 1998; Alarie *et al*. 1998, 2019; Michat & Archangelsky 2009) except for the following characteristics: seta FR5 close to pore FRd; pore ANi located more distally; A3 with one minute structure (possibly a spinula) posterior to seta AN2; a minute structure (possibly a pore) present on dorsal surface of A4; prementum with one or two additional setae on dorsal surface; seta FE1 inserted sub-medially; seta FE6 hair-like; femora with a variable number of additional setae (Table 1); despite thorough effort setae AB7 and AB14 could not be found, so they were coded as absent but with some hesitation; setae UR2 and UR3 contiguously inserted; seta UR4 either contiguously inserted to setae UR2 and UR3 or more distant; pore URc and one additional minute seta located near the articulation of setae UR5–UR8; setae UR5 and UR6 shorter than setae UR7 and UR8.

Instar II (Figs 76–78). As first-instar larva except as follows:

Head. HL = 0.95–1.35 mm; HW = 0.85–1.14 mm; FRL = 0.40–0.56 mm. Head capsule. Subovate to subtrapezoidal (HL/HW = 1.11–1.24, HW/OCW = 1.88–2.30); frontoclypeus with 20–31 spatulate setae; egg bursters lacking. Antenna. A/HW = 0.60–0.72; A4 the shortest, A3 the longest (A4/A3 = 0.44–0.66). Maxilla. MP3 the longest (MP3/MP2 = 1.17–1.54); Labium. MP/LP = 1.10–1.29; LP2 subequal or longer than LP1 (LP2/LP1 = 1.00–1.47).

Thorax. Legs. L3 = 2.56–3.64 mm, L3/HW = 2.89–3.43.

Abdomen. Segment VII completely sclerotized, ring-like; LAS = 0.34–0.57 mm, LAS/HW = 0.38–0.52. Urogomphi. U = 1.29–1.69 mm, U/HW = 1.27–1.62, longer than LAS (U/LAS = 2.56–4.12); U5, U6, U7 and U8 subequal or U8 slightly shorter than the others.

Chaetotaxy. Cephalic capsule with several minute secondary setae; parietale with 4–8 spine-like secondary setae on the lateral margin and several spine-like setae on ventral surface; mandible with one hair-like secondary seta along external margin, proximal to pore MNa, and some minute secondary setae along external margin; stipes with one minute secondary seta on ventral surface, near setae MX2 and MX3; prementum with one secondary pore on ventral surface, near seta LA1; CO with one secondary pore on posterior surface; LAS with numerous secondary setae on dorsal and lateral surfaces; secondary leg setation represented in Table 2.

Instar III (Figs 57–72, 79–82). As second-instar larva except as follows:

Head (Figs 57–60). HL = 1.40–1.99 mm; HW = 1.21–1.64 mm; FRL = 0.61–0.77 mm. Frontoclypeus with 26–51 spatulate setae in a double low along anterior margin. Antenna, A1, A2 and A3 the longest, subequal (A4/A3 = 0.29–0.53); A3' bulge-like. Maxilla. MP1, MP2 and MP3 subequal in length; Labium. LP2 shorter to longer than LP1 (LP2/LP1 = 0.73–1.20).

Thorax. Spiracular openings present on mesothorax. Legs (Figs 61–68). L3 = 3.87–5.51 mm, L3/HW = 3.03–3.81.

TABLE 1. Number and position of additional setae of selected species of *Platambus* Thomson, 1859: PIC = *P. pictipennis* (Sharp, 1873); CON = *P. convexus* Okada, 2011; FIM = *P. fimbriatus* (Sharp, 1884); SAW = *P. sawadai* (Kamiya, 1932); AV = anteroventral, PV = posteroventral, Total = total number of additional and secondary setae on segment; *n* = number of specimens examined.

Segment	Position	PIC (*n*= 14)	CON (*n*= 4)	FIM (*n*= 6)	SAW (*n*= 7)
Femur	AV	3-6/3-5/3-5	3/2-3/2-3	3-4/3-4/3-4	4/3-4/3-4
	PV	2-3/2/2	1/1/1	1/1/1	2/2/1-2
	Total	5-8/5-7/5-7	4/3-4/3-4	4-5/4-5/4-5	6/5-6/4-5

Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively.

TABLE 2. Number and position of secondary setae (including additional seta on femur) of selected species of *Platambus* Thomson, 1859: PIC = *P. pictipennis* (Sharp, 1873); CON = *P. convexus* Okada, 2011; FIM = *P. fimbriatus* (Sharp, 1884); SAW = *P. sawadai* (Kamiya, 1932); A = anterior, AD = anterodorsal, AV = anteroventral, CO = coxa, D = dorsal, Di = distal, FE = femur, PD = posterodorsal, Pr = proximal, PV = posteroventral, TA = tarsus, TI = tibia, TR = trochanter, V = ventral, *n* = number of specimens examined, Total = total number of secondary setae on segment.

Segment	Series	Instar II			Instar III			
		PIC	FIM	SAW	PIC	CON	FIM	SAW
		(*n*= 10)	(*n*= 2)	(*n*= 10)	(*n*= 10)	(*n*= 6)	(*n*= 10)	(*n*= 11)
ProCO	D	4-6	2-3	3-6	2-6	1-6	2-4	4-6
	A	0-4	1	0-2	1-4	1-4	0-2	0-4
	Total	4-9	3-4	4-7	4-9	5-8	2-6	4-9
ProFE	D	2	1-2	2	2	2	1-2	2
	AV	2-5	2-3	6-11	2-5	2-4	1-3	6-9
	PV	4-7	5	6-9	5-9	4-5	2-6	5-9
	Total	9-14	9	13-21	10-16	9-11	6-9	14-19
ProTI	AV	0	0	0	0	1	0	0
	PV	1	1	1	1-2	1-3	1	1
	Total	1	1	1	1-2	2-4	1	1
ProTA	D	1	1	0	1	0	1	0-1
	PV	1	0	1	1	1	0	1
	Total	2	1	1	2	1	1	1-2
MesoCO	D	3-5	1-2	3-5	3-5	2-5	2-3	2-6
	A	0-4	1-2	0-3	2-5	2-4	1-3	2-5
	Total	3-9	2-4	3-7	5-10	4-9	3-6	5-11
MesoFE	D	2	2	2-3	2	2	2	2-3
	AV	6-10	4-5	7-13	5-13	4-7	1-5	7-12
	PV	5-10	4-5	6-9	7-10	4-6	2-5	7-10
	Total	13-20	10-12	17-25	15-25	12-14	6-11	17-25
MesoTI	D	1	1	1-2	1	1-2	1-2	1-2
	AV	1-2	1	2-3	1-2	2-3	0-1	1-3
	PV	1	1-2	1-3	1-2	1-2	1	1-2
	Total	3-5	3-4	4-7	3-5	4-6	2-4	3-6
MesoTA	D	1	1	2	1	1-2	1	1-2
	AV	0	0	1-2	0	1-2	0-1	1-2
	PV	1-2	1	1	1	1-2	0-1	1
	Total	2-3	2	4-5	2	3-6	1-3	3-5
MetaCO	A	0-4	2	0-2	2-4	2-4	1-4	1-5
	V	2-4	2-3	2-4	2-4	2-3	2-4	1-4
	Total	2-7	4-5	2-4	5-8	5-7	3-7	3-7
MetaTR	Di	0	0	0-1	0	0	0	0-1
MetaFE	D	2-3	2	2	2	2	1-2	2-3
	AV	4-10	1-5	6-12	6-9	4-7	2-5	6-11
	PV	6-10	3	4-7	4-9	3-4	1-4	2-6
	Total	12-20	7-11	13-21	12-20	10-13	4-9	12-20
MetaTI	D	2-3	3	2-3	2-4	2-4	1-3	2-3
	AV	2-4	1	2-3	2-3	3-4	0-1	2-4
	PV	1-2	1	1	1-2	1-2	1	1-3
	Total	6-9	5	5-7	5-8	6-9	2-5	5-8
MetaTA	D	1-2	1	2-3	1-2	0-1	1-2	1-2

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TABLE 2. (Continued)

Segment	Series	Instar II			Instar III			
		PIC (*n*= 10)	FIM (*n*= 2)	SAW (*n*= 10)	PIC (*n*= 10)	CON (*n*= 6)	FIM (*n*= 10)	SAW (*n*= 11)
	AV	1-2	0	2-4	1-3	0-2	0	2-3
	PV	0-2	1	1-2	1-2	0-2	0-1	0-2
	Total	2-5	2	5-8	3-7	0-5	1-3	4-7

TABLE 3. Number and position of additional setae of selected species of *Platambus* Thomson, 1859: PIC = *P. pictipennis* (Sharp, 1873); CON = *P. convexus* Okada, 2011; FIM = *P. fimbriatus* (Sharp, 1884); SAW = *P. sawadai* (Kamiya, 1932); AV = anteroventral, PV = posteroventral, Total = total number of additional and secondary setae on segment; *n* = number of specimens examined.

Measure	Instar I				Instar II			Instar III			
	PIC (*n* = 14)	CON (*n* = 4)	FIM (*n* = 6)	SAW (*n* = 7)	PIC (*n* = 10)	FIM (*n* = 2)	SAW (*n* = 10)	PIC (*n* = 10)	CON (*n* = 6)	FIM (*n* = 10)	SAW (*n* = 11)
HL (mm)	0.70 - 0.78	0.84 - 0.86	0.64 - 0.71	0.86 - 0.92	1.04 - 1.19	0.95 - 1.00	1.23 - 1.35	1.56 - 1.80	1.86 - 1.92	1.40 - 1.52	1.79 - 1.99
HW (mm)	0.62 - 0.71	0.67 - 0.71	0.59 - 0.64	0.70 - 0.75	0.90 - 1.01	0.85 - 0.89	1.02 - 1.14	1.33 - 1.47	1.38 - 1.51	1.21 - 1.33	1.50 - 1.64
FRL (mm)	0.31 - 0.37	0.29 - 0.40	0.22 - 0.37	0.31 - 0.41	0.41 - 0.56	0.40 - 0.51	0.45 - 0.55	0.67 - 0.77	0.64 - 0.76	0.61 - 0.75	0.67 - 0.74
OCW (mm)	0.31 - 0.38	0.29 - 0.38	0.32 - 0.36	0.31 - 0.40	0.45 - 0.51	0.41 - 0.43	0.44 - 0.55	0.59 - 0.73	0.69 - 0.74	0.58 - 0.71	0.65 - 0.73
HL/HW	1.09 - 1.18	1.21 - 1.27	1.04 - 1.10	1.16 - 1.27	1.14 - 1.20	1.11 - 1.11	1.17 - 1.24	1.18 - 1.29	1.27 - 1.35	1.10 - 1.23	1.18 - 1.27
HW/OCW	1.78 - 2.09	1.74 - 2.47	1.76 - 1.97	1.80 - 2.38	1.93 - 2.14	2.00 - 2.16	1.88 - 2.30	2.02 - 2.33	2.01 - 2.07	1.89 - 2.26	2.11 - 2.35
A/HW	0.70 - 0.83	0.77 - 0.83	0.60 - 0.69	0.68 - 0.73	0.64 - 0.72	0.60 - 0.63	0.61 - 0.72	0.55 - 0.65	0.64 - 0.71	0.50 - 0.58	0.57 - 0.63
A4/A1	0.96 - 1.26	0.88 - 1.00	1.09 - 1.37	0.83 - 1.25	0.67 - 0.84	0.73 - 0.90	0.51 - 0.65	0.41 - 0.50	0.30 - 0.39	0.42 - 0.56	0.33 - 0.40
A4/A3	0.70 - 0.83	0.64 - 0.69	0.78 - 0.94	0.58 - 0.76	0.51 - 0.59	0.64 - 0.66	0.44 - 0.54	0.37 - 0.45	0.29 - 0.34	0.43 - 0.53	0.32 - 0.39
A/MP	1.22 - 1.37	1.15 - 1.19	1.13 - 1.27	1.13 - 1.20	1.25 - 1.39	1.27 - 1.30	1.17 - 1.28	1.32 - 1.39	1.23 - 1.36	1.26 - 1.41	1.24 - 1.35
MP3/MP2	1.51 - 1.78	1.52 - 1.75	1.70 - 2.06	1.66 - 1.94	1.17 - 1.46	1.43 - 1.54	1.33 - 1.54	0.96 - 1.10	1.08 - 1.29	1.04 - 1.18	1.04 - 1.22
MP3/MP1	1.70 - 2.14	1.87 - 2.13	1.77 - 2.13	1.90 - 2.43	1.35 - 1.76	1.52 - 1.90	1.51 - 1.84	1.05 - 1.26	1.17 - 1.28	1.07 - 1.22	1.20 - 1.32
MP/LP	1.12 - 1.37	1.31 - 1.47	1.08 - 1.25	1.20 - 1.39	1.13 - 1.26	1.10 - 1.16	1.15 - 1.29	1.10 - 1.25	1.25 - 1.38	1.04 - 1.24	1.12 - 1.23
LP2/LP1	1.17 - 1.57	1.75 - 2.00	1.26 - 1.44	1.33 - 1.63	1.01 - 1.20	1.04 - 1.14	1.00 - 1.47	0.84 - 0.95	0.94 - 1.20	0.73 - 1.02	0.83 - 1.05
L3 (mm)	1.88 - 2.19	2.31 - 2.37	1.61 - 1.81	2.21 - 2.36	2.84 - 3.19	2.56 - 2.72	3.23 - 3.64	4.24 - 4.77	5.15 - 5.51	3.87 - 4.11	4.85 - 5.26
L3/HW	2.90 - 3.21	3.33 - 3.48	2.66 - 2.87	3.07 - 3.33	2.89 - 3.22	3.00 - 3.04	3.05 - 3.43	3.13 - 3.29	3.60 - 3.81	3.03 - 3.28	3.09 - 3.40
L3/L1	1.24 - 1.30	1.29 - 1.32	1.22 - 1.29	1.25 - 1.36	1.28 - 1.38	1.30 - 1.35	1.28 - 1.42	1.34 - 1.42	1.42 - 1.46	1.30 - 1.36	1.36 - 1.41
L3 (CO/FE)	0.92 - 1.02	0.91 - 0.96	0.90 - 0.96	0.88 - 1.02	0.92 - 1.02	0.87 - 0.89	0.91 - 0.95	0.92 - 0.99	0.85 - 0.92	0.89 - 0.98	0.87 - 0.99
L3 (TI/FE)	0.64 - 0.74	0.68 - 0.72	0.59 - 0.65	0.69 - 0.77	0.66 - 0.73	0.59 - 0.62	0.67 - 0.76	0.66 - 0.71	0.66 - 0.70	0.55 - 0.63	0.67 - 0.76
L3 (TA/FE)	0.81 - 0.90	0.84 - 0.87	0.66 - 0.79	0.87 - 0.93	0.72 - 0.81	0.68 - 0.71	0.76 - 0.85	0.67 - 0.75	0.68 - 0.71	0.59 - 0.66	0.77 - 0.82
L3 (CL/TA)	0.58 - 0.70	0.45 - 0.49	0.66 - 0.81	0.39 - 0.48	0.45 - 0.65	0.72 - 0.79	0.41 - 0.46	0.40 - 0.50	0.40 - 0.51	0.63 - 0.74	0.34 - 0.41
LAS (mm)	0.16 - 0.21	0.20 - 0.23	0.16 - 0.19	0.22 - 0.27	0.34 - 0.46	0.37 - 0.41	0.47 - 0.57	0.73 - 0.91	1.00 - 1.12	0.77 - 0.90	0.93 - 1.06
LAS/HW	0.25 - 0.31	0.29 - 0.33	0.25 - 0.31	0.30 - 0.37	0.38 - 0.47	0.43 - 0.45	0.45 - 0.52	0.55 - 0.62	0.70 - 0.77	0.62 - 0.70	0.60 - 0.67
U (mm)	0.88 - 1.08	0.99 - 1.08	0.70 - 1.00	1.04 - 1.17	1.29 - 1.51	1.33 - 1.38	1.43 - 1.69	1.92 - 2.24	2.40 - 2.78	1.88 - 2.28	1.92 - 2.40
U/HW	1.33 - 1.68	1.39 - 1.61	1.18 - 1.60	1.47 - 1.58	1.27 - 1.55	1.49 - 1.62	1.33 - 1.55	1.38 - 1.58	1.68 - 1.84	1.50 - 1.81	1.24 - 1.53
U/LAS	4.86 - 6.00	4.45 - 5.28	4.19 - 5.44	4.11 - 5.09	2.84 - 4.12	3.29 - 3.75	2.56 - 3.28	2.26 - 2.86	2.25 - 2.62	2.24 - 2.71	1.88 - 2.47

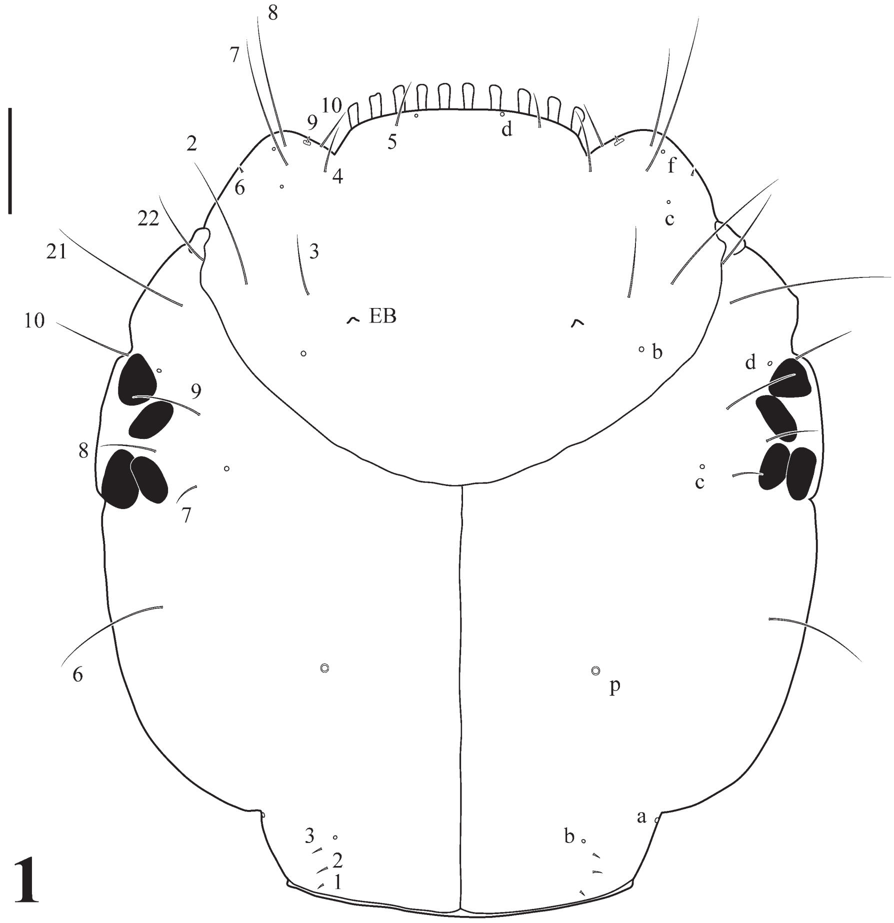
Abdomen. Spiracular openings present on segments I–VII; LAS = 0.73–1.12 mm, LAS/HW = 0.55–0.77. Urogomphi (Figs 69–72). U = 1.88–2.78 mm, U/HW = 1.24–1.84; U/LAS = 1.88–2.86.

Chaetotaxy (Figs 57–72). Stipes with 1–2 minutes secondary setae; prementum with two secondary pores; CO with two secondary pores; Secondary leg setation represented in Table 1 and Figures 61–68.

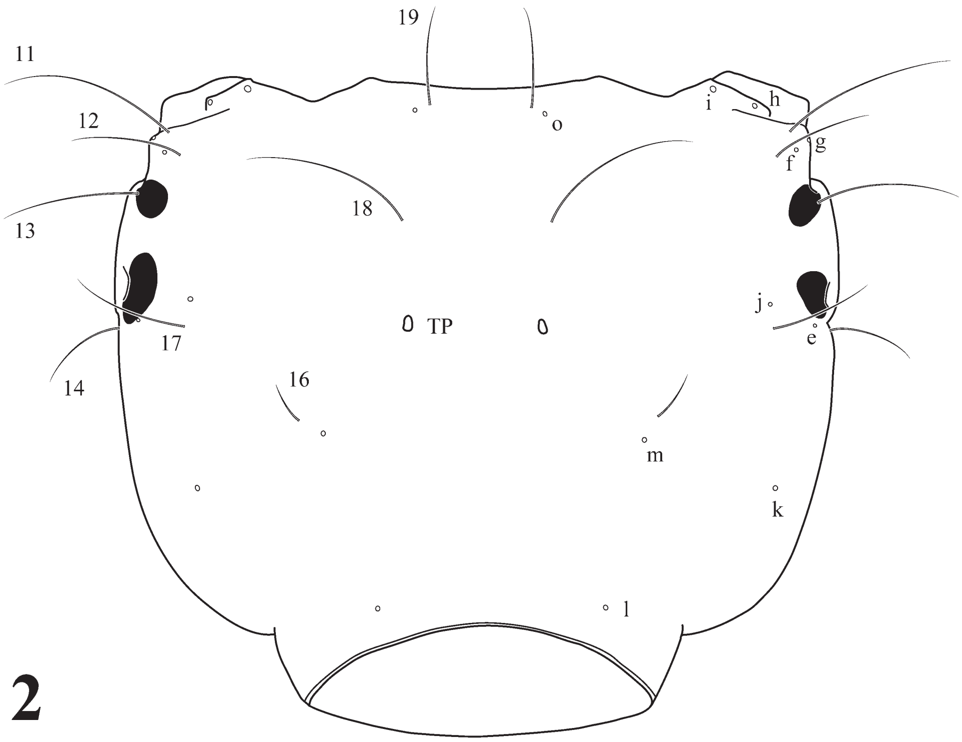
Description of the larvae of *Platambus pictipennis* (Sharp, 1873)

Source of material. 10 instar I, 10 instar II, 10 instar III, Japan: Echi riv., Tanesato, Notogawa-cho, Shiga Pref, 22.II.2015; 7.III.2015; 20.XII.2015; 6–10.I.2016; 6.II.2016; R. Okada leg; 3 instar **I,** Japan: Abukuma riv., Tsuruo, Saigo-mura, Fukushima Pref., 8.I.2017, R. Okada leg; 1 instar I, Japan: Shimokubo-dam, Fujioka-shi, Gunma Pref., 7.I.2016, N. Shimura leg. Larvae were reared *ex ovo* from adults collected at these localities

Diagnosis. First instar larva of *P. pictipennis* can be distinguished from the other species studied by the following combinations of features: frontoclypeus with less than 12 spatulate setae (Fig. 1); A3' short bulge-like (Fig. 4); seta FR3 shorter than seta FR2 (Fig. 1); seta PA6 longer than seta PA7 (Fig. 1); primary seta LA10 inserted subapically (Fig. 8); ratio L3/HW = 2.90–3.20. In addition to color patterns of head capsule (Fig. 57), last abdominal segment, and urogomphi (Figs 69, 73–82), the total number of spatulate setae on frontoclypeus, secondary setae on pro- and mesofemur, and the presence/absence of ventral setae on protarsus (Table 2) are helpful at discriminating later instars.

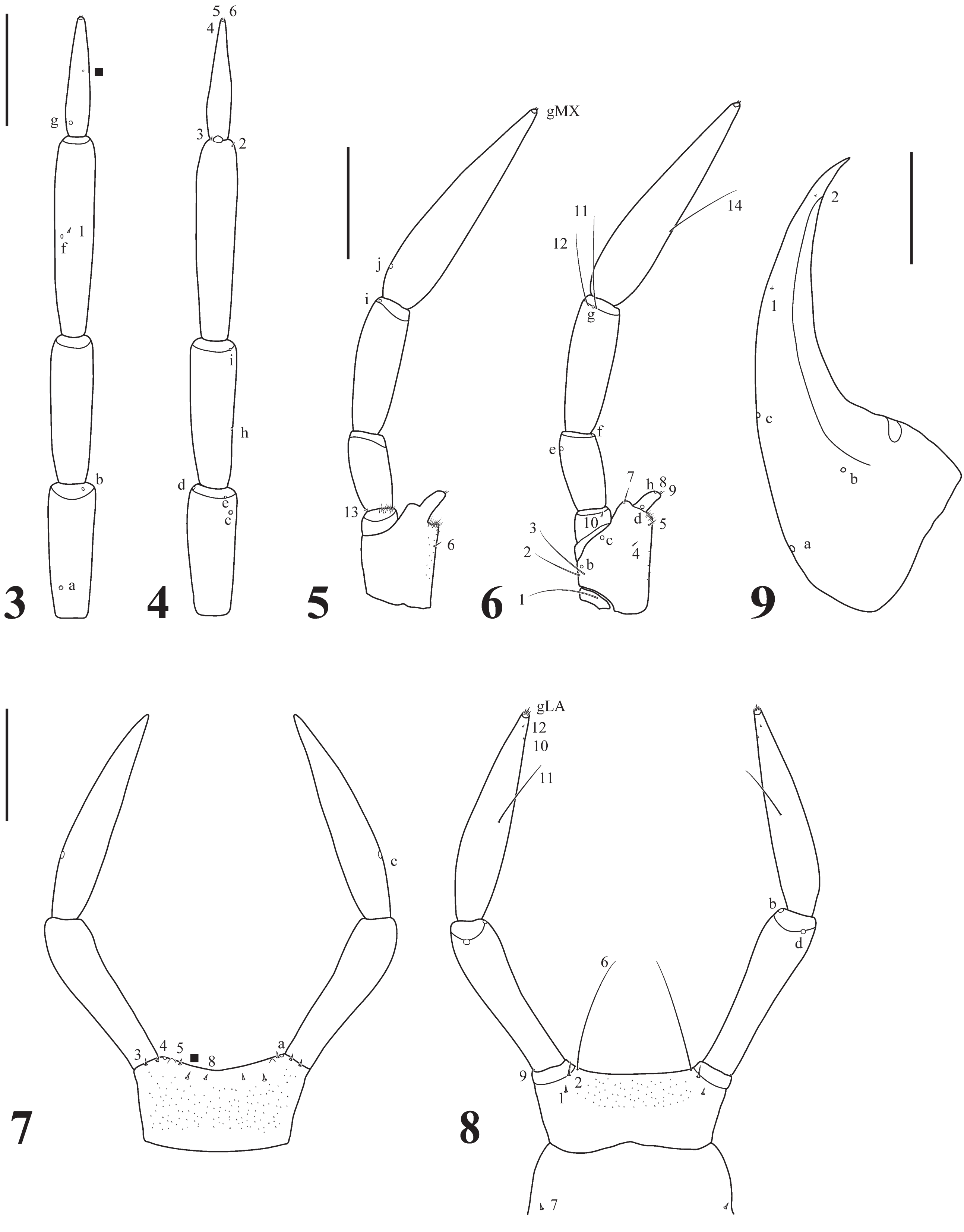


1

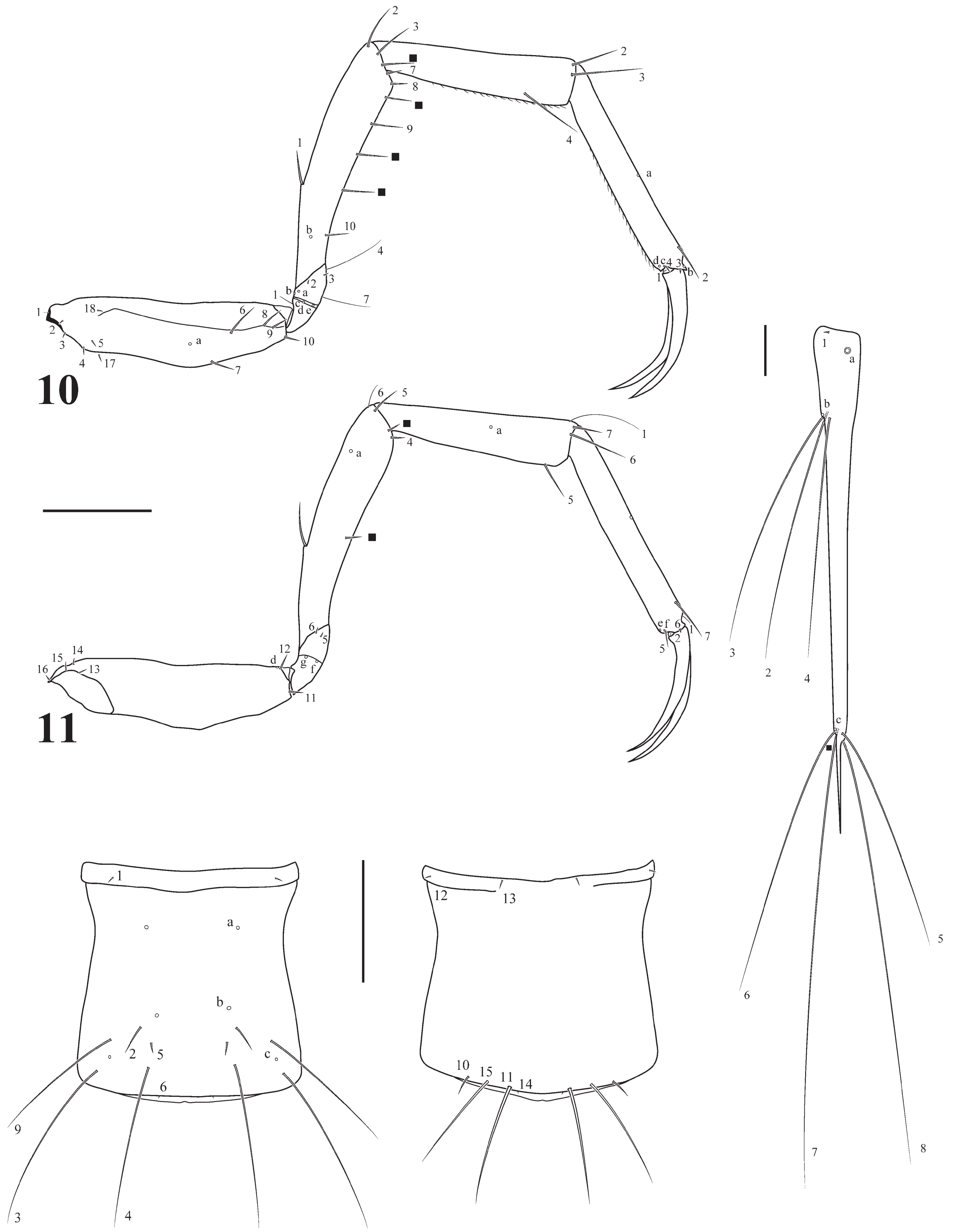


2

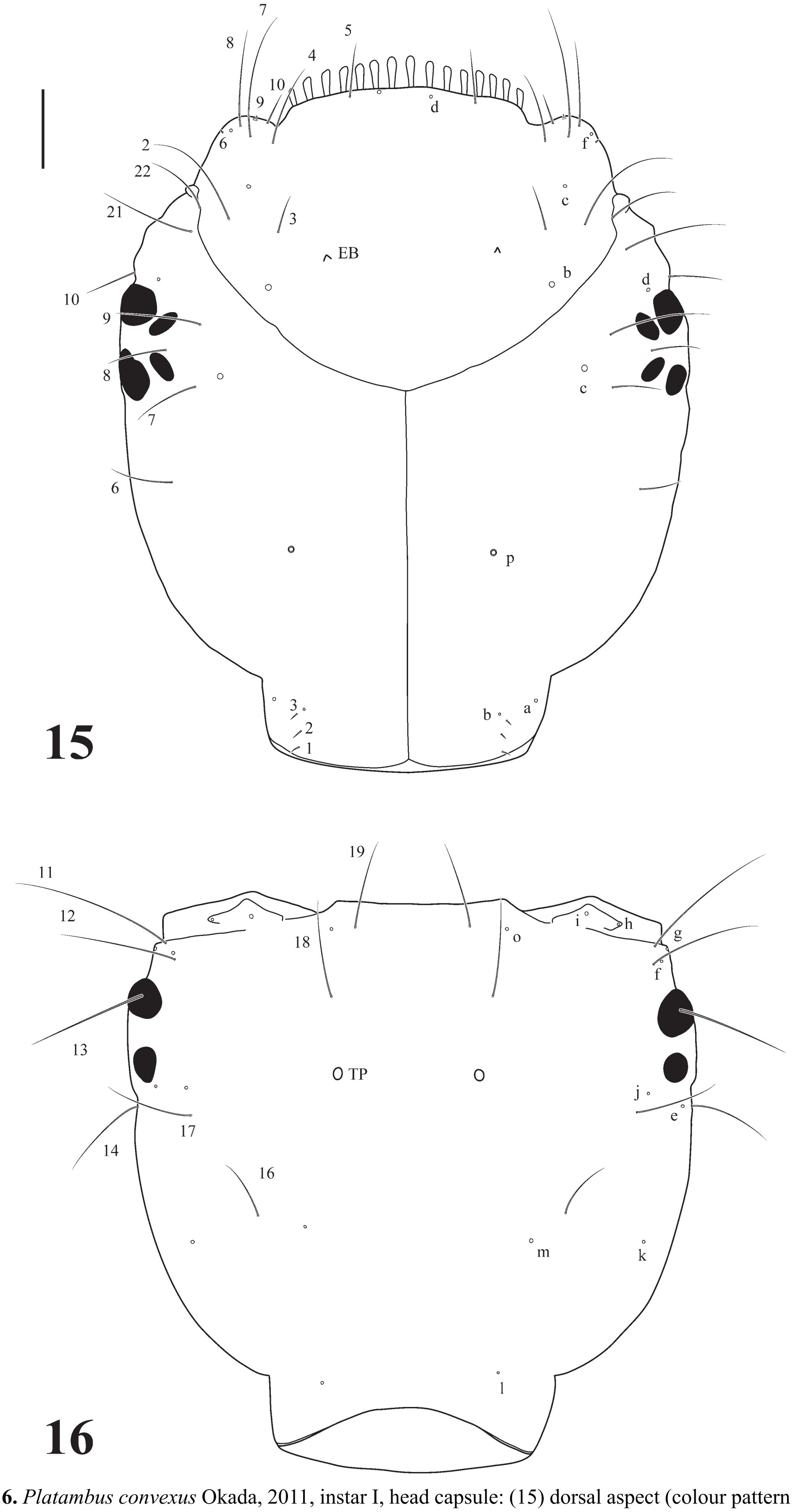
FIGURES 1–2. *Platambus pictipennis* (Sharp, 1873), instar I, head capsule: (1) dorsal aspect (colour pattern not represented); (2) ventral aspect. EB, egg bursters; TP, tentorial pits. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.



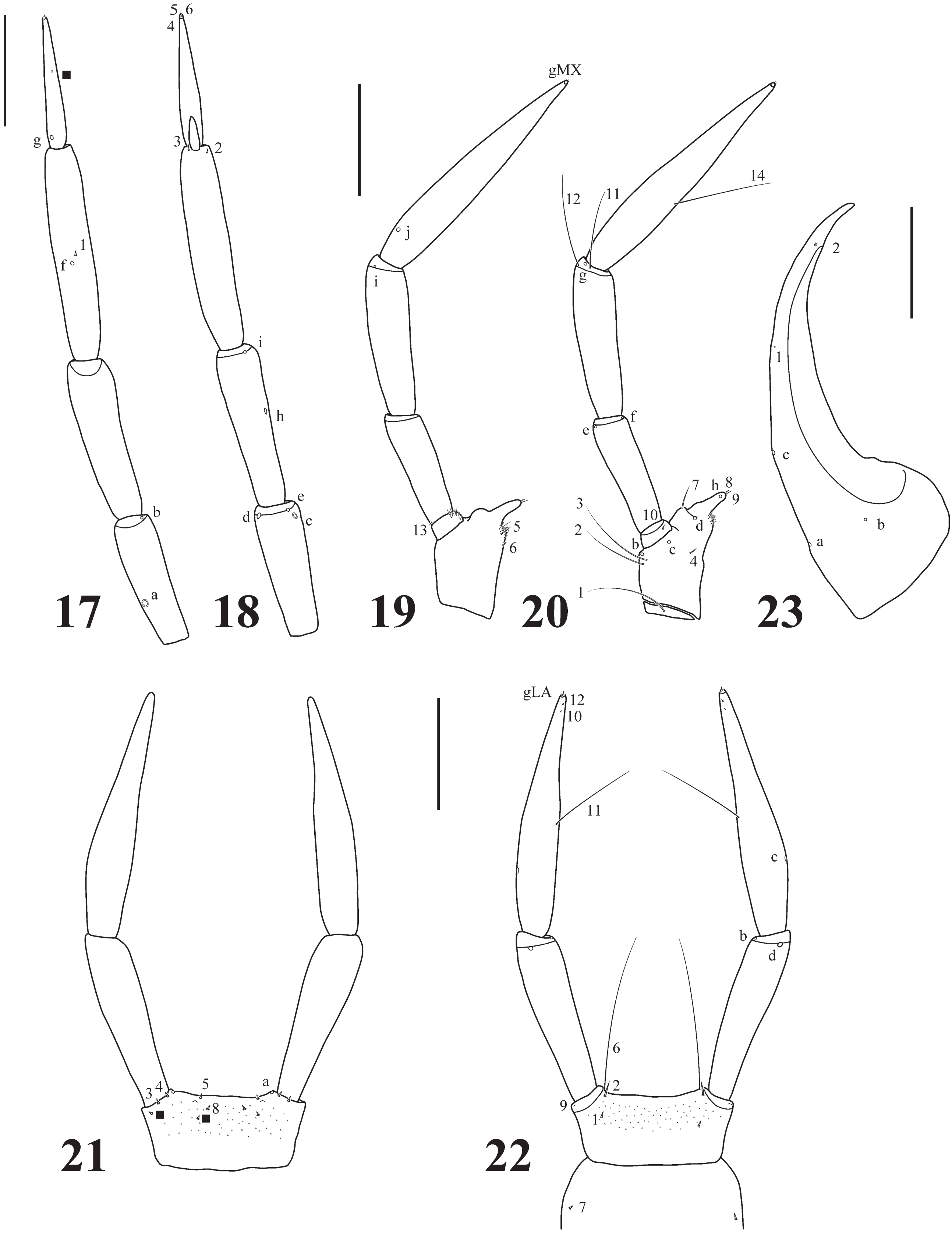
FIGURES 3–9. *Platambus pictipennis* (Sharp, 1873), instar I, head appendages: (3–4) antenna, (3) dorsal aspect; (4) ventral aspect; (5–6) maxilla, (5) dorsal aspect; (6) ventral aspect; (7–8) labium; (7) dorsal aspect; (8) ventral aspect; (9) mandible, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae. Scale bars = 0.10 mm.



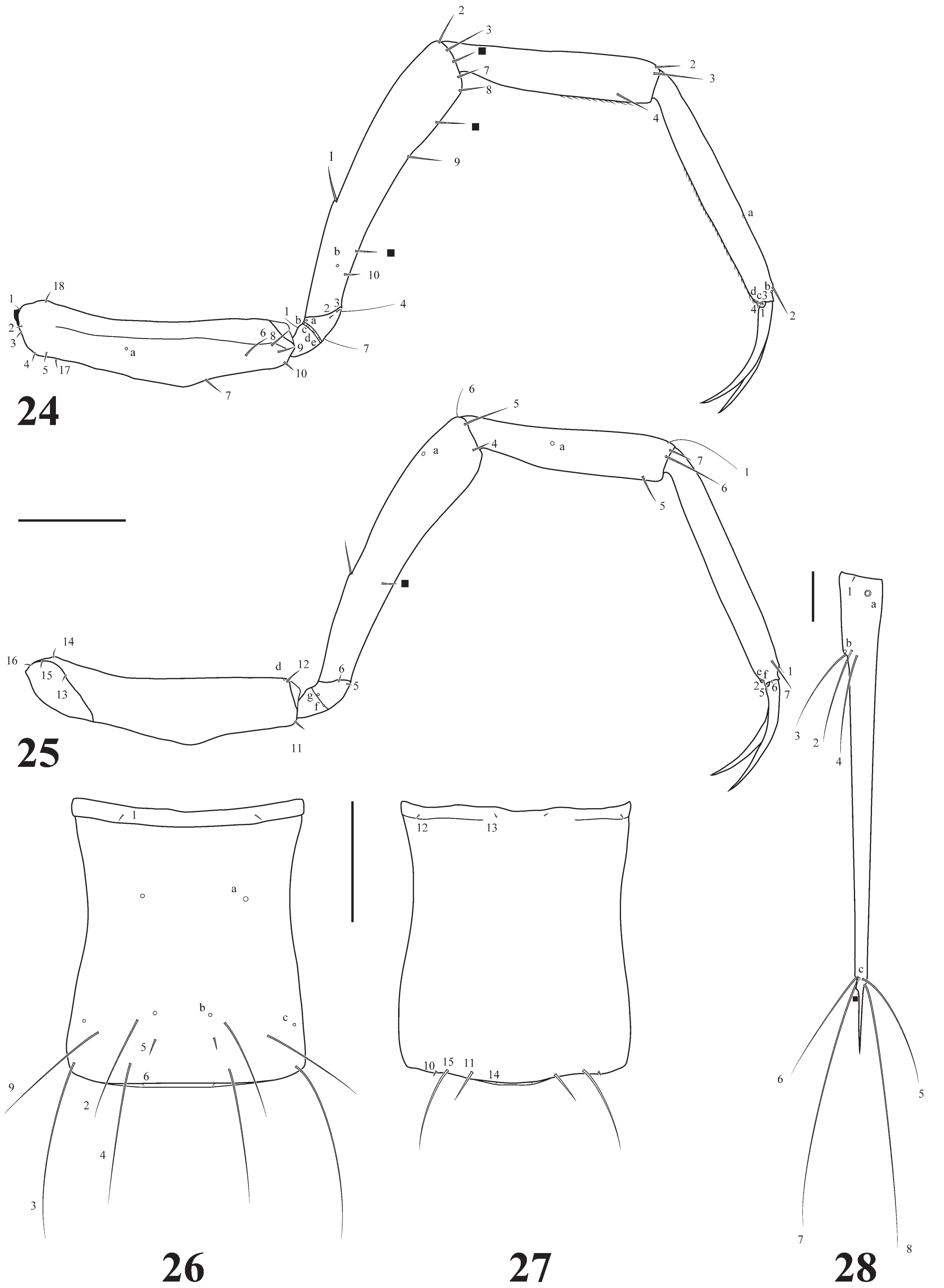
FIGURES 10–14. *Platambus pictipennis* (Sharp, 1873), instar I: (10–11) metathoracic leg; (10) anterior aspect; (11) posterior aspect; (12–13) last abdominal segment; (12) dorsal aspect; (13) ventral aspect; (14) urogomphi, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae. Scale bars = 0.20 mm in (10–11), 0.10 mm in (12–14).



FIGURES 15–16. *Platambus convexus* Okada, 2011, instar I, head capsule: (15) dorsal aspect (colour pattern not represented); (16) ventral aspect. EB, egg bursters; TP, tentorial pits. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.



FIGURES 17–23. *Platambus convexus* Okada, 2011, instar I, head appendages: (17–18) antenna, (17) dorsal aspect; (18) ventral aspect; (19–20) maxilla, (19) dorsal aspect; (20) ventral aspect; (21–22) labium; (21) dorsal aspect; (22) ventral aspect; (23) mandible, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae. Scale bars = 0.10 mm.



FIGURES 24–28. *Platambus convexus* Okada, 2011, instar I: (24–25) metathoracic leg; (24) anterior aspect; (25) posterior aspect; (26–27) last abdominal segment; (26) dorsal aspect; (27) ventral aspect; (28) urogomphi, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae. Scale bars = 0.20 mm in (24–25), 0.10 mm in (26–28).

Instar I (Figs 1–14, 73). **Color.** Dorsal surface of head capsule predominantly dark brown; frontoclypeus creamy white distally, dark brown around each egg burster; parietale dark brown to black with a paired pale macula distal margin of ecdysial suture; head appendages pale yellow, A3, A4, MP3, and LP2 infuscate apically; thoracic and abdominal terga I to VII brown; LAS dark brown over 1/3 to 1/2 of anterior region, yellowish posteriorly; urogomphi pale yellow, basal region of median and distal group of sensilla dark brown; legs pale yellow.

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule (Figs 1–2). Rounded, sides subparallel; frontoclypeus with 10–11 spatulate setae. Antenna (Figs 3–4). A3' bulge-like.

Chaetotaxy. Seta FR3 shorter than seta FR2; seta PA6 shorter than seta PA7; seta PA13 subequal or longer than seta PA12; prementum with one additional seta; setae TI2, TI3, TI6, TI7, TA6, and TA7 acute apically; seta AB2 shorter than seta AB9; seta AB15 subequal or slightly shorter than seta AB11; setae UR2, UR3 and UR4 inserted contiguously; position and number of additional setae on legs are shown in Table 1.

Instar II (Fig. 76). As first-instar larva except as follows:

Color. Dorsal surface of head capsule predominantly yellowish with W-shaped dark brown macula at about middle; thoracic and abdominal segments yellowish with several brown maculae.

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule. Frontoclypeus with 20–22 spatulate setae.

Chaetotaxy. Parietale with 5–8 spine-like secondary setae on the lateral margin; position and number of secondary setae on legs are shown in Table 2; anterodorsal secondary setae on TI and TA acute apically.

Instar III (Figs 57, 61–62, 69, 79). As second-instar larva except as follows:

Color. Thoracic and abdominal segments predominantly brown with several yellowish maculae.

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule (Fig. 57). Frontoclypeus with 35–42 spatulate setae.

Chaetotaxy. Parietale with 6–8 spine-like secondary setae along lateral margin; position and number of secondary setae on legs are shown in Table 2.

Habitat. Larvae were collected along the quiet margin of moderate size rivers (Figs 83–85). First-instar larvae were generally collected in shallower areas, among roots of small grass whilst second- and third- instar larvae were mainly found along banks with withered grass hanging (Fig. 83).

Description of the larvae of *Platambus convexus* Okada, 2011

Source of material. 4 instar I, 6 instar III, Japan: Nishinopporo-sawa, Nopporo, Ebetsu-shi, Hokkaido Pref., 22.III.2014, 21.III.2015, R. Okada leg; 26.XII.2015, D. Sumikawa leg; Japan: Ishihoko riv., Hatori, Ten-ei-mura, Fukushima Pref., 26.X.2016, K. Hirasawa leg. First instar larvae were reared *ex ovo* from adults collected at that locality. The identification of instar III is firm as *P. convexus* is the only *Platambus* species found at those localities (Okada 2011).

Diagnosis. First instar larva of *P. convexus* can be distinguished from the other species studied by the following combinations of features: frontoclypeus with more than 15 spatulate setae (Fig. 15); seta FR3 shorter than seta FR2 (Fig. 15); seta PA6 subequal in length to seta PA7 (Fig. 15); primary seta LA10 inserted subapically (Fig. 22); ratio L3/HW = 3.30–3.50. In addition to color patterns of head capsule (Fig. 58), last abdominal segment, and urogomphi (Figs 70, 73–82), the total number of spatulate setae on frontoclypeus, secondary setae on pro- and mesofemur, and the presence/absence of ventral setae on protarsus (Table 2) are helpful at discriminating later instars.

Instar I (Figs 15–28). **Color (alcohol preserved).** Dorsal surface of head capsule predominantly creamy white; frontoclypeus creamy white apically, dark brown around each egg burster; parietale creamy white with a dark brown V-shaped macula across the ecdysial suture along with some pale brown maculae. Head appendages creamy white; thoracic and abdominal terga I to VII creamy white; LAS dark brown over anterior 1/2, paler posteriorly; urogomphi creamy white; legs creamy white.

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule (Figs 15–16). Subovate, sides subparallel; frontoclypeus with 15–16 spatulate setae. Antenna (Figs 17–18). A3' protruding, finger-like.

Chaetotaxy. Seta FR3 shorter than seta FR2; seta PA6 shorter than seta PA7; seta PA13 subequal or longer than seta PA12; prementum with two additional setae on dorsal surface; setae TI2, TI3, TI6, TI7, TA6, and TA7 acute apically; seta AB2 subequal to seta AB9; seta AB15 longer than seta AB11; setae UR2, UR3 and UR4 inserted contiguously; position and number of additional setae on legs are shown in Table 1.

Instar II. No specimen was available for study.

Instar III (Figs 58, 63–64, 70, 82). As first-instar larva except as follows:

Color. Dorsal surface of head capsule yellowish; parietale yellowish with W-shaped pale brown marking and pale spot maculae across distal margin of ecdysial suture; thoracic and abdominal segments pale brown with several pale yellowish maculae; LAS brown over anterior 1/2, yellowish posteriorly.

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule (Fig. 58). Frontoclypeus with 42–45 spatulate setae. Antenna. A3' bulge-like.

Chaetotaxy. Position and number of secondary setae on legs are shown in Table 2; parietale with 6–7 spine-like secondary setae along lateral margin.

Habitat. Larvae were collected along the quiet margin of a shallow creek flowing under broadleaved trees (Fig. 86). Whereas frozen in winter, we were able to collect some larvae under ice.

Description of the larvae of *Platambus fimbriatus* (Sharp, 1884)

Source of material. 1 instar I, 1 instar II, 10 instar III, Japan: Echi riv., Tanesato, Notogawa-cho, Shiga Pref., 22.II.2015; 20.XII.2015; 10.I.2016; R. Okada leg; 5 instar I, 1 instar II, Japan: Abukuma riv., Tsuruo, Saigo-mura, Fukushima Pref., 8.I.2017 R. Okada leg. Larvae were identified *ex societate imaginis*. Both *Platambus fimbriatus* and *P. pictipennis* occur at these two localities. Larvae of *P. fimbriatus*, however, could readily be recognized using features listed below.

Diagnosis. First instar larva of *P. fimbriatus* can be distinguished from the other species studied by the following combinations of features: frontoclypeus with less than 10 spatulate setae (Fig. 29); seta FR3 shorter than seta FR2 (Fig. 29); seta PA6 subequal in length to seta PA7 (Fig. 29); primary seta LA10 inserted subapically (Fig. 36); setae TI2, TI3, TI6, TI7, TA6, and TA7 bluntly pointed apically; seta UR4 not inserted contiguously to setae UR2 and UR3; ratio L3/HW < 2.90. In addition to color patterns of head capsule (Fig. 59), last abdominal segment, and urogomphi (Figs 71, 73–82), the total number of spatulate setae on frontoclypeus, secondary setae on pro- and mesofemur, and the presence/absence of ventral setae on protarsus (Table 2) are helpful at discriminating later instars.

Instar I (Figs 29–42, 74). Color. Dorsal surface of head capsule predominantly dark brown; frontoclypeus yellowish anteriorly, dark brown around each egg burster; parietale dark brown, paler over occipital region; head appendages pale yellow, A3, A4, MP3, MP2, MP3 and LP2 infuscate apically; thoracic and abdominal terga I to VII pale brown; LAS predominantly dark brown; urogomphi pale yellow basally, dark brown over distal half; legs predominantly pale yellow, dark brown apically.

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule (Figs 29–30). Rounded, sides slightly diverging posteriorly; frontoclypeus with 10 spatulate setae. Antenna (Figs 31–32). A3' finger-like.

Chaetotaxy. Seta FR3 shorter than seta FR2; seta PA6 subequal or longer than seta PA7; seta PA13 shorter than PA12; prementum with one additional seta on dorsal surface; setae TI2, TI3, TI6, TI7, TA6, and TA7 bluntly pointed apically; seta AB2 shorter than seta AB9; seta AB15 longer than seta AB11; seta UR4 not inserted contiguously to setae UR2 and UR3; position and number of additional setae on legs are shown in Table 1.

Instar II (Fig. 77). As first-instar larva except as follows:

Color. Dorsal surface of LAS yellowish anteriorly, dark brown over posterior half.

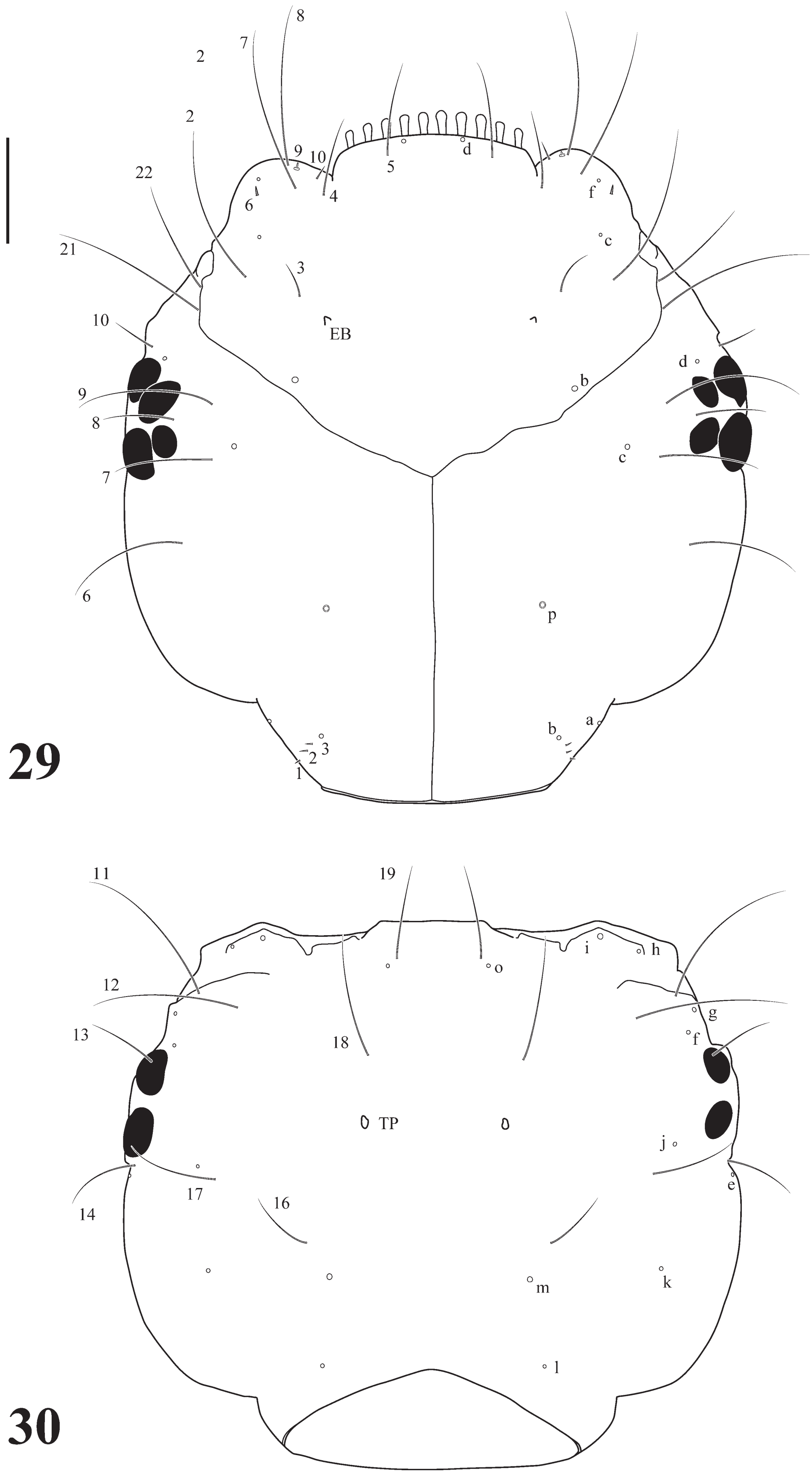
Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule. Frontoclypeus with 20–21 spatulate setae. Antenna. A3' bulge-like.

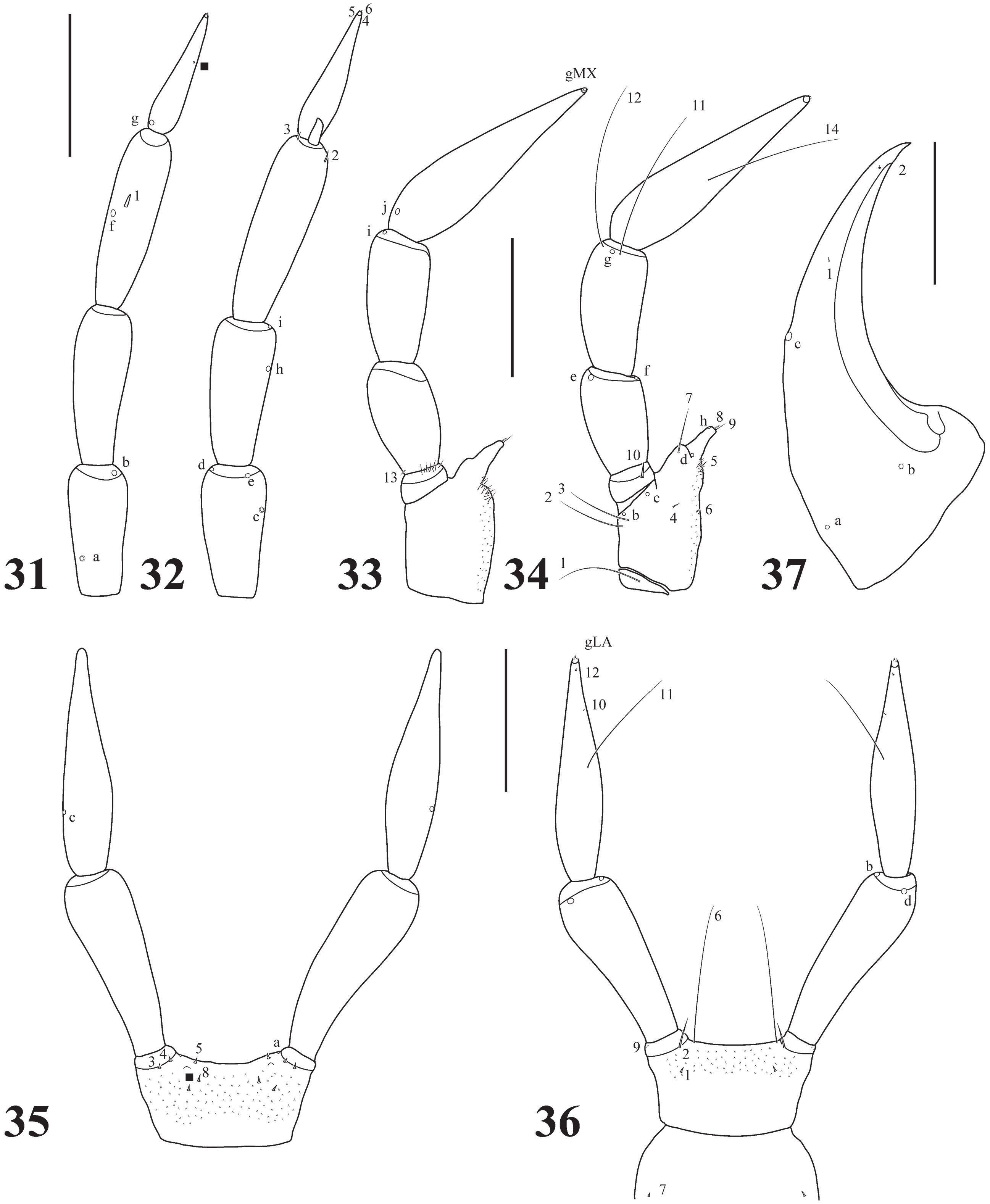
Chaetotaxy. Position and number of secondary setae on legs are shown in Table 1; parietale with 4 spine-like secondary setae on lateral margin of each side; anterodorsal secondary setae on TI and TA bluntly pointed apically.

Instar III (Figs 59, 65–66, 71, 80). As second-instar larva except as follows:

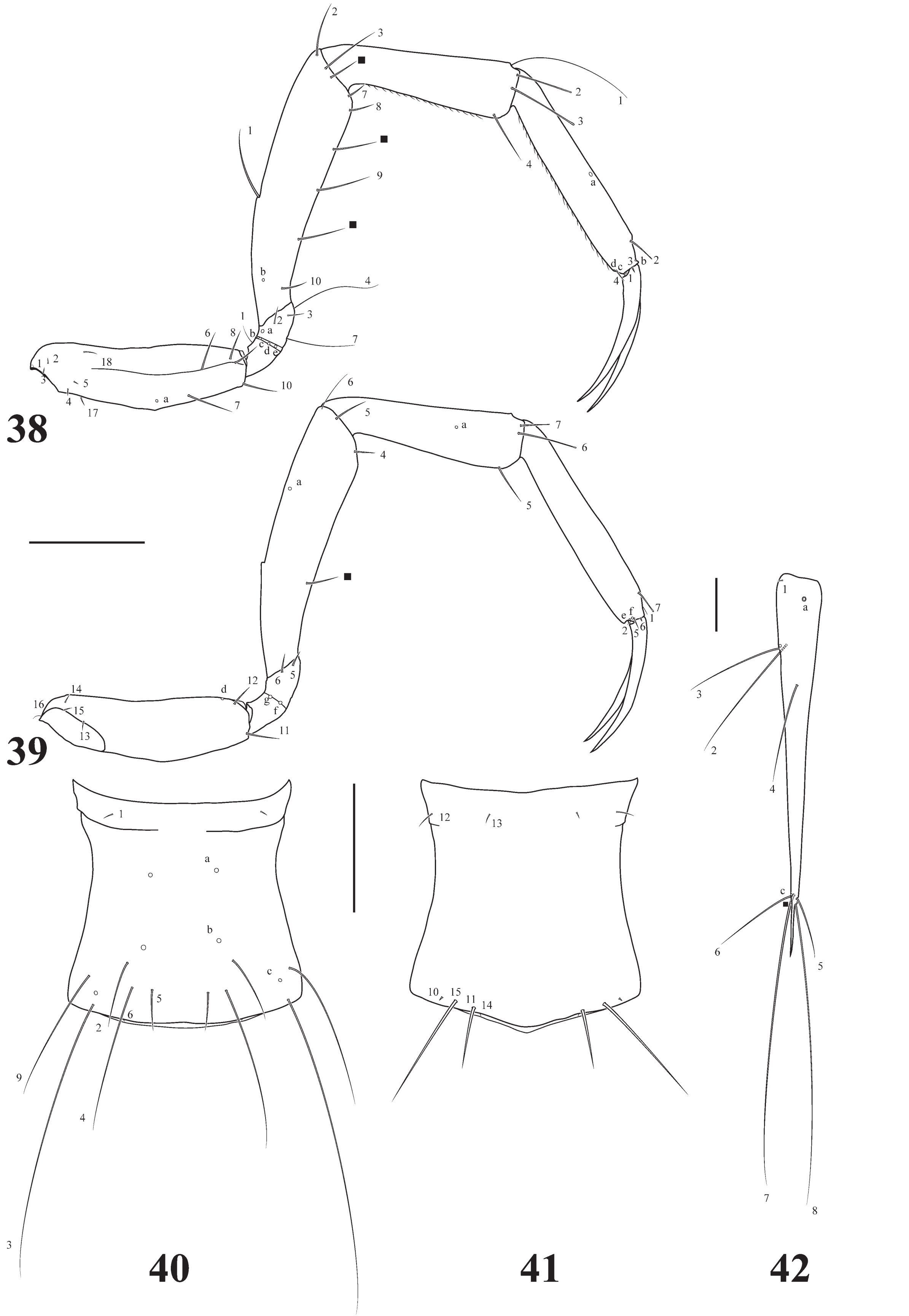
Color. Dorsal surface of head capsule yellowish; parietale yellowish with a narrow V-shaped dark brown marking across capsule at about mid-length and some brown maculae posteriorly; pro- and mesotergum and abdominal segments yellowish with several brown maculae, metanotum predominantly dark brown; LAS yellowish anteriorly, dark brown over distal 1/3 to 1/2; urogomphi predominantly yellow.



FIGURES 29–30. *Platambus fimbriatus* (Sharp, 1884), instar I, head capsule: (29) dorsal aspect (colour pattern not represented); (30) ventral aspect. EB, egg bursters; TP, tentorial pits. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.



FIGURES 31–37. *Platambus fimbriatus* (Sharp, 1884), instar I, head appendages: (31–32) antenna, (31) dorsal aspect; (32) ventral aspect; (33–34) maxilla, (33) dorsal aspect; (34) ventral aspect; (35–36) labium; (35) dorsal aspect; (36) ventral aspect; (37) mandible, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae. Scale bars = 0.10 mm.



FIGURES 38–42. *Platambus fimbriatus* (Sharp, 1884), instar I: (38–39) metathoracic leg; (38) anterior aspect; (39) posterior aspect; (40–41) last abdominal segment; (40) dorsal aspect; (41) ventral aspect; (42) urogomphi, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae. Scale bars = 0.20 mm in (38–39), 0.10 mm in (40–42).

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule (Fig. 59). Frontoclypeus with 26–31 spatulate setae.

Chaetotaxy. Position and number of secondary setae on legs are shown in Table 1; parietale with 6–8 spine-like secondary setae along lateral margin.

Habitat. Larvae occur along quiet margins of moderate sized rivers flowing on sandy bottom. First-instar larvae are mainly collected along the banks under stones in shallow water. Whereas also collected in shallow parts, both second- and third- instar larvae appear to be more abundant in dry grass deposits (Fig. 85).

Description of the larvae of *Platambus sawadai* (Kamiya, 1932)

Source of material. 7 instar I, 10 instar II, 10 instar III, Japan: Happudani riv., Ishigure pass, Higashiomi-shi, Shiga Pref., 28.XI.2015; 20.XII.2015; 10.I.2016; 6.II.2016, R. Okada leg. Larvae were identified *ex societate imaginis*. The identification is firm since *P. sawadai* is the only *Platambus* species known at this locality.

Diagnosis. First instar larva of *P. sawadai* can be distinguished from the other species studied by the following combinations of features: frontoclypeus with more than 13 spatulate setae (Fig. 43); seta FR3 subequal in length to seta FR2 (Fig. 43); seta PA6 longer than seta PA7 (Fig. 43); primary seta LA10 inserted submedially (Fig. 50); ratio L3/HW = 3.10–3.30. In addition to color patterns of head capsule (Fig. 60), last abdominal segment, and urogomphi (Figs 73–82), the total number of spatulate setae on frontoclypeus, secondary setae on pro- and mesofemur and the presence/absence of ventral setae on protarsus (Table 2) are helpful at discriminating later instars.

Instar I (Figs 43–56, 75). Color. Dorsal surface of head capsule predominantly pale yellow; frontoclypeus pale yellow anteriorly, dark grey around each egg burster; parietale pale yellow with dark V-shaped band across ecdysial suture; head appendages pale yellow; thoracic and abdominal terga I to VII dark grey; LAS dark grey over anterior 2/3, yellowish posteriorly; urogomphi pale yellow; legs pale yellow.

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule (Figs 43–44). Subovate, sides subparallel; frontoclypeus with 13–15 spatulate setae. Antenna (Figs 45–46). A3' finger-like.

Chaetotaxy. Seta FR3 subequal or longer than seta FR2; seta PA6 longer than seta PA7; seta PA13 longer than seta PA12; prementum with two additional setae on dorsal surface; setae TI2, TI3, TI6, TI7, TA6, and TA7 acute apically; seta AB2 shorter than seta AB9; seta AB15 subequal or shorter than seta AB11; setae UR2, UR3 and UR4 inserted contiguously; position and number of additional setae on legs are shown in Table 1.

Instar II (Fig. 78). As first-instar larva except as follows:

Color. Thoracic and abdominal segments dark brown with several yellowish maculae.

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

Head. Head capsule. Frontoclypeus with 28–31 spatulate setae. Antenna. A3' bulge-like.

Chaetotaxy. Position and number of secondary setae on legs are shown in Table 2; parietale with 4–6 spine-like secondary setae along lateral margin; anterodorsal secondary setae on TI and TA acute apically.

Instar III (Figs 60, 67–68, 72, 81). As second-instar larva except as follows:

Body. Measurements and ratios that characterize the body shape are shown in Table 3.

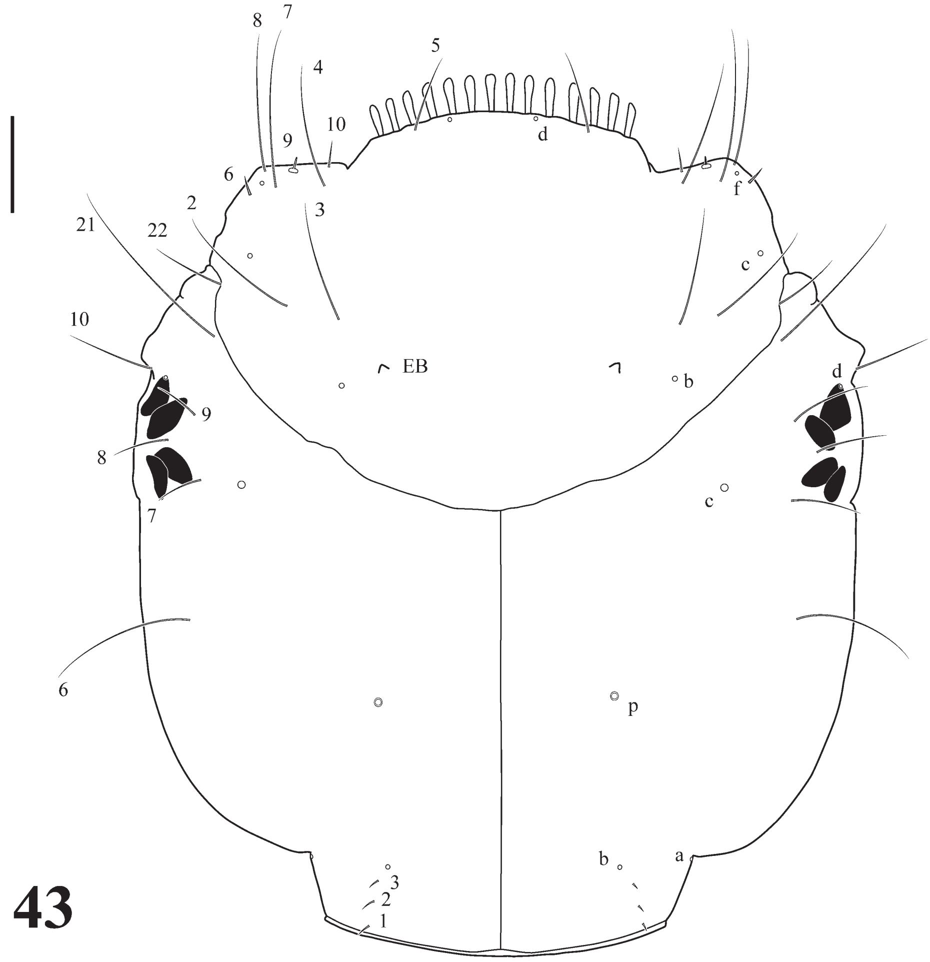
Head. Head capsule (Fig. 60). Frontoclypeus with 40–51 spatulate setae.

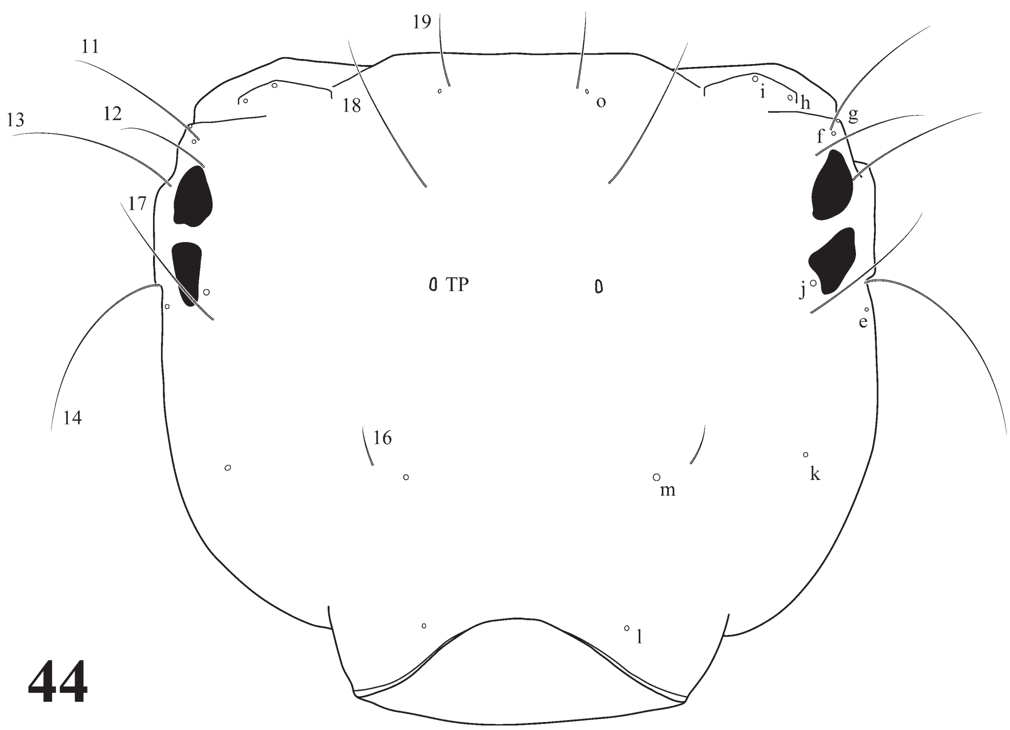
Chaetotaxy. Position and number of secondary setae on legs are shown in Table 2; parietale with 4–6 spine-like secondary setae along lateral margin.

Ecology. Larvae were collected from eddies of clear mountain stream (Fig. 87), particularly in road-side gutters with constantly flowing clear water (Fig. 88). Larvae occur amongst fallen leaves deposited in the gutter.

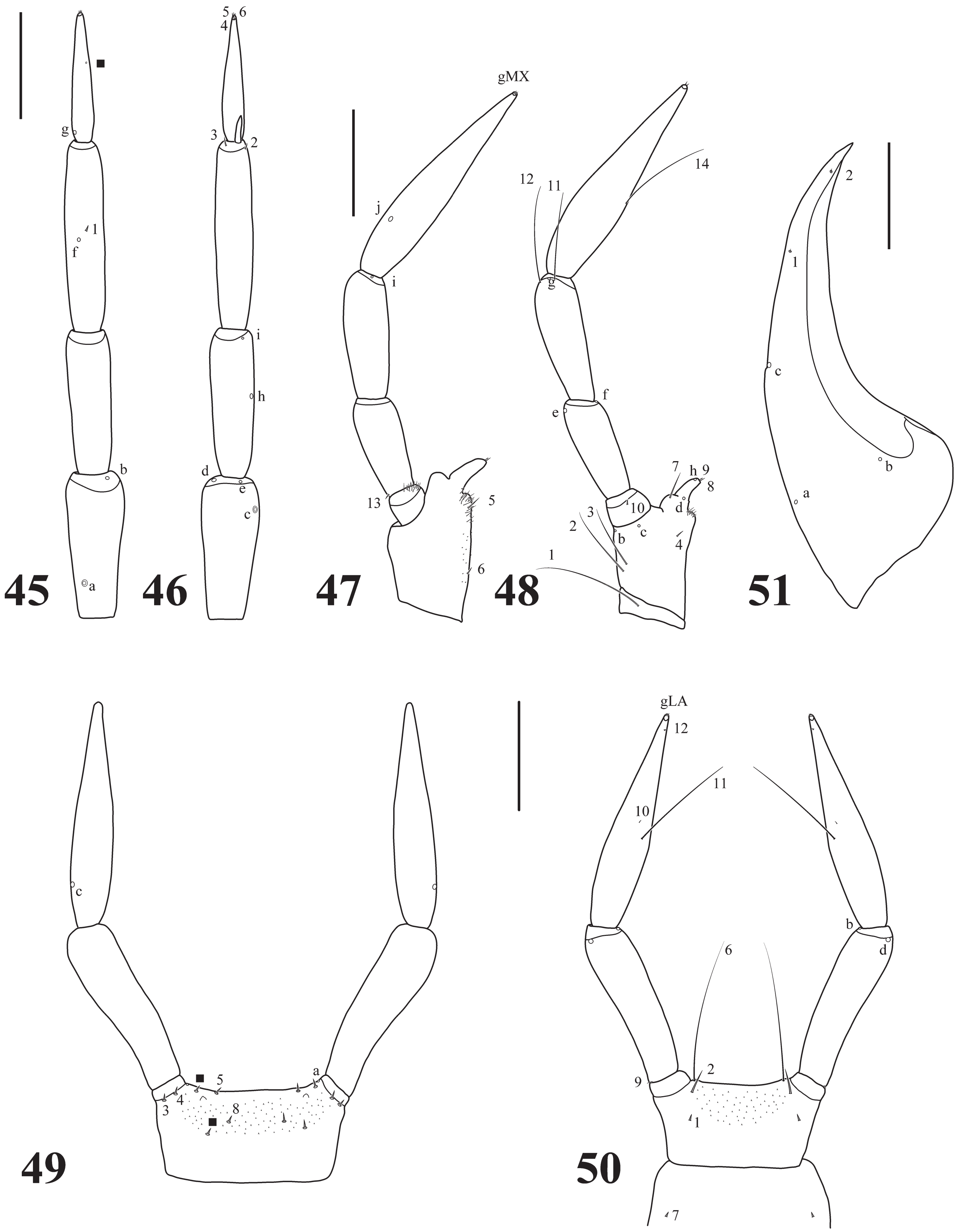
Character analysis

The analysis of the data matrix with TNT resulted in six most parsimonious trees of 79 steps (CI = 0.57; RI = 0.72). The strict consensus was calculated (Fig. 89), in which most of the genera collapsed in a polytomy. The monophyly of *Platambus*, however, is well supported, although the identity of its sister group remains obscure. Character state changes are mapped on one of the most parsimonious trees (Fig. 90).

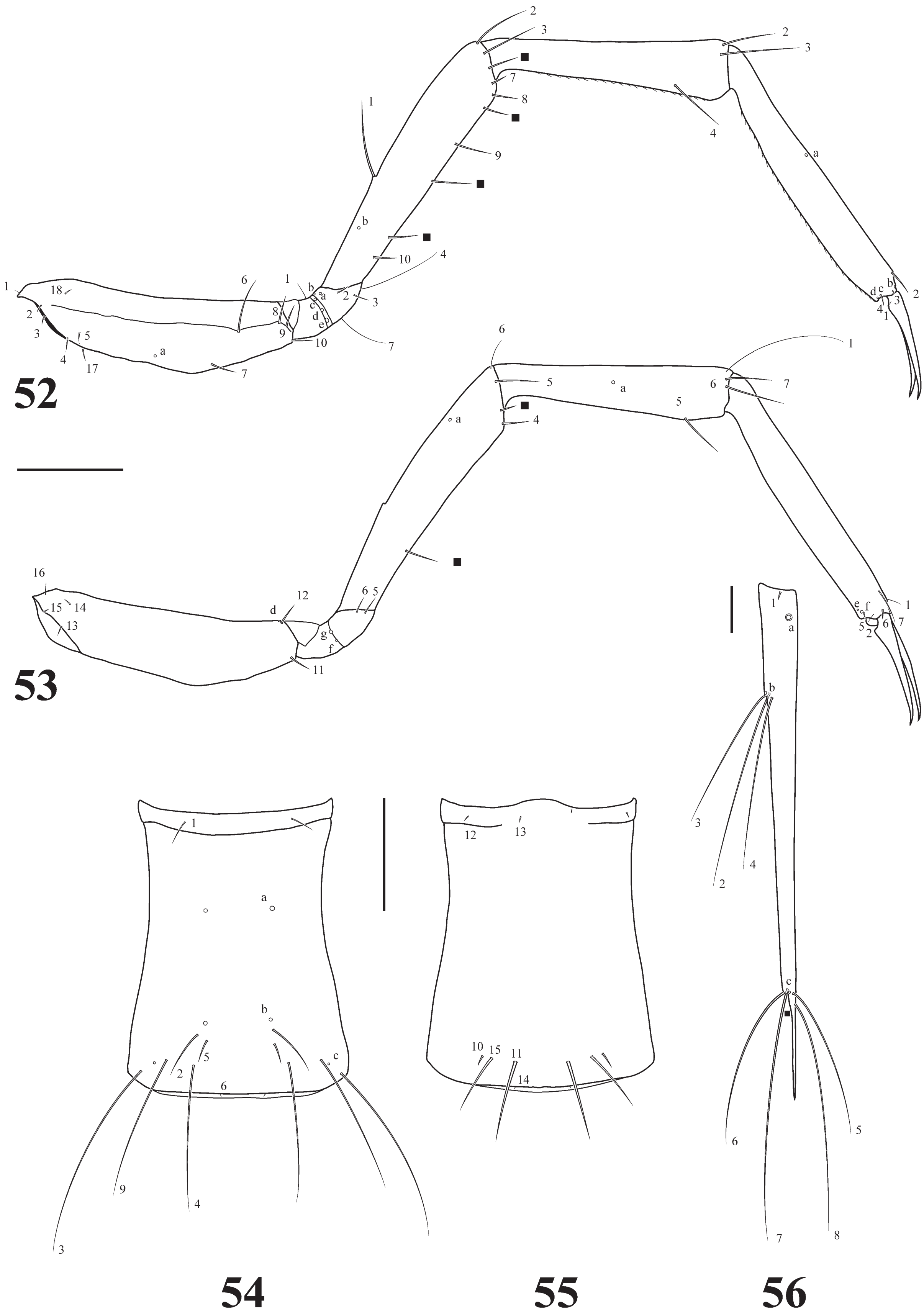




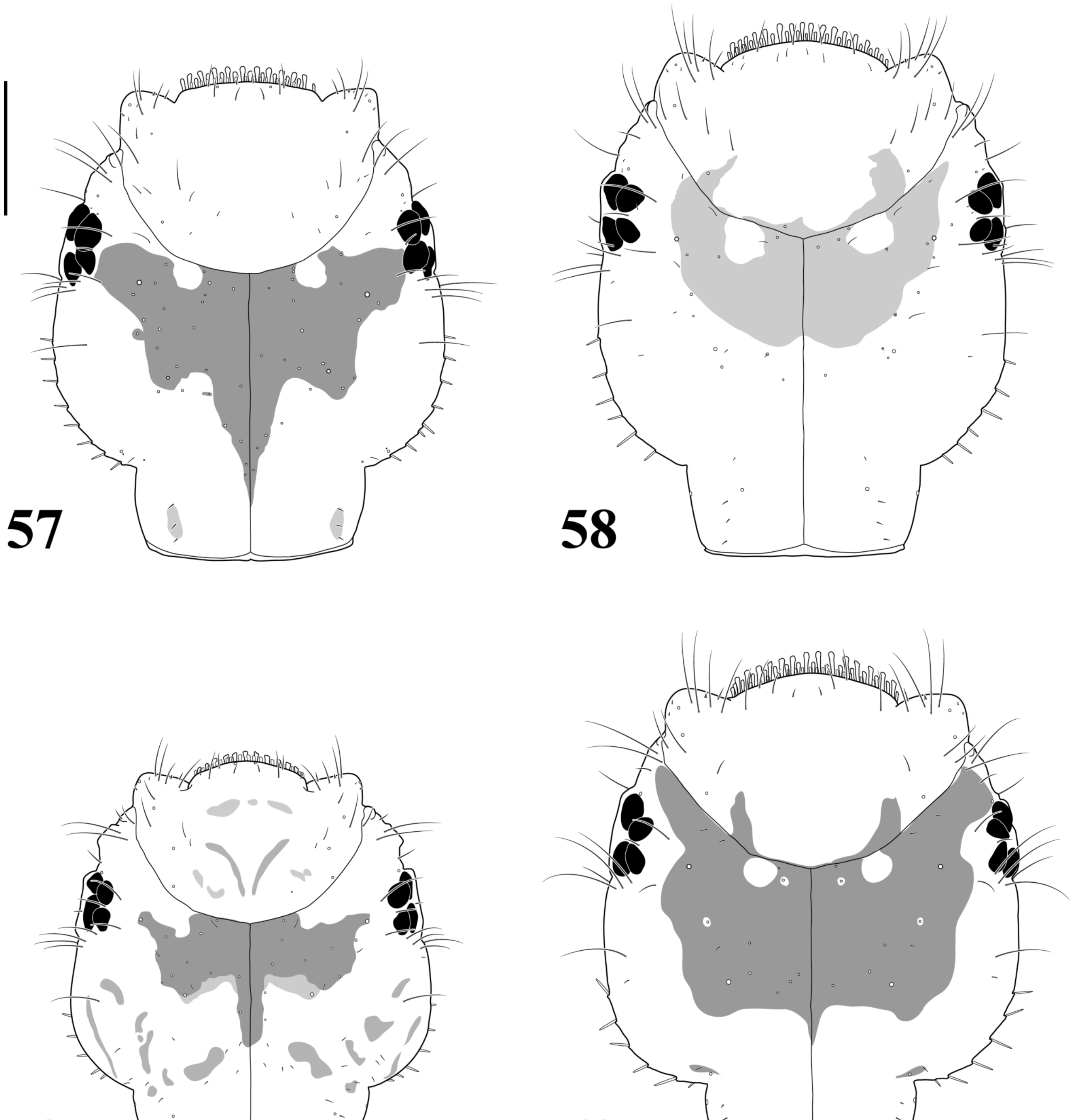
FIGURES 43–44. *Platambus sawadai* (Kamiya, 1932), instar I, head capsule: (43) dorsal aspect (colour pattern not represented); (44) ventral aspect. EB, egg bursters; TP, tentorial pits. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.



FIGURES 45–51. *Platambus sawadai* (Kamiya, 1932), instar I, head appendages: (45–46) antenna, (45) dorsal aspect; (46) ventral aspect; (47–48) maxilla, (47) dorsal aspect; (48) ventral aspect; (49–50) labium; (49) dorsal aspect; (50) ventral aspect; (51) mandible, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae. Scale bars = 0.10 mm.



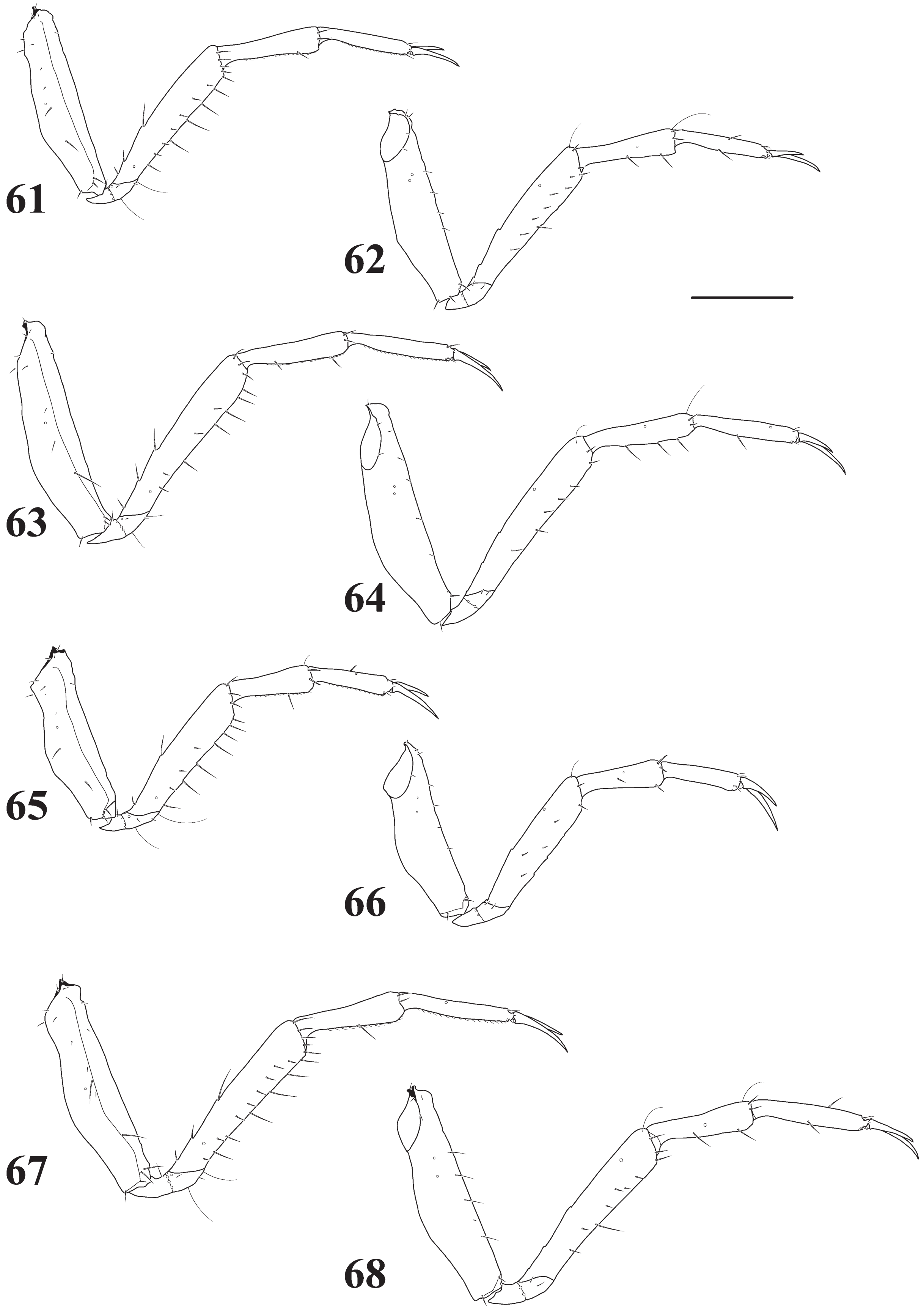
FIGURES 52–56. *Platambus sawadai* (Kamiya, 1932), instar I: (52–53) metathoracic leg; (52) anterior aspect; (53) posterior aspect; (54–55) last abdominal segment; (54) dorsal aspect; (55) ventral aspect; (56) urogomphi, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae. Scale bars = 0.20 mm in (52–53), 0.10 mm in (54–56).



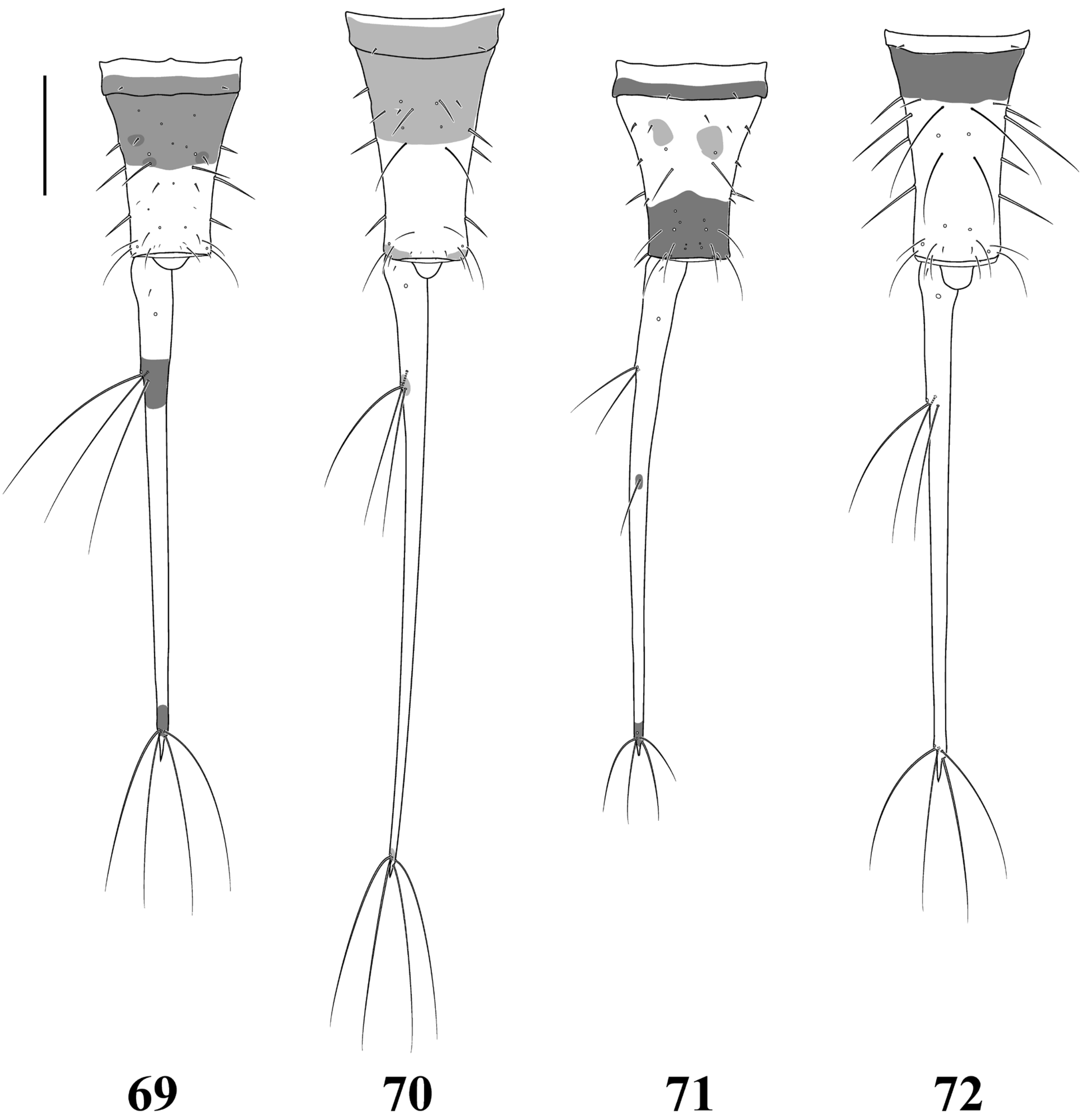
FIGURES 57–60. Head capsule of selected species of *Platambus* Thomson, 1859, instar III, dorsal aspect: (57) *P. pictipennis* (Sharp, 1873); (58) *P. convexus* Okada, 2011; (59) *P. fimbriatus* (Sharp, 1884); (60) *P. sawadai* (Kamiya, 1932). Scale bar = 0.50 mm.

Discussion

Agabinae is comprised of more than 400 species worldwide (Nilsson & Hájek 2019). Our study therefore must be seen as provisional owing to the limited number of taxa included. It is obviously open to reconsideration when larvae of additional Agabinae taxa will be described.

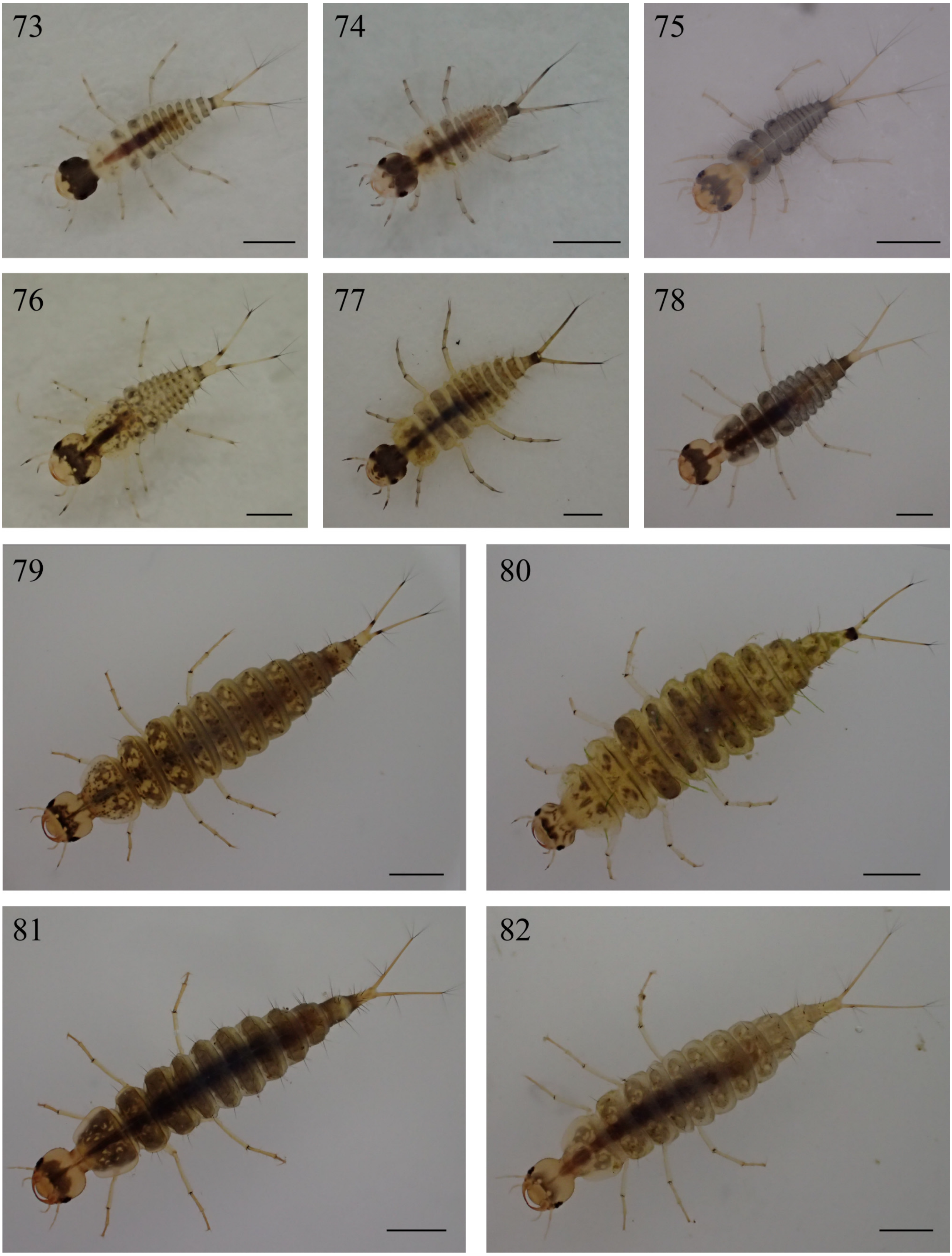


FIGURES 61–68. Prothoracic leg of selected species of *Platambus* Thomson, 1859, instar III: (61–62) *P. pictipennis* (Sharp, 1873), (61) anterior aspect; (62) posterior aspect; (63–64) *P. convexus* Okada, 2011, (63) anterior aspect; (64) posterior aspect; (65–66) *P. fimbriatus* (Sharp, 1884), (65) anterior aspect; (66) posterior aspect; (67–68) *P. sawadai* (Kamiya, 1932), (67) anterior aspect; (68) posterior aspect. Scale bar = 0.50 mm.



FIGURES 69–72. Last abdominal segment and urogomphi of selected species of *Platambus* Thomson, 1859, instar III, dorsal aspect: (69) *P. pictipennis* (Sharp, 1873); (70) *P. convexus* Okada, 2011; (71) *P. fimbriatus* (Sharp, 1884); (72) *P. sawadai* (Kamiya, 1932). Scale bar = 0.50 mm.

Following this study, a placement of *Platambus* within Agabinae seems rather clear based on larval morphology. High bootstrap (0.92) and Bremer (9) values (Figure 89) indicate strong support for the monophyly of Agabinae with respect to the chosen out-groups. Larvae of *Platambus* share with other Agabinae studied the following unique character states (Fig. 90): (1) absence of an occipital suture (Figs 1, 2, 15, 16,2 9, 30, 43, 44, 57–60; character 06); (2) absence of natatory setae on legs (Figs 61–68; characters 19, 25, 29), and (3) presence in instar I larva of a short and spine-like seta TI6 (Figs 11, 25, 39, 53; character 29).



FIGURES 73–82. Dorsal habitus of selected species of *Platambus* Thomson, 1859: (73– 75) instar I; (76–78) instar II; (79-82) instar III; (73, 76, 79) *P. pictipennis* (Sharp, 1873); (74, 77, 80) *P. fimbriatus* (Sharp, 1884); (75, 78, 81) *P. sawadai* (Kamiya, 1932); (82) *P. convexus* Okada, 2011. Scale bar = 1.00 mm in (73–78), 2.00 mm in (79–82).

FIGURES 83–88. Collecting localities of the larvae of *Platambus* Thomson, 1859: (83–85) Echi river, Shiga Prefecture, Western Japan, (83) moderate sized river, with withered grass hanging; (84) river bank with gravel bed; (85) shallow area with dry grass deposited; (86) Nishinopporo-sawa river, Hokkaido Prefecture, Northern Japan, small stream flowing under broadleaved trees; (87–88) Happudani river, Shiga Prefecture, Western Japan, (87) mountain stream; (88) gutters with constantly flowing clear water.

TABLE 4. Characters used for the phylogenetic analysis and the coding of states using the genera *Matus* Aubé, 1836 and *Rhantus* Dejean, 1833 as outgroups.

---

00. Cephalic capsule (instar I): (0) maximum width at level of stemmata; (1) maximum width posterior to stemmata.
01. Egg bursters (instar I): (0) located close to frontal suture; (1) located far from frontal suture.
02. Seta FR5 (instar I): (0) inserted anteriorly; (1) inserted anterolaterally.
03. Number of lamellae clypeales (excluding FR10) (instar I): (0) four; (1) six; (2) eight; (3) 10 or more.
04. Parietals (at level of occipital suture) (instar I): (0) not constricted; (1) constricted.
05. Parietals (at level of occipital suture) (instars II–III): (0) not constricted; (1) constricted.
06. Occipital suture (instar I): (0) absent; (1) present.
07. Occipital suture (instars II–III): (0) absent; (1) present.
08. Apical lateroventral process of antennomere 3 (instars I–III): (0) protruding; (1) not protruding.
09. Pore ANc (instar I): (0) inserted distally; (1) inserted submedially.
10. Additional ventroapical pores on antennomere 3 (instar I): (0) absent; (1) present.
11. Secondary setae on antennomere 1 (instars II–III): (0) absent; (1) present.
12. Mandibular channel (instars I–III): (0) absent; (1) present.
13. Inner ventral margin of mandible (instars I–III): (0) serrate; (1) not serrate.
14. Additional setae on stipes (instar I): (0) absent; (1) a single seta inserted contiguously to seta MX6.
15. Seta LA10 (instar I): (0) inserted distally; (1) inserted submedially.
16. Additional setae on dorsal surface of prementum (instar I): (0) absent; (1) present.
17. Seta FE1 (instar I): (0) inserted proximally; (1) inserted submedially.
18. Additional posteroventral setae on femur (instar I): (0) absent; (1) present.
19. Natatory posterodorsal setae on femur (instars II–III): (0) absent; (1) present.
20. Secondary anterodorsal setae on femur (instars II–III): (0) absent; (1) present.
21. Seta TI4 (instar I): (0) not inserted more proximally on protibia than on metatibia; (1) inserted more proximally on protibia than on metatibia.
22. Seta TI6 on metatibia (instar I): (0) short, spine-like; (1) elongate, hair-like.
23. Secondary setae on tibiae (instars II–III): (0) absent; (1) present.
24. Primary setae TI2, TI3, TI6, TI7, TA6, TA7 (instars II–III): (0) acute; (1) bluntly pointed.
25. Natatory posterodorsal setae on tibia (instars II–III): (0) absent; (1) present.
26. Seta TA1 (instar I): (0) elongate to very elongate; (1) very short.
27. Secondary dorsal setae on protarsus (instar III): (0) absent; (1) present.
28. Secondary posteroventral setae on pro- and metatarsus (instar III): (0) absent; (1) present.
29. Natatory posterodorsal setae on tarsus (instars II–III): (0) absent; (1) present.
30. Abdominal segment 8 (instar III): (0) extensively extending posteriorly beyond bases of urogomphi; (1) moderately extending posteriorly beyond bases of urogomphi; (2) not extending posteriorly beyond bases of urogomphi.
31. Seta AB14 (instar I): (0) not lanceolate; (1) lanceolate.
32. Additional setae on abdominal segment VIII (instar I): (0) absent; (1) 1-2 spine-like setae inserted on dorsolateral surface; (2) numerous.
33. Siphon (instars I–III): (0) rounded; (1) deeply sinuate medially; (2) lacking.
34. Urogomphus (instars I): (0) composed of one urogomphomere; (1) composed of two urogomphomeres.
35. Seta UR5 (instar I): (0) elongate, as long as seta UR7; (1) short, much shorter than seta UR7.
36. Seta UR6 (instar I): (0) elongate, as long as seta UR7; (1) short, much shorter than seta UR7.
37. Seta UR8 (instar I): (0) elongate, hair-like; (1) short, spine-like
38. Pore URc (instar I): (0) not inserted apically on urogomphomere 1; (1) inserted apically on urogomphomere 1.
39. Additional setae on urogomphomere 1 (instar I): (0) absent; (1) 1-2 spine-like setae inserted dorsolaterally.

Compared to the other Agabinae studied, larvae of *Platambus* examined in this study are deemed monophyletic owing to the unique subquadrate shape of the last abdominal segment not extending posteriorly into a siphon (Figs 12–13, 26–27, 40–41, 54–55, 69–72; characters 30, 33) as well as by the relatively short seta UR5 compared to seta UR7 on the urogomphi of instar I larvae (Figs 14, 28, 42, 56; character 35). The typical shape of the last abdominal segment of the four *Platambus* species studied is noteworthy knowing that in *P. flavovittatus* and *P. stagninus* of the

TABLE 5. Data matrix used for the cladistic analysis.

Species	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20
Matus bicarinatus	0	0	1	2	0	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1
Meridiorhantus calidus	0	0	0	3	0	1	1	1	1	0	1	0	1	1	1	0	0	0	0	1	1
Agabinus glabrellus	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1
Agabus ambiguus	0	0	1	3	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1
Agabus anthracinus	0	0	1	3	0	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1
Hydrotrupes chinensis	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Hydrotrupes palpalis	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Ilybiosoma seriatum	0	0	0	3	1	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1
Ilybius biguttulus	0	1	1	3	1	1	0	0	1	0	0	0	1	1	1	1	1	1	1	0	1
Ilybius vittiger	0	1	1	3	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1
Platynectes bakewelli	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	1	0	0	1	0	0
Platynectes curtulus	0	0	0	3	1	1	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1
Platynectes reticulosus	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	1	1	0	1	0	0
Platambus convexus	0	0	0	3	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1	0	1
Platambus fimbriatus	0	0	0	3	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1	0	1
Platambus pictipennis	0	0	0	3	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1	0	1
Platambus sawadai	0	0	0	3	1	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1

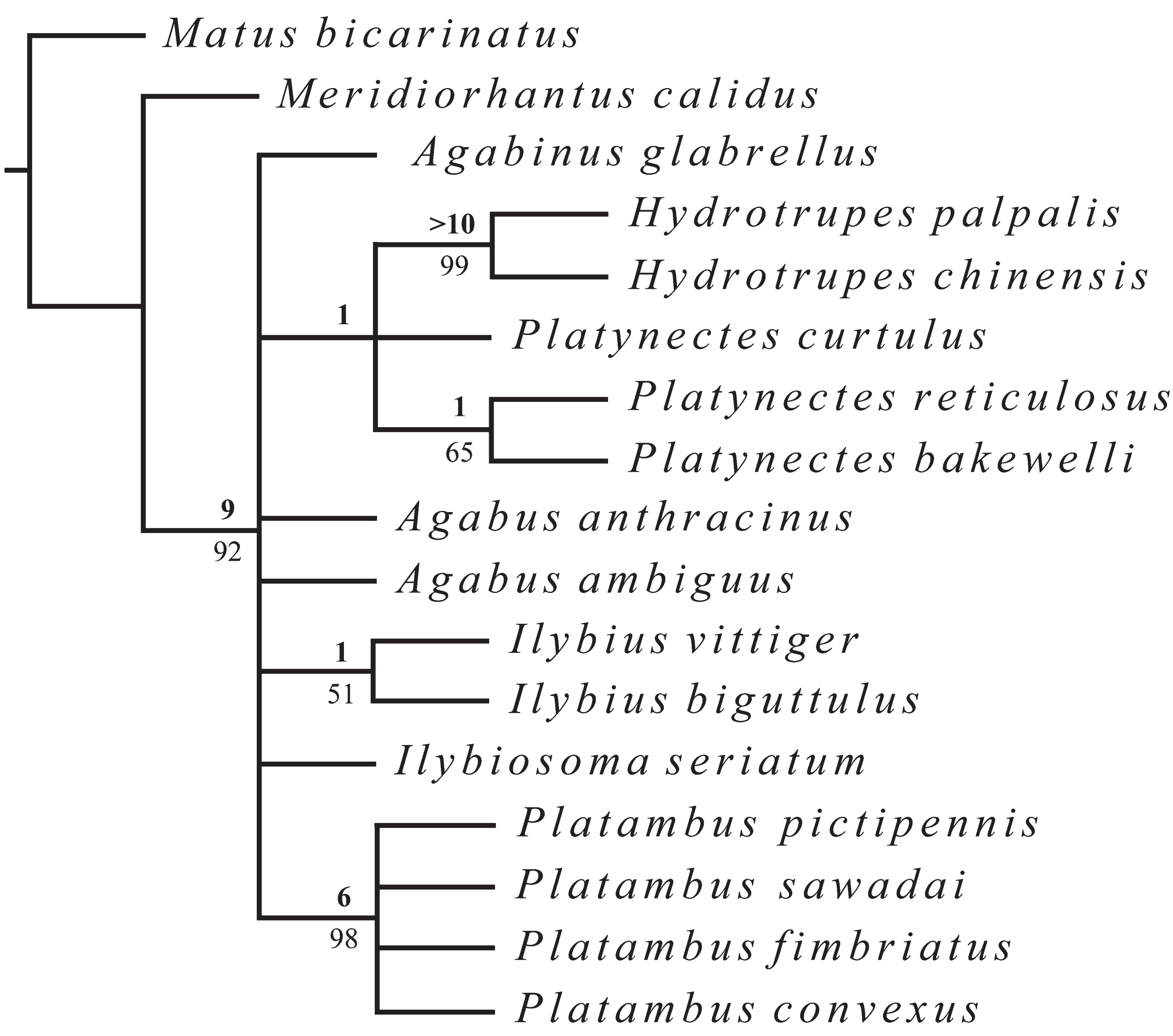
......continued on the next page

TABLE 5. (Continued)

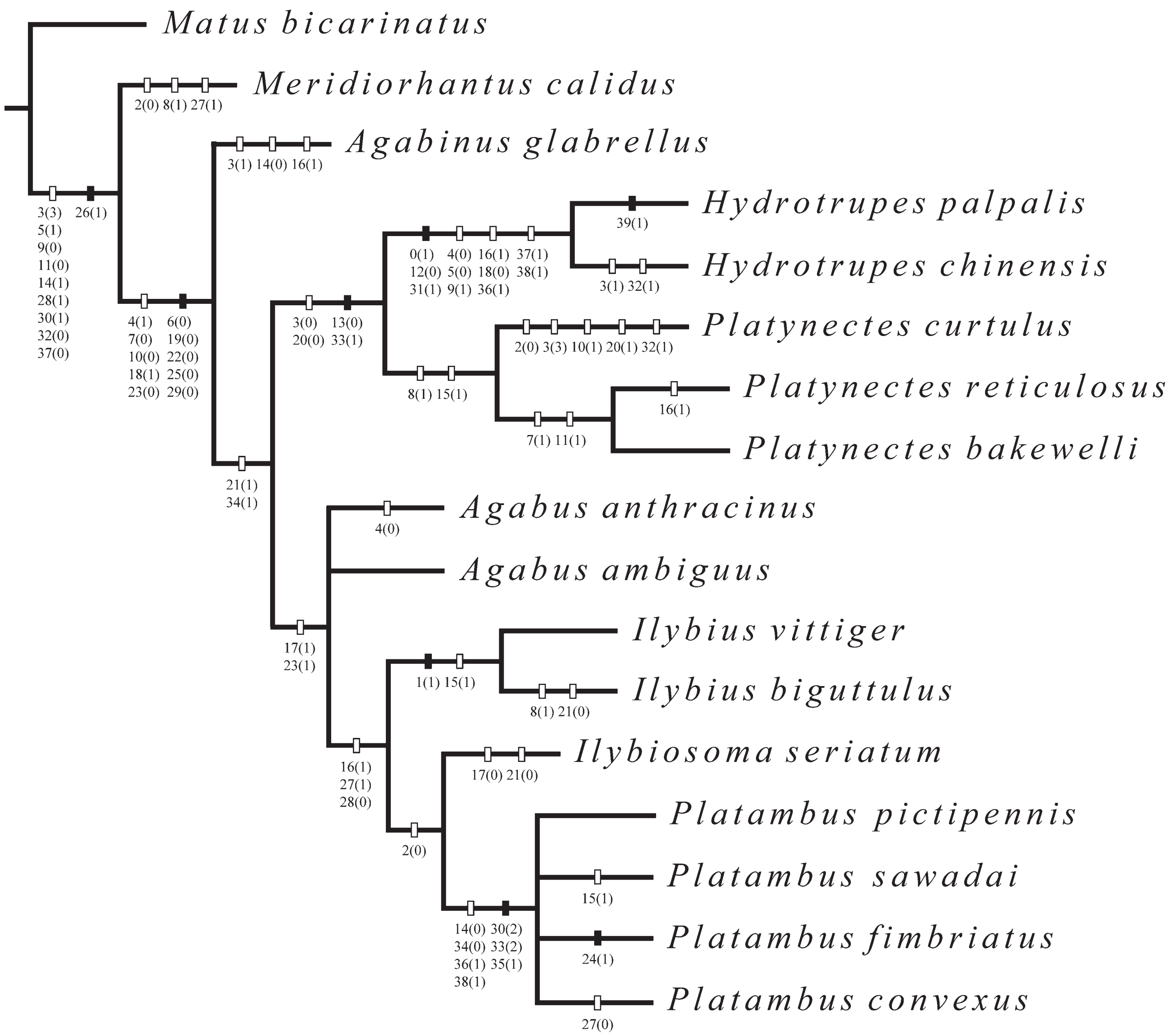
Species	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9
Matus bicarinatus	0	1	1	0	1	0	0	1	1	0	0	2	0	0	0	0	1	0	0
Meridiorhantus calidus	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0
Agabinus glabrellus	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Agabus ambiguus	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
Agabus anthracinus	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
Hydrotrupes chinensis	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	1	1	1	0
Hydrotrupes palpalis	1	0	0	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1
Ilybiosoma seriatum	0	0	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0
Ilybius biguttulus	0	0	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0
Ilybius vittiger	1	0	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0
Platynectes bakewelli	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0
Platynectes curtulus	1	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0
Platynectes reticulosus	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0
Platambus convexus	1	0	1	0	0	1	0	1	0	2	0	0	2	0	1	1	0	1	0
Platambus fimbriatus	1	0	1	1	0	1	1	1	0	2	0	0	2	0	1	1	0	1	0
Platambus pictipennis	1	0	1	0	0	1	1	1	0	2	0	0	2	0	1	1	0	1	0
Platambus sawadai	1	0	1	0	0	1	1	1	0	2	0	0	2	0	1	1	0	1	0

semivittatus-group and *P. koreanus* of the *optatus*-group the last abdominal segment is deemed to extend posteriorly into a siphon (Nilsson 1996; Barman *et al*. 1999; Wilkes *et al*. 2013). A more thorough analysis of the larvae of other species groups of *Platambus* would help to determine if the typical shape of the last abdominal segment observed within the four Japanese species could be generalized to the entire genus or if it represents an evolutionary novelty within *Platambus*.

Whereas inclusion of *Platambus* amongst Agabinae seems rather clear based on larval morphology its relationship with the other Agabini genera studied remains equivocal (Fig. 89). This result is, to some extent, not surprising knowing that Agabinae is a difficult group, which always has shown bad resolution in recent analysis of the Dytiscidae based on larval morphology (cf., Michat *et al*. 2017). Moreover, as a limited number of species groups were included in our study, such result was likely. In that regard the relative position of the genus *Agabinus* must be interpreted cautiously. Nilsson (2000) noted that *Agabinus* shared with *Platambus* the posteriorly expanded lateral beads of the prosternal process, a historically important synapomorphy for the latter genus, which once led in the expansion of *Platambus* to include the genus *Agabinus* (Miller & Bergsten 2016). Nilsson (2015) subsequently resurrected that genus name. Such an apparent similarity between *Agabinus* and *Platambus* argues against the topology proposed in this paper.



FIGURES 89. Strict consensus cladogram obtained from the cladistic analysis of 15 terminal taxa of Agabinae and two outgroups, with Bremer support values indicated above branches and Bootstrap support values indicated below branches.



FIGURES 90. One of the most parsimonious trees obtained from the cladistic analysis of 15 terminal taxa of Agabinae and two outgroups, with character changes mapped for each clade. Solid rectangles indicate unique character state transformations; open rectangles indicate homoplastic character state transformations.

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