Larval morphology of genus *Lancetes* (Coleoptera: Adephaga: Dytiscidae): the hypothesis of sister-group relationship with the subfamily Dytiscinae revisited

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Abstract—Descriptions of the larvae of *Lancetes angusticollis* (Curtis), *L. lanceolatus* (Clark), *L. subseriatus* Zimmermann, *L. flavoscutatus* Enderlein, *L. delkeskampi* Ríha, and *L. nigriceps* (Erichson) are provided. Characters from larval morphology are analyzed to infer the phylogenetic relationships of the genus *Lancetes* Sharp with other genera of Dytiscidae. A parsimony analysis based on 51 informative larval characteristics was conducted with the program NONA. The most parsimonious tree supports a sister-group relationship between the genus *Lancetes* and members of the subfamily Dytiscinae. The only unambiguous synapomorphy in support of this hypothesis is the secondary subdivision of some cephalic appendages. Other putative synapomorphies are the proximal articulation of the primary seta CO7 both on meso- and meta-coxa and the presence of additional primary setae on the ventral margin of the tibiae. Based on several character states including the presence of multifragmented urogomphi, the genus *Lancetes* is monophyletic.

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Résumé—Les stades larvaires des espèces *Lancetes angusticollis* (Curtis), *L. lanceolatus* (Clark), *L. subseriatus* Zimmermann, *L. flavoscutatus* Enderlein, *L. delkeskampi* Ríha, and *L. nigriceps* (Erichson) sont décrits. Une analyse par parcimonie de 51 caractères larvaires significatifs fut effectuée à l'aide du logiciel NONA afin de déterminer la position phylogénétique du genre *Lancetes* Sharp parmi les Dytiscidae. L'arbre les plus parcimonieux suggère que le genre *Lancetes* est le groupe consoeur de la sous-famille Dytiscinae. Cette hypothèse est fortement supportée par la division secondaire de certains articles des appendices céphaliques, caractère présumément synapomorphique, ainsi que par la position proximale de la soie primaire CO7 sur la méso- et la méta-coxa et par la présence de soies primaires additionnelles sur la marge ventrale des tibias. L'origine monophylétique du genre *Lancetes* est

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elle-même supportée par plusieurs caractères parmi lesquels la présence d'un urogomphe plurifragmenté.

Introduction

The genus *Lancetes* Sharp includes medium-sized beetles (7.50–13.00 mm long), and is the only genus of the family Dytiscidae with a predominantly southern-most, transantarctic distribution pattern (Ruhnau and Brancucci 1984). The genus *Lancetes* comprises 22 species worldwide, most of which occur in South America, a few in subantarctic islands (Falkland islands, South Georgia, Tristan da Cunha), and one in south Australia, Tasmania, and New Zealand (Ríha 1961).

Members of the genus *Lancetes* are considered as monophyletic based on the synapomorphy of truncate and sinuate elytral apices (Miller 2001). Whereas the genus *Lancetes* could be taken as a relatively well-supported monophyletic group, available evidence is still equivocal regarding the systematic placement of the genus within the family Dytiscidae. Indeed, Sharp (1882) placed it among his group of "seven unrelated genera" (along with *Aglymbus* Branden, *Lacconectus* Motschulsky, *Agabetes* Crotch, *Matus* Aubé, *Copelatus* Erichson, and *Coptotomus* Say). Traditionally, the genus *Lancetes* has been included within the subfamily Colymbetinae either as a distinct tribe, the Lancetini (Pederzani 1995), or as a member of the tribes Coptotomini (Brinck 1948) and Colymbetini (Guignot 1931, 1933, 1933; Ordish 1966; Franciscolo 1979). Beier (1928), Ruhnau and Brancucci (1984), and Nilsson (1989), however, called in question the usual assignment of the genus *Lancetes* to the Colymbetinae postulating a putative relationship with either the Dytiscinae or the Laccophilinae.

Recently, in what is seen as the first extensive study of the phylogenetic relationships of the family Dytiscidae using a cladistic approach, Miller (2001) postulated a sister-group relationship between the genus *Lancetes* and members of the subfamily Dytiscinae (based on common presence of a ventral sclerite on the male median lobe and fused gonocoxae) and reinstated the subfamily name Lancetinae Van den Branden (1885) [previously suggested by Nilsson and Roughley 1997]. The elevation of the genus *Lancetes* to the subfamily level, and in particular, its placement as sister group to the Dytiscinae merit further investigation. Given the relatively weak Bremer support value (Bremer 1994) obtained by Miller (2001), this placement would benefit from being reanalyzed by incorporating new characters such as those provided by larvae. In a phylogenetic perspective, it is useful to study additional taxa and search for new characters to increase knowledge about the group being studied and to improve hypotheses formulated in different contexts. It is generally held that the more characters which support a clade, the more plausible is the hypothesis that the clade represents a natural group (De Salle and Brower 1997). When a phylogenetic hypothesis is supported by several independant lines of evidence, we gain confidence in it as an estimate of phylogenetic history (it is an analogue to an increase in statistical power) (Lanyon 1993).

Assessment of larval morphology has proven useful in studying phylogenetic relationships among selected groups of the family Dytiscidae (Alarie 1997; Alarie *et al.* 1999, 2000, 2001, 2002). With regard to systematics of the Dytiscidae, the use of the positions and shapes of the setae and pores on larvae has proven useful for reconsidering classifications based mainly on adult characteristics. Recent publications of preliminary larval phylogenetic reconstruction in the dytiscid subfamilies Laccophilinae (Alarie *et al.* 2000, 2002), Colymbetinae (Alarie *et al.* 1998), and Matinae (Alarie *et al.* 2001) provide a basic framework to evaluate the taxonomic status of the genus *Lancetes*. Morphology of the larvae of the genus *Lancetes*, however, is poorly known and of unequal value (Mjöberg 1906; Beier 1928; Brinck 1948; Watts 1963; Gressitt 1970; Cekalovic and Spano 1981; Bachmann and Trémouilles 1981; Crespo 1987), and

published descriptions can hardly be used for phylogenetic comparisons. Moreover, as these descriptions are rather superficial and do not include detailed chaetotaxic analysis, comparison in the context of recent works on larval Dytiscidae is difficult.

This paper is meant to be a step towards a better knowledge of the larval morphology of the genus *Lancetes*. It has the following goals: (*i*) descriptions or redescriptions of the larvae of *L. angusticollis* (Curtis), *L. lanceolatus* (Clark), *L. subseriatus* Zimmermann, *L. flavoscutatus* Enderlein, *L. delkeskampi* Ríha, and *L. nigriceps* (Erichson), with an emphasis on chaetotaxic analysis of the head capsule, cephalic appendages, legs, last badominal segment, and urogomphi; (*ii*) identification of generic-level larval characters for the genus *Lancetes*; and (*iii*) analysis of the phylogenetic position of the genus *Lancetes* within the Dytiscidae based on larval features.

Material and methods

Specimens representative of each of the three instars were disarticulated and mounted on standard glass slides with Hoyer's medium. Voucher specimens are deposited in the research larval collection of Yves Alarie (Laurentian University, Department of Biology, Sudbury, Ontario, Canada) and in the South Australian Museum (*L. lanceolatus*) (North Terrace, Adelaide, SA 5000, Australia, CHS Watts).

Morphometric analysis

All measurements were made with a compound microscope equipped with a micrometer eyepiece. The part to be measured was adjusted so that it was, as nearly as possible, parallel to the plane of the objectives.

The characters and terms used in the morphometric analysis are mainly those used in previous papers dealing with larval morphology of the Colymbetinae (Alarie *et al.* 1998, 2001; Alarie and Larson 1998; Alarie and Balke 1999) and of the Laccophilinae (Alarie *et al.* 2000, 2002), and some are defined as follows: **Head length (HL)** was total head length including the frontoclypeus measured medially along the epicranial stem. **Head width (HW)** was maximum width measured posterior to the stemmata. **Length of frontoclypeus (FCL)** was from apex of the nasal to the back of the ecdysial suture. **Occipital foramen width (OcW)** was maximum width measured along the dorsal margin of the occipital foramen. **Length of antenna** was derived by adding the length of each individual antennomere; comparison among antennomeres was made using the capital letter A with a number corresponding to the segment considered (*e.g.*, A1 for antennomere 1); A3′ is used as an abbreviation for the lateral elongation of antennomere 3. **Length of maxillary palpus** was derived by adding the length of each individual palpomere (*e.g.*, MX1 for palpomere 1). **Length of maxillary galea** was maximal length measured from apex of the galea to margin of the maxillary stipes. **Length of palpifer** was maximal length measured along lateral margin. **Length of labial palpus** was derived by adding the length of each individual palpomere (*e.g.*, LB1 for palpomere 1). **Length of legs** was derived by adding the length of each individual segment including the longest claw; the length of each segment was taken at the longest point except for the trochanter, which includes only the proximal portion (the length of distal portion being included in the femoral length). **Dorsal length of last abdominal segment (LLAS)** included the whole sclerite measured dorsally along mid-line from the anterior margin to the posterior margin.

The individual measurements defined above were used in calculating several ratios aimed at characterizing the body shape. Most of the ratios used in this paper are similar to those mentioned in previous papers dealing with larval morphology of the

Colymbetinae (Alarie and Balke 1999; Alarie and Larson 1998; Alarie *et al.* 1998, 2001, 2002), and as such, are not defined herein.

Chaetotaxic analysis

Primary and secondary setae and pores were distinguished on the head capsule, head appendages, legs, last abdominal segment, and urogomphi. The setae and pores were coded according to Alarie (1995) for the legs, the last abdominal segment, and urogomphi, and Alarie (1998) for the head capsule and head appendages. Setae are coded by two capital letters corresponding to the first two letters of the name of the structure on which the seta is located (AB, last abdominal segment; AN, antenna; CO, coxa; FE, femur; FR, frontoclypeus; MX, maxilla; LA, labium, PA, parietals; TA, tarsus; TI, tibia; TR, trochanter; UR, urogomphus) and a number. Pores are coded in a similar manner except that the number is replaced by a lower case letter. The position of the sensilla is described by adding the following abbreviations: A, anterior; AV, anteroventral; D, dorsal; Di, distal; Pr, proximal; PV, posteroventral.

Instar I larvae of the genus *Lancetes* are characterized by the presence of additional setae on femora and tibiae. As their number and position vary among species, they were included in the count of secondary setae.

Color

Description of color is given for all species from ethanol-preserved specimens.

Parsimony analysis

To examine the phylogenetic signal of the characters observed on the larvae of the species of *Lancetes* studied and test the monophyly of the genus, a phylogenetic analysis was conducted, rooting the cladogram with the Matinae. The Matinae are postulated to represent the sister group of other Dytiscidae (Miller 2001). Initially, all species of *Lancetes* were included in the analysis. The three species not represented by instar I (*L. lanceolatus*, *L. flavoscutatus*, *L. nigriceps*) were removed from the analysis to minimize the number of missing entries in the data matrix and to facilitate faster tree searches. The other species (n = 52) included in the analysis were from the subfamilies Agabinae, Colymbetinae, Copelatinae, Dytiscinae, and Laccophilinae (Appendix A). Many species of Agabinae had the same combination of character states as *Ilybius vittiger* (Gyllenhal), and thus, were deleted from the analysis (*i.e.*, they were condensed to a single terminal to facilitate faster tree searches). Species were used as terminals to avoid any assumption of monophyly of higher taxa. A total of 60 characters were used (Table 1). The distribution of character states is given for all 52 terminal taxa (Table 2).

The parsimony analysis was based on 51 informative characters within the data matrix (Table 2). The single multistate character (*i.e.*, character 16, Table 1) was treated as nonadditive. A search in the program NONA (Goloboff 1995) (commands: hold*; hold/100; mult*100) found one shortest tree of length 107 (Fig. 34). The consistency index (CI) (Kluge and Farris 1969) and retention index (RI) (Farris 1989) were calculated. The tree was produced in WINCLADA using the unambiguous optimization (*i.e.*, only the unambiguous characters were mapped). MacClade 4.0 (Maddison and Maddison 2000) was used to examine the distributions of characters on the phylogeny.

Description of larvae of the genus *Lancetes* Sharp

(Figs. 1–33)

Diagnostic combination

Head capsule (Figs. 1–4, 22–23) subovate to subquadrate; occipital suture lacking; egg bursters (Figs. 1, 3–4) located to posterior half of frontoclypeus, contiguous to primary pore FRb (instar I); apical margin of frontoclypeus with two lamellae clypeales (instar I) (Figs. 1, 3–4); spinulose epipharyngeal band present; mandibular channel present; lateral elongation of antennomere 3 short, A3′/A4 < 0.15; antennomeres 2, 3, and 4, maxillary palpomeres 2 and 3, and labial palpomere 2 fractured proximally (instar III); natatory setae present on dorsal margin of tibiae and tarsi (instars II and III) (Figs. 29, 31); LAS truncate posteriorly, siphon weakly delineated (Fig. 33); urogomphus elongate, >3 times LLAS, with secondary setae, and with a variable number of divisions (Figs. 20, 21, 33).

Description

Instar I (Figs. 1–21)

HEAD (Figs. 1–12). HL = 0.88–0.95 mm; HW = 0.77–0.93 mm; FCL = 0.40–0.48 mm. **Head capsule** (Figs. 1–4): rounded to obovate, as long or longer than broad (HL/HW = 1.04–1.22), constricted or not at level of occipital region, HW/OcW = 1.81–2.05; ecdysial suture well developed, coronal suture about 0.50 times as long as HL; occipital suture lacking; frontoclypeus strongly convex mesally, 0.44–0.50 times as long as HL, extending mesally to about level of lateral lobes [= adnasalia]; dorsal surface of frontoclypeus with two egg bursters (ruptor ovi of Bertrand 1972) located in posterior half, contiguous to primary pore FRb; apical margin of frontoclypeus with two spatulate setae (lamellae clypeales of Bertrand 1972); spinulose epipharyngeal band ["area o banda spinulosa del palato" of DeMarzo (1979)] present; gular suture not visible; ocularium present, stemmata visible ventrally and subdivided into two vertical series; tentorial pits visible ventrally on each side of middle at about mid-length; occipital foramen indented ventrally. **Antenna** (Figs. 5–6): four-segmented, subequal or longer than HW (length of antenna/HW = 1.04–1.20); A1 = A2 = A3 = A4, A2/A3 = 0.91–1.00; lateral elongation of antennomere 3 short, A3′/A4 = 0.07–0.13; antennomere 3 with a ventroapical spinula. **Mandible** (Fig. 7): falciform, innner margin minutely toothed ventrally, 2.20–2.30 times as long as broad, about 0.50 times as long as HL; mandibular channel present, pubescence present on ventral margin. **Maxilla** (Figs. 8–9): stipes trapezoidal; cardo and galea present, lacinia lacking; galea short, 0.25–0.36 times as long as length of palpomere 1; palpifer similar to a palpomere, 0.13–0.30 times as long as palpomere 1; palpus three-segmented, shorter than antenna (length of antenna/length of maxillary palpus = 1.71–1.80); palpomere 1 = 2 < 3; length of palpomere 3/length of palpomere 2 = 1.37–1.52. **Labium** (Figs. 10–11): prementum subrectangular, broader than long; palpus two-segmented, subequal in length to maxillary palpus (length of maxillary palpus/length of labial palpus = 0.97–1.09), palpomere 2 is 0.97–1.45 as long as palpomere 1. **Chaetotaxy and porotaxy:** all primary setae and pores of generalized Colymbetinae larva present. Antennomere 3 with ventroapical spinulae and two additional pores (Figs. 5–6); prementum with two additional setae and one additional pore dorsally (Fig. 10). **THORAX.** Pronotum elliptical dorsally; length of pronotum about twice that of mesonotum; metanotum subequal to mesonotum in length, both slightly wider than pronotum; terga lacking transverse carina; maximum body width at level of prothorax; thoracic venter membranous; spiracular openings absent. **LEGS** (Figs. 13–16). Five-segmented; metathoracic legs longest, about 1.30–1.50 times as long as length

TABLE 1. Characters used for the phylogenetic analysis and the coding of states using the tribe Matini as outgroup; 0 indicates plesiomorphic state and number >0 indicates progressively more apomorphic states.

Code	Character	States
01	Egg bursters (instar I)	(0) at about level of pore FRb; (1) posterior to pore FRb, contiguous to coronal suture
02	Egg bursters (instar I)	(0) spine-like; (1) blade-like
03	Frontoclypeus (instar I)	(0) rounded posteriorly; (1) truncate posteriorly
04	Frontal suture (instar I)	(0) concave, not/more or less sinuate; (1) deeply sinuate
05	Lamellae clypeales (instar I)	(0) >4; (1) 2
06	Frontoclypeus	(0) adnasalia delineated; (1) adnasalia not delineated
07	Pore FRe	(0) lacking; (1) present
08	Labial palpomere 2 (instar III)	(0) <1.70 times length of palpomere 1; (1) >2.20 times length of palpomere 1
09	Spinulose epipharyngeal band	(0) lacking; (1) present
10	Setae LA10 and LA12	(0) present; (1) lacking
11	Pore ANf	(0) present; (1) lacking
12	Head appendages (excluding mandible) (instars II and III)	(0) with several secondary setae; (1) lacking or with a few secondary setae
13	Seta MX5	(0) present; (1) lacking
14	Prementum	(0) additional pore lacking; (1) additional pore present
15	Occipital suture	(0) present; (1) lacking
16	Antennomere III, ventroapical spinula	(0) spine-like; (1) hole-like; (2) lacking
17	Antennomere III, additional ventroapical pores (instar I)	(0) present; (1) absent
18	Antennomere IV	(0) pore ANg inserted basally; (1) pore ANg inserted medially
19	Antennomere III, lateral projection (A3′)	(0) short, <0.20 times length of A4; (1) elongate, equals 0.30 times length of A4
20	Mandible, additional setae (instar I)	(0) absent; (1) present
21	Maxilla, galea	(0) longer than palpifer; (1) shorter or subequal to palpifer
22	Maxillary stipes, additional setae (instar I)	(0) absent; (1) present
23	Mandible	(0) with a mandibular channel; (1) lacking a mandibular channel
24	Legs, natatory setae (instars II and III)	(0) present; (1) lacking
25	Seta CO7, meso- and meta-coxa	(0) articulated distally; (1) articulated proximally
26	Coxa, pectens	(0) lacking; (1) present
27	Trochantera, (instars II and III)	(0) with a few (<10) secondary setae; (1) with several (>20) secondary setae
28	Femur, pectens	(0) lacking; (1) present
29	Seta FE5, metafemur (instar I)	(0) elongate, hair-like; (1) short, spine-like
30	Seta FE5, mesofemur (instar I)	(0) short, spine-like; (1) elongate, hair-like
31	Seta FE6, metafemur (instar I)	(0) elongate; (1) short
32	Seta FE1	(0) proximal; (1) distal
33	Femur, dorsal margin (instar I)	(0) lacking additional setae; (1) with additional setae
34	Tibia, ventral additional setae (instar I)	(0) absent; (1) present

TABLE 1 (*concluded*).

Code	Character	States
35	Seta TI2, pro- and meso-femur	(0) present; (1) absent
36	Seta TI6, metatibia	(0) elongate, hair-like; (1) short, spine-like
37	Seta TI7	(0) short; (1) elongate
38	Protibia	(0) seta TI6 present; (1) seta T16 absent
39	Tibia (instar I)	(0) lacking additional natatory setae; (1) with additional natatory setae
40	Pretarsal claws	(0) marginal spinulae absent; (1) marginal spinulae present
41	Pro- and meso-tibiae	(0) normal shape; (1) chelate
42	Pronotum	(0) lacking a neck constriction; (1) with a neck constriction
43	Abdominal venter 6	(0) membranous; (1) sclerotized
44	Siphon	(0) lacking a cresent shape setal pattern; (1) with a crescent shape setal pattern
45	Abdominal segment 8 (instar I)	(0) additional setae present; (1) additional setae absent
46	Setae AB8 and AB14	(0) spine-like; (1) lanceolate
47	Urogomphus	(0) one-segmented; (1) two-segmented
48	Urogomphus	(0) elongate >0.70 HW; (1) short, <0.60 HW
49	Urogomphus, additional setae (instar I)	(0) absent; (1) present
50	Urogomphomere 1 (instars II and III)	(0) with secondary setae; (1) lacking secondary setae
51	Urogomphomere 1 (instars II and III)	(0) lacking a subbasal suture; (1) with a subbasal suture
52	Temporal secondary spines	(0) present; (1) absent
53	Antennomere 1 (instar III)	(0) longer than broad; (1) shorter than broad
54	Abdominal venter 4–5	(0) membranous; (1) sclerotized
55	Head appendages (excluding mandible) (instar III)	(0) articles not fractured proximally; (1) some articles fractured proximally
56	Urogomphus (instar I)	(0) not fractured; (1) fractured
57	Ligula	(0) absent; (1) present
58	Legs	(0) lacking ventral natatory setae; (1) with verntral natatory setae
59	Abdominal segment 8 (instar I)	(0) lacking additional natatory setae along lateral margin; (1) with additional natatory setae along lateral margin
60	Abdominal segments 7 and 8 (instars II and III)	(0) lacking natatory setae along lateral margin; (1) with natatory setae along lateral margin

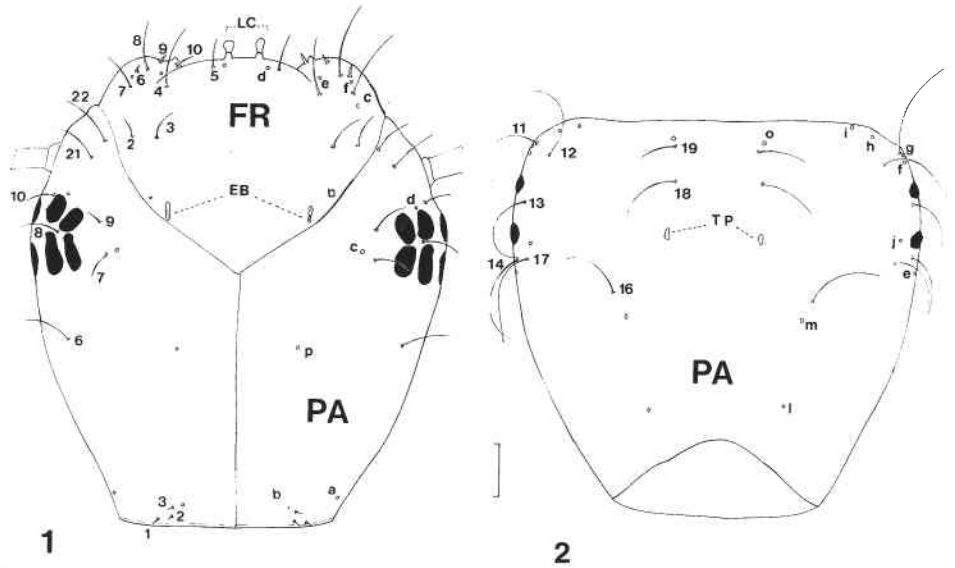
of prothoracic legs, and 3.40–4.10 times HW; meta-[femur > coxa = tarsus > tibia > trochanter]; tarsus with two claws, posterior claw slightly shorter than anterior claw; anterior metathoracic claw 0.53–0.65 times as long as metatarsus; spinulae strongly developed on ventral margin of tibia and tarsus, weakly developed or absent on ventral margin of femur. **Chaetotaxy and porotaxy:** all primary setae and pores of generalized Colymbetinae larva present; seta CO7 inserted proximally on all legs; primary seta FE1 inserted distally; seta TI7 elongate; additional setae are observed on femora and tibiae (Table 3). **ABDOMEN** (Figs. 17–19). LLAS = 0.30–0.44 mm. Eight-segmented, dorsally sclerotized; segments 1–6 membranous ventrally, segment 7 with a ventral plate distinct from tergite, segment 8 completely sclerotized; all terga lacking anterodorsal

TABLE 2. Matrix of 60 morphological characters of larvae of 52 species of the family Dytiscidae.

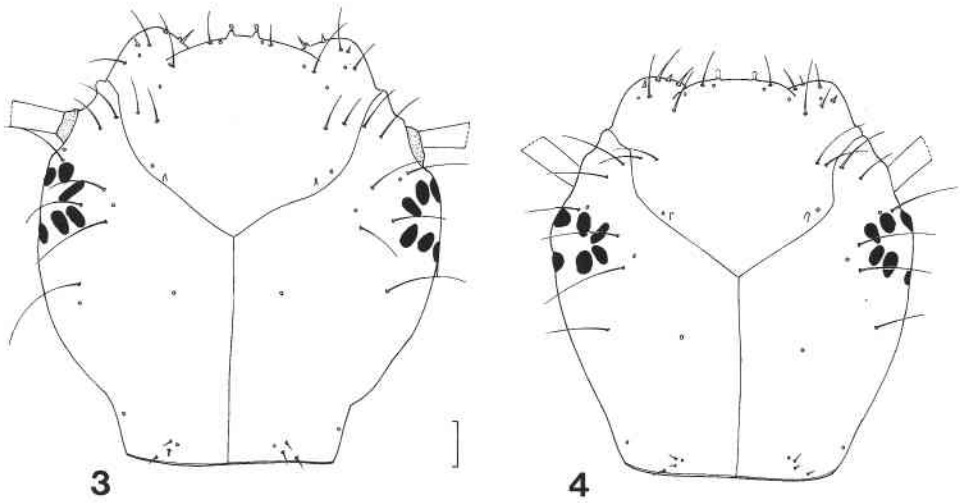
Taxon	Characters											
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60
Allomatus nannup	00000	00000	00000	10000	00000	01000	00110	00110	00000	00010	00000	00000
Batrachomatus daemeli	00000	00000	00000	10100	00000	01000	00000	00110	00000	00010	00000	00000
Matus bicarinatus	00000	10000	00000	10010	00000	00000	00001	00000	10000	00000	00000	00000
Copelatus sp.	0000?	01000	01010	01010	01110	00010	10000	10000	00001	01101	00000	00000
Ilybiosoma bjorkmanae	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Ilybiosoma roguus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Ilybiosoma seriatus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Hydrotrupes palpalis	00000	00010	01001	01000	11110	00010	11000	10000	00001	11001	00000	00000
Agabus anthracinus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus arcticus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus bifarius	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus confinis	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus discolor	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus elongatus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus falli	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus phaeopterus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus semipunctatus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus strigulosus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Agabus subfuscatus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Ilybius wasastjernae	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Ilybius angustior	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Ilybius biguttulus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Ilybius picipes	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Ilybius subaeneus	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Ilybius vittiger	00000	00000	01001	01000	11010	00010	11000	10000	00001	01001	00000	00000
Platambus glabrellus	00000	00000	01001	01000	10010	00010	11000	10000	00001	00001	00000	00000
Rhantus (R.) binotatus	00000	01000	01000	00100	00000	00001	00010	01001	00001	00000	00000	00000

Rhantus (R.) consimilis	00000	01000	01000	00100	00000	00001	00010	01001	00001	00000	00000	00000
Rhantus (R.) suturellus	00000	01000	01000	00100	00000	00001	00010	01001	00001	00000	00000	00000
Rhantus (R.) wallisi	00000	01000	01000	00100	00000	00001	00010	01001	00001	00000	00000	00000
Rhantus (N.) grapii	00000	01000	01000	20100	00000	00001	00110	01001	00001	00000	00000	00000
Colymbetes dolabratus	00000	01000	01000	00100	00000	00010	00000	01001	00001	00000	00000	00000
Colymbetes paykulli	00000	01000	01000	00100	00000	00010	00000	01001	00001	00000	00000	00000
Colymbetes sculptilis	00000	01000	01000	00100	00000	00010	00000	01001	00001	00000	00000	00000
Neoscutopterus hornii	00000	01000	01000	20101	00000	00000	00110	01001	00000	00010	00000	00000
Agabetes acuductus	11001	00111	01011	21010	10010	00110	10000	10000	00101	00101	00000	00000
Neptosternus meridianus	10011	00001	11111	21010	10001	00001	10000	00000	01101	01000	00000	00000
Neptosternus hydaticoides	?????	0?001	11111	21010	10001	000??	?0??0	??0?0	0110?	010?0	00000	00000
Africophilus montalentii	?????	0?011	01001	21010	1?010	00010	10000	10000	0010?	01101	01110	00000
Australphilus montanus	?????	0?001	01101	21010	10001	000??	?0??0	??0?0	0110?	010?0	00000	00000
Australphilus saltus	?????	0?001	01101	21010	10001	000??	?0??0	??0?0	0110?	010?0	00000	00000
Laccophilus maculosus	10101	00011	01001	21010	10001	10100	10000	00000	00111	01000	10000	00000
Laccophilus minutus	10101	00011	01001	21010	10001	10100	10000	00000	00111	01000	10000	00000
Laccophilus hyalinus	10101	00011	01001	21010	10001	10100	10000	00000	00111	01000	10000	00000
Lancetes angusticollis	00001	01010	01011	00000	10001	00010	01010	11000	00001	00000	00001	10000
Lancetes delkeskampi	00001	01010	01011	00000	10001	00010	01110	11000	00001	00010	00001	10000
Lancetes subseriatus	01001	01010	01011	00000	10001	00010	01010	11000	00001	00100	00001	10000
Acilius semisulcatus	00000	0?010	010?0	01000	01001	000??	10010	?0?10	00000	00001	00001	01111
Graphoderus liberus	00000	0?010	010?0	01000	01001	000??	10010	?0?10	00000	00001	00001	01111
Thermonectus marmoratus	00000	0?010	010?0	01000	01001	000??	10010	?0?10	00000	00001	00001	01111
Hydaticus aruspex	00000	0?000	010?0	00010	11001	010??	00110	?1?10	00000	00001	00001	00111
Dytiscus cordieri	00000	0?000	010?0	00000	11001	010??	10110	?0?10	00000	00010	01001	00111

NOTE: The 60 columns correspond to the character number (Table 3); state 0, plesiomorphic state; ?, missing data.

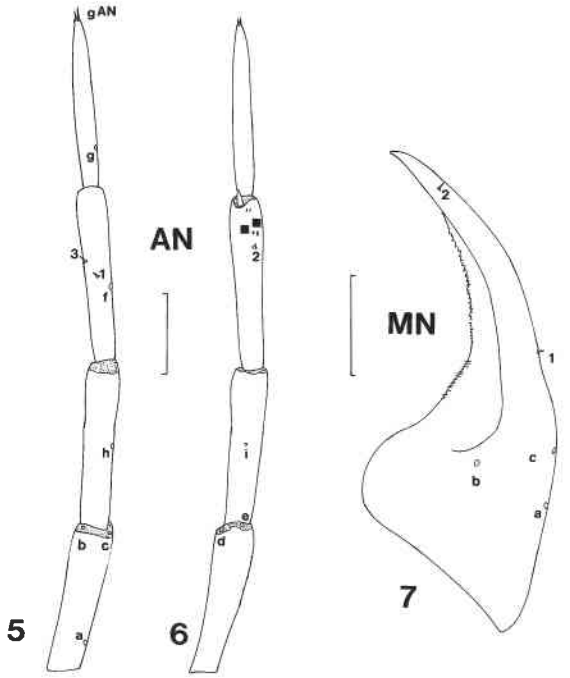


FIGURES 1–2. *Lancetes subseriatus*, cephalic capsule, instar I: (1) dorsal aspect and (2) ventral aspect. EB, egg bursters; LC, lamellae clypeales; FR, frontoclypeus; PA, parietale; TP, tentorial pits. Numbers and lowercased letters refer to primary setae and pores, respectively (color pattern not represented). Scale bar = 0.10 mm.

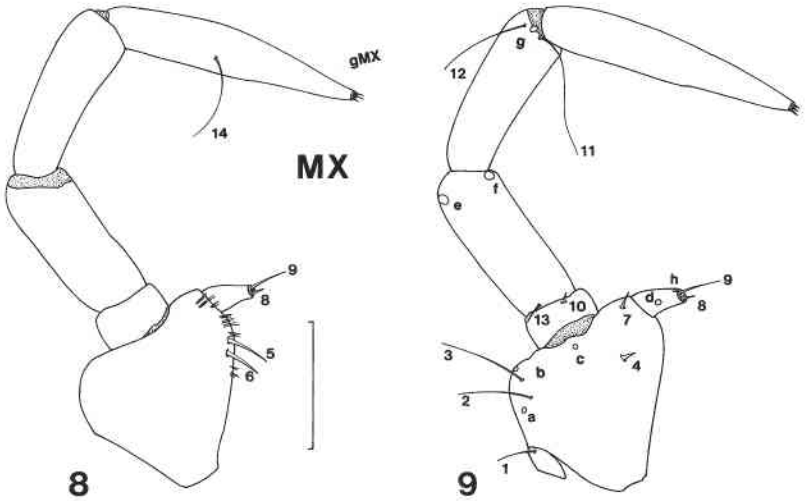


FIGURES 3–4. Dorsal surface of cephalic capsule of selected species of the genus *Lancetes*, instar I: (3) *L. delkeskampi* and (4) *L. angusticollis* (color pattern not represented). Scale bar = 0.10 mm.

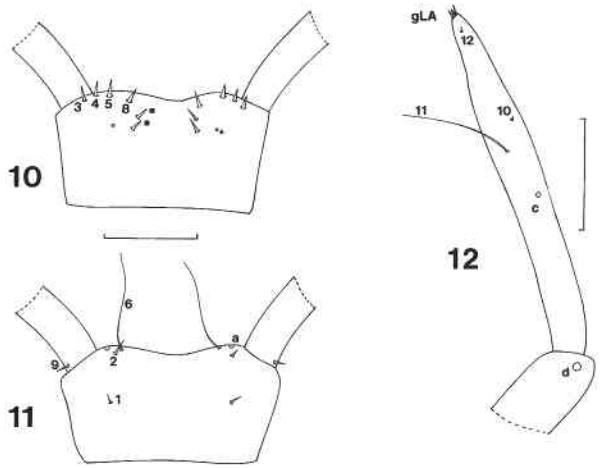
transverse carina; spiracular openings absent; segment 8 subquadrate to subrectangular, shorter than HW, LLAS/HW = 0.36–0.52. **Siphon:** reduced in size. **Chaetotaxy and porotaxy:** all primary setae and pores of generalized Colymbetinae larva present. **UROGOMPHUS** (Figs. 20–21). Total length of urogomphus = 2.38–3.05 mm; one segmented, with three to four divisions, 5.40–10.03 times as long as LLAS, 2.80–3.87 times as long as HW. **Chaetotaxy and porotaxy:** all primary setae and pores of



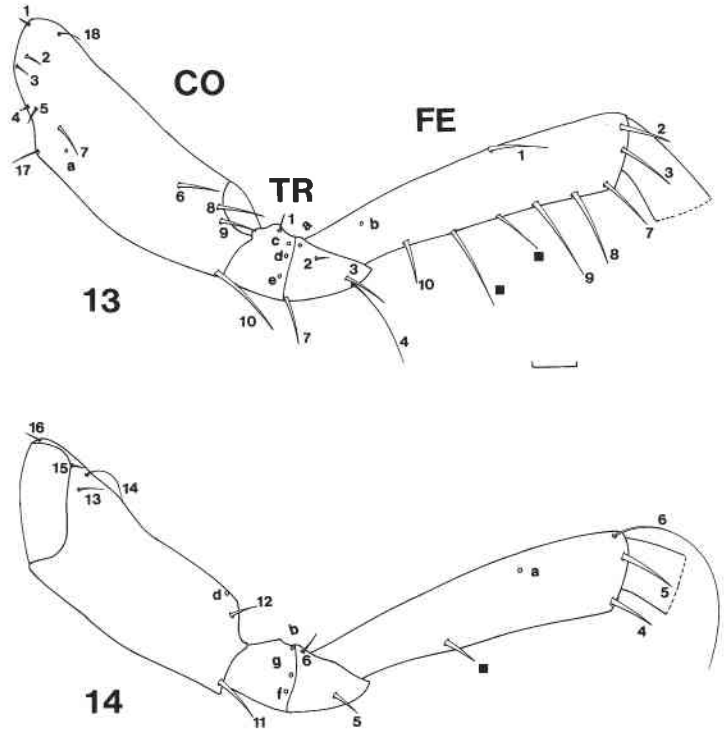
FIGURES 5–7. Cephalic appendages of selected species of the genus *Lancetes*, instar I. (5–6) Antenna of *L. subseriatus*: (5) dorsal aspect and (6) ventral aspect. (7) Mandible of *L. delkeskampi*, dorsal aspect. AN, antenna; gAn, antennal group; MN, mandible; Sp, spinula. Numbers and lowercased letters refer to primary setae and pores, respectively, and solid squares are additional setae. Scale bars = 0.10 mm.



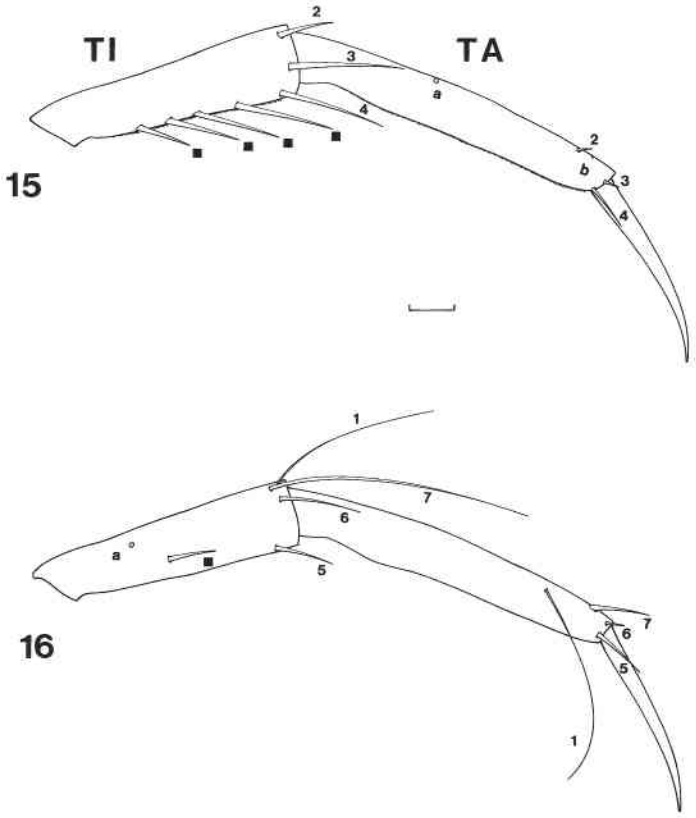
FIGURES 8–9. Maxilla of *Lancetes subseriatus*, instar I: (8) dorsal aspect and (9) ventral aspect. MX, maxilla; gMX, maxilla group. Numbers and lowercased letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.



FIGURES 10–12. Labium of *Lancetes delkeskampi*, instar I: (10) prementum, dorsal aspect; (11) prementum, ventral aspect; and (12) palpomere II, ventral surface. LA, labium; gLA, labial group. Numbers and lowercased letters refer to primary setae and pores, respectively, and solid squares are additional setae and solid triangle is additional pore. Scale bars = 0.10 mm.



FIGURES 13–14. *Lancetes angusticollis*, metathoracic leg (metacoxa, metatrochanter, metafemur), instar I: (13) anterior surface and (14) posterior surface. CO, coxa; FE, femur; TR, trochanter. Numbers and lowercased letters refer to primary setae and pores, respectively, and solid squares are additional setae. Scale bar = 0.10 mm.

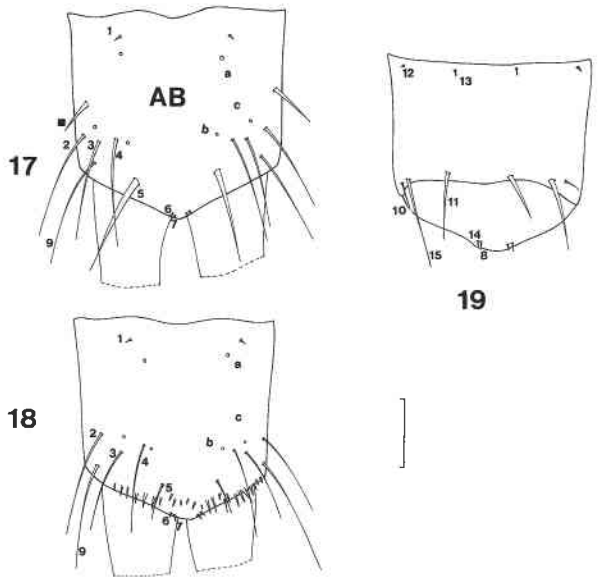


FIGURES 15–16. ***Lancetes angusticollis*****, metatibia and metatarsus, instar I: (15) anterior surface and (16) posterior surface. TI, tibia, TA, tarsus. Numbers and lowercased letters refer to primary setae and pores, respectively, and solid squares are additional setae. Pretarsus not represented. Scale bar = 0.10 mm.**

generalized Colymbetinae larva present; additional setae present or absent; seta UR8 inserted either apically (Fig. 20) or subapically (Fig. 21).

Instar II

As instar I except as follows. **HEAD.** HL = 1.43–1.73 mm; HW = 1.23–1.61 mm; FCL = 0.59–0.77 mm. **Head capsule:** subquadrate, lateral margin constricted posteriorly at level of occipital region, HL/HW = 1.04–1.24, HW/OcW = 1.69–2.12; frontoclypeus 0.40–0.45 times as long as HL; dorsal surface of frontoclypeus lacking egg bursters; apical margin of frontoclypeus with 20–30 spatulate setae; parietals with 9–11 lateral temporal spines. **Antenna:** length of antenna/HW = 0.87–1.20; A1 = A2 = A3 > A4; A2/A3 = 0.91–1.14; A3′/A4 = 0.08–0.11. **Mandible:** 2.20–2.50 times as long as broad. **Maxilla:** galea 0.21–0.34 as long as palpomere 1; palpifer 0.21–0.28 times as long as palpomere 1; palpomere 3 > 2 = 1; length of antenna/length of maxillary palpus = 1.66–1.98; length of palpomere 3/length of palpomere 2 = 1.06–1.28. **Labium:** length of maxillary palpus/length of labial palpus = 0.90–1.00; palpomere 2 is 0.76–1.00 as long as palpomere 1. **Chaetotaxy and porotaxy:** head capsule with several secondary setae; head appendages lacking secondary setae except for several minute setae on

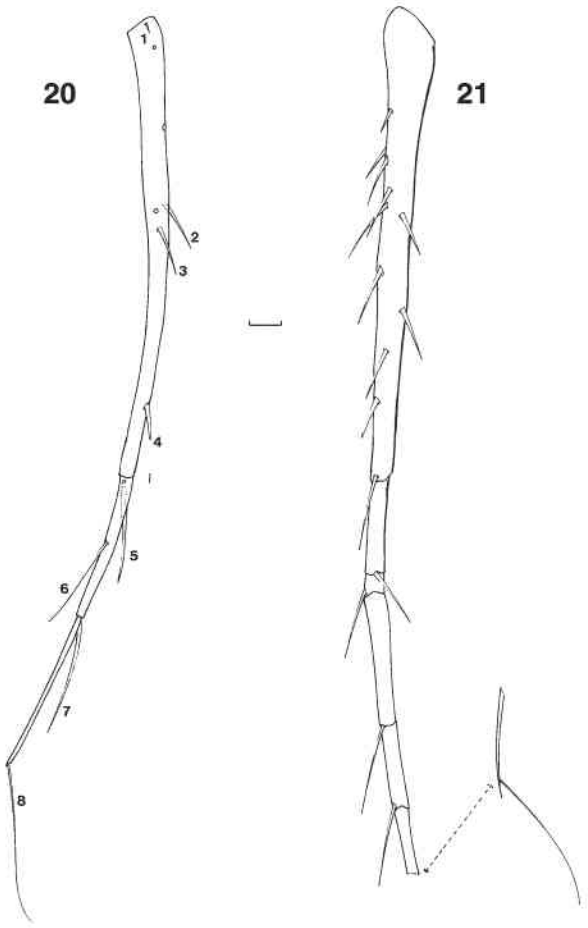


FIGURES 17–19. Abdominal segment 8 of selected species of the genus *Lancetes*, instar I: (17) *L. delkeskampi*, dorsal surface; (18–19) *L. subseriatus*, (18) dorsal aspect and (19) ventral aspect. AB, abdominal segment 8. Numbers and lowercased letters refer to primary setae and pores, respectively, and solid square is additional seta. Scale bar = 0.10 mm.

mandible. **THORAX.** Pronotum elliptical to subtrapezoidal dorsally; secondary setation on each tergum. **LEGS.** Metathoracic legs 1.30–1.50 times length of prothoracic legs, and 3.20–3.90 times HW; anterior metathoracic claw 0.47–0.58 times as long as metatarsus; spine-like spinulae strongly developed on ventral margin of tibia and tarsus, more weakly developed on femur. **Chaetotaxy and porotaxy:** position and number of secondary setae (Table 4); natatory setae present on dorsal margin of tibia and tarsus. **ABDOMEN.** LLAS = 0.59–1.05 mm. Terga 1–7 with an anterodorsal transverse carina; segment 7 fully sclerotized; LLAS/HW = 0.41–0.66. **Chaetotaxy and porotaxy:** secondary tergal setation present. **UROGOMPHUS.** Total length of urogomphus = 3.90–5.33, 3.90–7.80 times as long as LLAS, 2.50–4.00 times as long as HW. **Chaetotaxy and porotaxy:** urogomphus with several secondary setae.

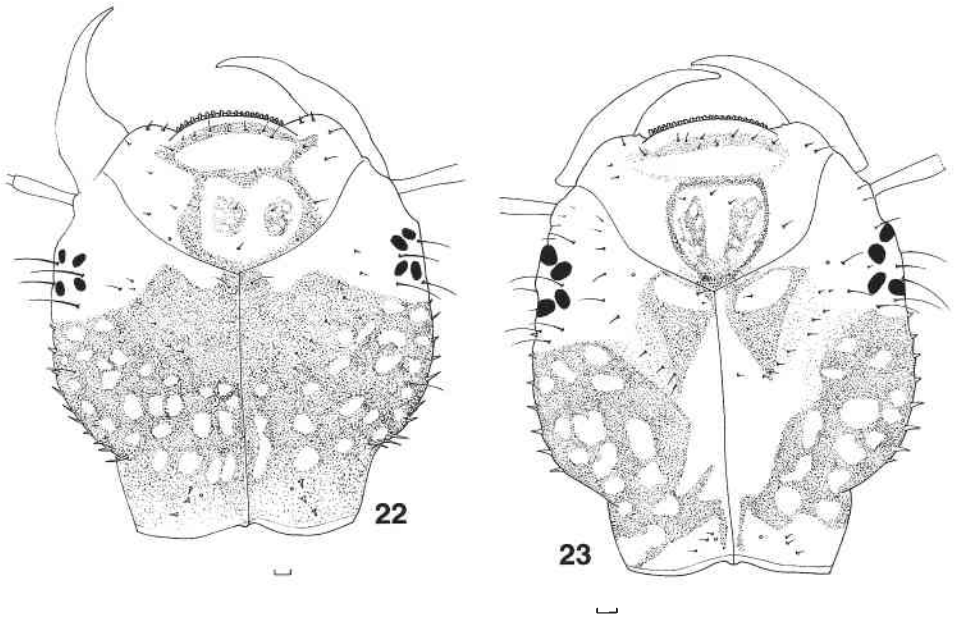
Instar III (Figs. 22–33)

As instar II except as follows. **HEAD** (Figs. 22–23). HL = 2.13–2.85 mm; HW = 1.85–2.75 mm; FCL = 0.83–1.38 mm. **Head capsule:** HL/HW = 1.04–1.19, subquadrate, lateral margin constricted at level of occipital region, HW/OcW = 1.50–2.00; frontoclypeus 0.40–0.50 times as long as HL, with ~40–50 finger-like to spatulate lamellae clypeales; parietals with 8–12 lateral temporal spines. **Antenna:** length of antenna/HW = 0.68–0.92; A1 = A2 = A3 > A4; A2/A3 = 1.05–1.21; A3′/A4 = 0.06–0.10; A2, A3 and A4 fractured proximally. **Mandible:** 2.50–2.90 times as long as broad. **Maxilla:** galea 0.26–0.31 times as long as palpomere 1; palpifer 0.25–0.36 as long as palpomere 1; palpomere 1 = 2 = 3; length of antenna/length of maxillary palpus = 1.49–1.91; length of palpomere 3/length of palpomere 2 = 0.89–1.14; MX2 and MX3 fractured proximally. **Labium:** length of maxillary palpus/length of labial palpus = 0.90–1.05; palpomere 2 is 0.70–1.00 as long as palpomere 1; LB2 fractured proximally.



FIGURES 20–21. Dorsal aspect of urogomphus of selected species of the genus *Lancetes*, instar I: (20) *L. angusticollis* and (21) *L. delkeskampi*. UR, urogomphus. Scale bar = 0.10 mm.

Chaetotaxy and porotaxy: mandible with several minute secondary setae. **THORAX.** Mesopleural region with spiracular opening on each side. **LEGS** (Figs. 24–31). Metathoracic legs 1.36–1.50 times as long as prothoracic legs, and 3.10–3.85 times HW; meta-[femur > coxa = tarsus = tibia > trochanter]; anterior metathoracic claw 0.40–0.53 times as long as metatarsus; spine-like spinulae strongly developed on ventral margin of tibia and tarsus. **Chaetotaxy and porotaxy:** position and number of secondary setae (Table 4); natatory setae present on dorsal margin of tibia and tarsus (Figs. 29, 31). **ABDOMEN** (Fig. 33). LLAS = 1.02–2.08 mm. Terga 1–7 with an anterodorsal transverse carina; segment 8 with an anterotransverse carina present or absent, LLAS/HW = 0.50–0.80; segments 1–7 each with pair of spiracular openings. **Chaetotaxy and porotaxy:** secondary tergal setation present. **UROGOMPHUS** (Fig. 33). Total length of urogomphus = 5.70–8.85 mm, 3.20–5.80 times as long as LLAS, 2.32–4.35 times as long as HW. **Chaetotaxy and porotaxy:** urogomphus with several secondary setae.



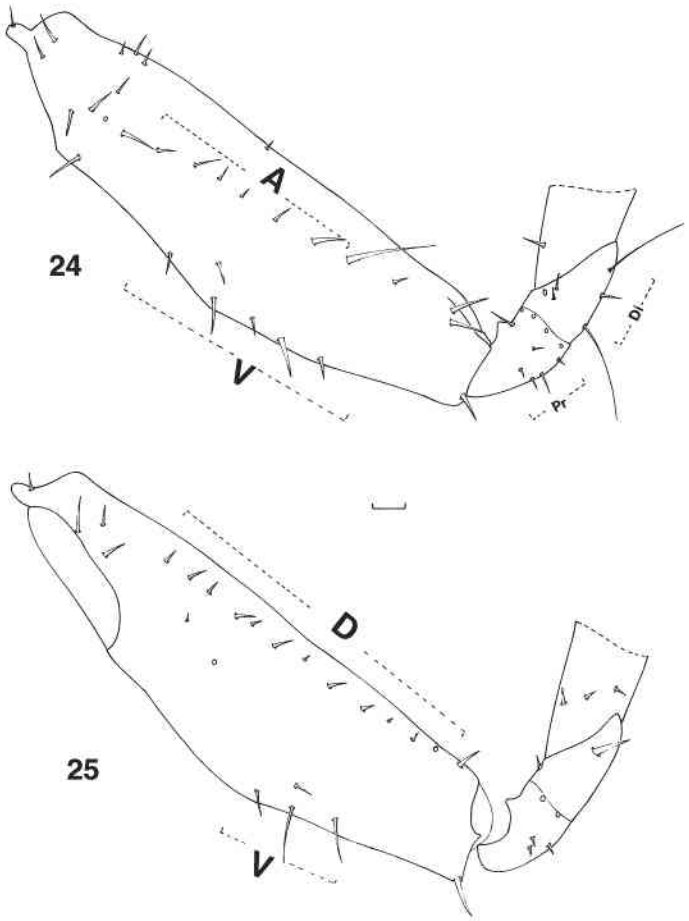
FIGURES 22–23. Dorsal aspect of cephalic capsule of selected species of the genus *Lancetes*, instar III: (22) *L. delkeskampi* and (23) *L. subseriatus*. Scale bars = 0.10 mm.

Distribution

Species of the genus *Lancetes* are distributed in Australia, New Zealand, southern South America, Antarctic, and Subantarctic Islands.

Key to instar III of species of the genus *Lancetes* of the world

1. Profemur with a submarginal PV keel covered with elongate spinulae (Fig. 32); coxae with >12 secondary V setae; femora with >15 D secondary setae . . . . . *L. flavoscutatus*
– Profemur lacking a keel covered with elongate spinulae; coxae with <1 secondary V setae; femora with <11 D secondary setae 2
2. Antenna elongate, length of antenna/HW > 0.90; profemur with >29 V setae . . . . . *L. lanceolatus*
– Antenna shorter, length of antenna/HW < 0.80; profemur with <26 V setae 3
3. Tarsi and protibia lacking secondary spiniform setae (Figs. 30–31); metathoracic leg shorter, about 3.10 times HW 4
– Tarsi and protibia with secondary spiniform setae (Figs. 28–29); metathoracic legs longer, >3.50 times HW 5
4. Meso- and meta-femora with >25 V setae; metacoxa with <8 dorsal setae, larger species, HL >2.50 mm . . . . . *L. delkeskampi*
– Meso- and meta-femora with <22 V setae; metacoxa with >11 D setae, smaller species, HL <2.50 mm . . . . . *L. nigriceps*
5. Coxae with <9 D secondary setae; metatarsus with >9 V secondary setae; mesofemur with <17 secondary setae . . . . . *L. angusticollis*
– Coxae with >11 D secondary setae; metatarsus with <4 V secondary setae; mesofemur with >28 secondary setae . . . . . *L. subseriatus*



FIGURES 24–25. Procoxa and protrochanter of *Lancetes flavoscutatus*, instar III: (24) anterior surface and (25) posterior surface. A, anterior; D, dorsal; Di, distal; Pr, proximal; V, ventral. Scale bar = 0.10 mm.

Larvae of *Lancetes delkeskampi* Ríha

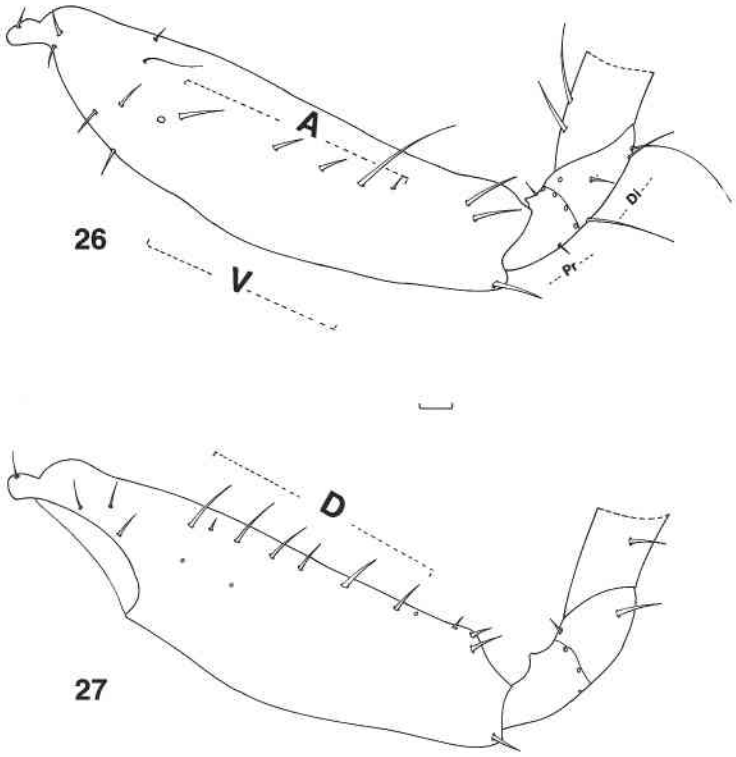
(Figs. 3, 7, 10–12, 17, 21, 22, 26, 27, 30, 31)

Source of material

The larvae studied (three instar I, four instar II, and four instar III) were collected in association with adults at the following locality: **Argentina**, R del Peñón, Camino a Laguna Brava, 2925 m, algae and rocks, 5.iv.1998.

Diagnostic combination (instar III)

Profemur lacking a submarginal PV keel with elongate spinulae; metathoracic leg about 3.10 times HW; coxae with <26 secondary setae; trochanter with <8 secondary setae; protibia and tarsi lacking secondary spiniform setae; protarsus with secondary ventral setae; larger species, HL >2.50 mm.



FIGURES 26–27. Procoxa and protrochanter of *Lancetes delkeskampi*, instar III: (26) anterior surface and (27) posterior surface. A, anterior; D, dorsal; Di, distal; Pr, proximal; V, ventral. Scale bar = 0.10 mm.

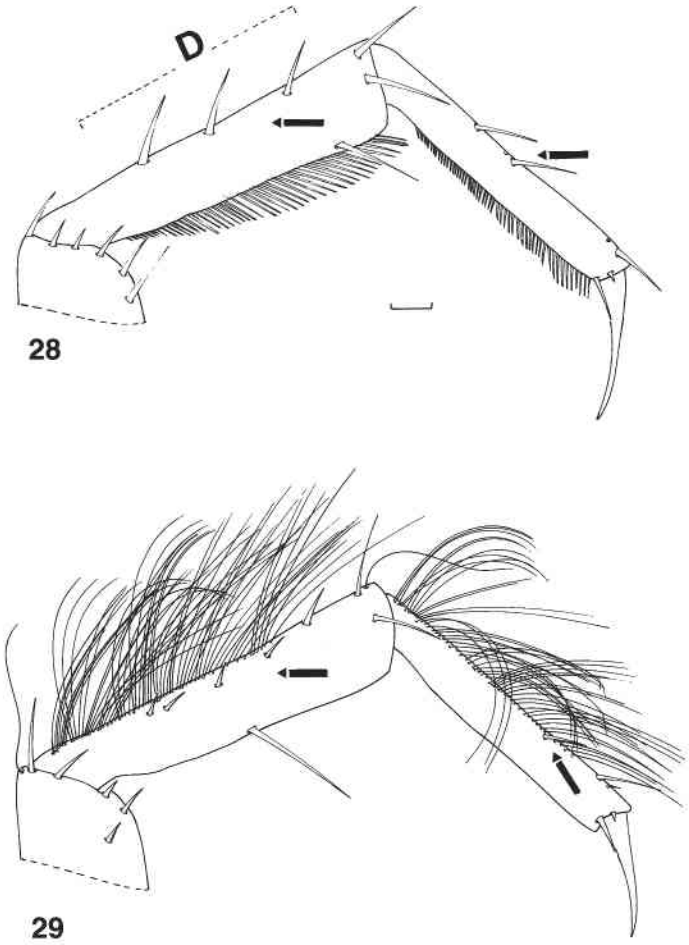
Description

Instar I (Figs. 3, 7, 10–12, 17, 21)

COLOR. Head capsule: predominantly brownish posteriorly, yellowish anteriorly; **head appendages:** predominantly yellow, most articles infuscate proximally and distally; **thoracic and abdominal terga:** predominantly brown; **legs:** yellow to pale brown; **urogomphus:** yellow, infuscate apically. **HEAD. Head capsule** (Fig. 3): HL = 0.93–0.98 mm (mean = 0.97 mm, n = 3); HW = 0.90–0.93 mm (mean = 0.91 mm, n = 3); FCL = 0.47–0.48 mm (mean = 0.47 mm, n = 3); HL/HW = 1.04–1.08. **Antenna:** length of antenna/HW = 1.17–1.20. **Maxilla:** length of antenna/length of maxillary palpus = 1.72–1.73. **Labium** (Fig. 10–12): palpomere 2 is 0.95–0.99 as long as palpomere 1. **LEGS.** Metathoracic leg about 3.50 times as long as HW; position and number of additional setae (Table 3). **ABDOMEN** (Fig. 17). LLAS = 0.32–0.33 mm (mean = 0.33 mm, n = 3); LLAS/HW = 0.35–0.36. **UROGOMPHUS** (Fig. 21). Total length of urogomphus = 2.94–3.05 mm (mean = 2.99 mm, n = 3), 9.14–9.25 times as long as LLAS, 3.25–3.33 times as long as HW.

Instar II

COLOR. As instar I except dorsal surface of head capsule yellowish with a reticulate brown pattern. **HEAD. Head capsule:** HL = 1.57–1.73 mm (mean = 1.62 mm,

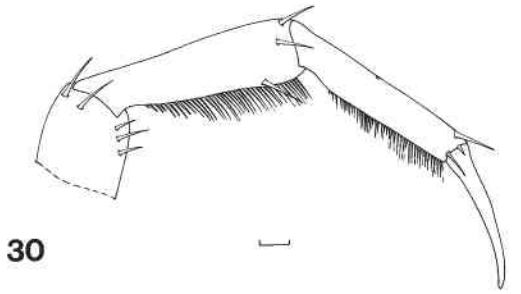


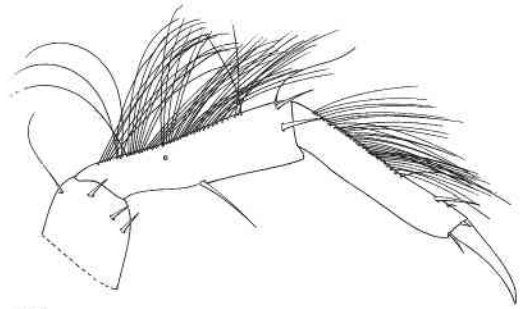
FIGURES 28–29. Protibia and protarsus of *Lancetes flavoscutatus*, instar III: (28) anterior surface and (29) posterior surface. D, dorsal; arrows, secondary spiniform setae. Scale bar = 0.10 mm.

n = 4); HW = 1.45–1.57 mm (mean = 1.50 mm, n = 4); FCL = 0.69–0.71 mm (mean = 0.70 mm, n = 4); HL/HW = 1.09–1.09. **Antenna:** length of antenna/HW = 0.87–0.89. **Maxilla:** length of antenna/length of maxillary palpus = 1.66–1.69. **Labium:** palpomere 2 is 0.76–0.82 as long as palpomere 1. **LEGS.** Metathoracic leg about 3.20 times HW; position and number of secondary setae (Table 4). **ABDOMEN.** LLAS = 0.59–0.74 mm (mean = 0.66 mm, n = 4); LLAS/HW = 0.41–0.47. **UROGOMPHUS.** Total length of urogomphus = 4.60–5.33 mm (mean = 4.96 mm, n = 2), 7.17–7.47 times as long as LLAS, 3.18–3.38 times as long as HW.

Instar III (Figs. 22, 26, 27, 30, 31)

COLOR. As in instar II except pronotum broadly yellow laterally; legs paler. **HEAD. Head capsule** (Fig. 22): HL = 2.53–2.80 mm (mean = 2.65 mm, n = 4); HW = 2.29–2.60 mm (mean = 2.45 mm, n = 4); FCL = 1.00–1.10 mm (mean = 1.05 mm, n = 4); HL/HW = 1.04–1.10. **Antenna:** length of antenna/HW = 0.70–0.72. **Maxilla:** length of antenna/length of maxillary palpus = 1.49–1.60. **Labium:** palpomere 2 is 0.71–0.74





FIGURES 30–31. Protibia and protarsus of *Lancetes delkeskampi*, instar III: (30) anterior surface and (31) posterior surface. Scale bar = 0.10 mm.

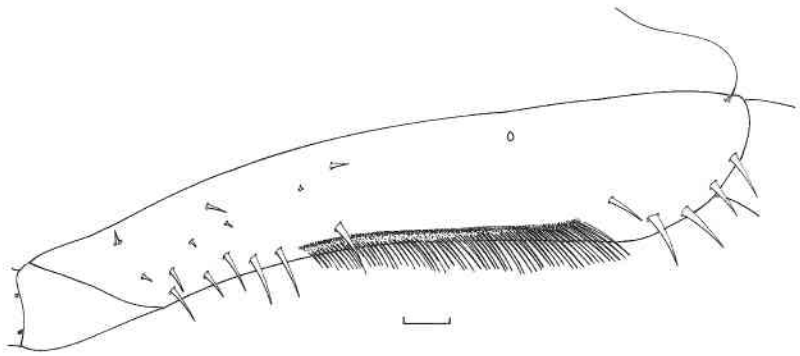


FIGURE 32. Posterior surface of profemur of *Lancetes flavoscutatus*, instar III. Scale bar = 0.10 mm.

as long as palpomere 1. **LEGS** (Figs. 26, 27, 30, 31). Metathoracic leg about 3.10 times HW; position and number of secondary setae (Table 4). **ABDOMEN.** LLAS = 1.45–1.60 mm (mean = 1.53 mm, n = 3); LLAS/HW = 0.55–0.66. **UROGOMPHUS.** Total length of urogomphus = 7.33–8.85 mm (mean = 8.03 mm, n = 4), 5.05–5.77 times as long as LLAS, 3.20–4.25 times as long as HW.

Distribution

South America (Argentina) (Ríha 1961; Bachmann and Trémouilles 1981).

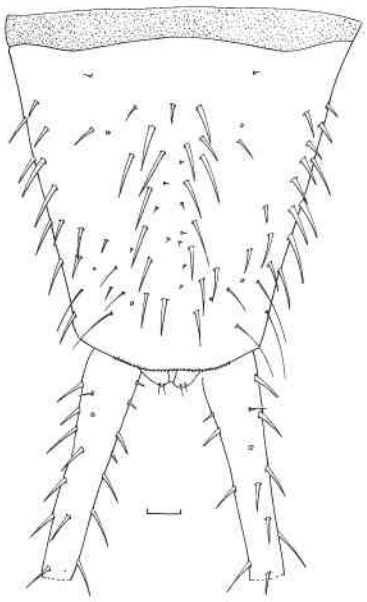


FIGURE 33. Dorsal aspect of last abdominal segment of *Lancetes nigriceps* (Erichson), instar III. Scale bar = 0.10 mm.

Remarks

As instar I, *L. delkeskampi* can readily be distinguished from either *L. subseriatus* or *L. angusticollis* (the only two other species of the genus *Lancetes* known as instar I) by several unique features: (*i*) head capsule constricted at level of the occipital region (Fig. 3), (*ii*) posterior margin of LAS lacking spinulae (Fig. 17), (*iii*) LAS with one additional seta (Fig. 17), (*iv*) primary seta AB5 elongate (Fig. 17), (*v*) urogomphus with several additional setae (Fig. 21), (*vi*) presence of additional D setae on femora (Table 3), and (*vii*) presence of one additional seta on meso- and meta-tibia (compared with >2) (Table 3).

Larvae of *Lancetes subseriatus* Zimmermann

(Figs. 1, 2, 5, 6, 8, 9, 18, 19, 23)

Source of material

The larvae studied (three instar I, six instar II, and eight instar III) were collected in association with adults at **Falkland Islands.** No locality labels were included with the specimens. Ríha (1961) recognized three species of the genus *Lancetes* on the Falkland Islands: *L. subseriatus*, *L. flavoscutatus*, and *L. falklandicus* (Régimbart). The identity of *L. falklandicus* is, however, uncertain. Two different morphotypes were found among the larvae obtained from the Falkland Islands. *Lancetes subseriatus* is known to be smaller than *L. flavoscutatus* (Ríha 1961), and accordingly the smaller of the two morphotypes obtained was identified as *L. subseriatus*.

Diagnostic combination (instar III)

Profemur lacking a submarginal PV keel with elongate spinulae; metathoracic leg about 3.80 times HW; coxae with <26 secondary setae; trochanter with <8 secondary

TABLE 3. Number and position of additional setae in instar I of selected species of the genus *Lancetes*.

Segment*	Position†	*Lang* (*n* = 1)	*Ldel* (*n* = 3)	*Lsub* (*n* = 3)
ProFE	D	0	3	0
	AV	2	4–5	2–3
	PV	1	3	0
MesoFE	D	0	4	0
	AV	2	5–6	3–4
	PV	1	2–3	0
MetaFE	D	0	4–5	0
	AV	2	5–7	2–3
	PV	1	2–3	0
ProTI	AV	0	0	0–1
	PV	3	0	0
MesoTI	AV	4	1	2–3
	PV	1	0	0
MetaTI	AV	3	1	3
	PV	1	0	0

NOTE: *Lang*, *L. angusticollis*; *Ldel*, *L. delkeskampi*; *Lsub*, *L. subseriatus*.

* Leg segments: FE, femur; TI, tibia.

† Position: D, dorsal; AV, anteroventral; PV, posteroventral.

setae; protibia and tarsi with secondary spiniform setae; protarsus lacking secondary ventral setae; smaller species, HL <2.40 mm.

Description

Instar I (Figs. 1, 2, 5, 6, 8, 9, 18, 19)

COLOR. Head capsule: pale brown, yellow around ocularium; **head appendages:** predominantly pale yellow except A4, apex of A3, MX3, and LB2 piceous; **thorax:** terga predominantly brown; **legs:** predominantly creamy white; **abdomen:** terga predominantly brown; **urogomphi:** greyish black, paler proximally over a short distance. **HEAD. Head capsule** (Figs. 1, 2): HL = 0.88–0.95 mm (mean = 0.91 mm, *n* = 3); HW = 0.77–0.78 mm (mean = 0.78 mm, *n* = 3); FCL = 0.40–0.44 mm (mean = 0.41 mm, *n* = 3); HL/HW = 1.14–1.22. **Antenna** (Figs. 5, 6): length of antenna/HW = 1.06–1.16. **Maxilla** (Figs. 8, 9): length of antenna/length of maxillary palpus = 1.76–1.84. **Labium:** palpomere 2 is 1.09–1.19 as long as palpomere 1. **LEGS.** Metathoracic leg about 4.10 times as long as HW; position and number of additional setae (Table 3). **ABDOMEN** (Figs. 18, 19). LLAS = 0.30–0.31 mm (mean = 0.30 mm, *n* = 3); LLAS/HW = 0.39–0.40. **UROGOMPHUS** (Fig. 21). Total length of urogomphus = 2.86–3.03 mm (mean = 2.95 mm, *n* = 2), 9.32–10.03 times as long as LLAS, 3.71–3.87 times as long as HW.

Instar II

COLOR. As instar I except head capsule paler. **HEAD. Head capsule:** HL = 1.43–1.48 mm (mean = 1.46 mm, *n* = 4); HW = 1.23–1.27 mm (mean = 1.25 mm, *n* = 4); FCL = 0.59–0.61 mm (mean = 0.60 mm, *n* = 4); HL/HW = 1.14–1.20. **Antenna:** length of antenna/HW = 0.91–0.92. **Maxilla:** length of antenna/length of maxillary palpus = 1.83–1.85. **Labium:** palpomere 2 is 0.90–1.00 as long as palpomere 1. **LEGS.**

Metathoracic leg about 3.80 times HW; position and number of secondary setae (Table 4). **ABDOMEN.** LLAS = 0.62–0.68 mm (mean = 0.65 mm, *n* = 4); LLAS/HW = 0.50–0.54. **UROGOMPHUS.** Total length of urogomphus = 4.63–4.98 mm (mean = 4.87 mm, *n* = 4), 7.25–7.77 times as long as LLAS, 3.70–4.01 times as long as HW.

Instar III (Fig. 23)

COLOR. As in instar II except dorsal surface of head capsule yellow with a reticulate brown pattern (Fig. 23); pronotum broadly pale yellow laterally. **HEAD. Head capsule** (Fig. 23): HL = 2.13–2.33 mm (mean = 2.24 mm, *n* = 5); HW = 1.85–2.00 mm (mean = 1.92 mm, *n* = 5); FCL = 0.83–0.93 mm (mean = 0.87 mm, *n* = 5); HL/HW = 1.15–1.17. **Antenna:** length of antenna/HW = 0.72–0.75. **Maxilla:** length of antenna/length of maxillary palpus = 1.62–1.66. **Labium:** palpomere 2 is 0.87 as long as palpomere 1. **LEGS.** Metathoracic leg about 3.80 times as long as HW; position and number of secondary setae (Table 4). **ABDOMEN.** LLAS = 1.19–1.28 mm (mean = 1.24 mm, *n* = 4); LLAS/HW = 0.59–0.66. **UROGOMPHUS.** Total length of urogomphus is not determined (broken).

Distribution

Falkland Islands (Ríha 1961).

Remarks

As instar I, *L. subseriatus* can readily be distinguished from either *L. delkeskampi* or *L. angusticollis* (the only two other species of the genus *Lancetes* known as instar I) by (*i*) the shorter urogomphus (5.00 times LLAS compared with 9.00 times) and (*ii*) by the more elongate labial palpomere 2 compared with labial palpomere 1 (>1.40 compared with <1.20). See also under *L. delkeskampi* and *L. angusticollis*.

Larvae of *Lancetes angusticollis* (Curtis)

(Figs. 4, 13–16, 20)

Source of material

The instar I studied was reared from adults collected in **South Georgia**; the four instar III studied were collected in association with adults in **South Georgia**, ii.1981.

Diagnostic combination (instar III)

Profemur lacking a submarginal PV keel with elongate spinulae; metathoracic leg about 3.50 times HW; coxae with <26 secondary setae; trochanter with <8 secondary setae; protibia and tarsi with secondary spiniform setae; protarsus with secondary ventral setae; smaller species, HL <2.40 mm.

Redescription

Instar I (Figs. 4, 13–16, 20)

COLOR. Head capsule: yellowish to pale brown; parietals brownish with an irrorate creamy white pattern; **head appendages:** creamy white to pale yellow except A4, and apex of MX3 infuscate; **thorax:** terga yellowish to pale brown; **legs:** creamy white to pale yellow; **abdomen:** terga yellowish to pale brown; **urogomphus:** creamy white to pale yellow. **HEAD. Head capsule** (Fig. 4): HL = 0.94 mm (*n* = 1); HW = 0.84 mm (*n* = 1);

TABLE 4. Number of secondary setae on the legs of instars II and III of the genus *Lancetes*.

		Instar II				Instar III				
Segment*	Sensillar series†	*Ldel* (n = 4)	*Llan* (n = 6)	*Lsub* (n = 4)	*Lang* (n = 4)	*Ldel* (n = 4)	*Lfla* (n = 3)‡	*Llan* (n = 5)	*Lnig* (n = 5)	*Lsub* (n = 4)
ProCO	D	5–8	3–7	6–7	5–8	9–11	18–26	9–12	10–14	11–15
	A	0–2	0–1	2	5–6	3–6	10–16	7–11	3–7	4–9
	V	0	0	0	0	0	12–18	0	0	0–1
	Range	6–10	3–7	8–9	10–13	13–15	42–60	16–23	13–18	18–24
ProTR	Pr	0–1	0–1	0	1	1–2	6–9	2–6	0–1	2–4
	Di	0	0–1	0	0–1	0–1	1–5	0	0–1	0–3
	Range	0–1	0–2	0	1–2	1–3	10–11	2–6	0–2	2–5
ProFE	AD	3–4	4–6	2	3–4	3	9–13	4–6	2–4	2
	AV	11–12	7–13	7–10	7–13	9–17	12–15	16–22	8–9	8–12
	PD	0	0	0	0	0	7–8	0	0	0
	PV	6–8	7–9	4–7	5–9	6–9	12–17	13–21	3–4	6–9
	Range	21–23	18–25	14–19	15–25	18–27	43–51	35–46	14–17	16–21
ProTI	NS(PD)	Present	Present	Present	Present	Present	Present	Present	Present	Present
	AD	0	2–3	1–2	2–3	0	3	2–3	0	1–2
	AV	0	1–2	0	1–2	0	0	0–2	0	0
	PD	0	0	0	0	0	4–6	0	0	0
	PV	0	0–2	0	1–2	0	0–1	0–2	0	0
	Range	0	4–6	1–2	4–7	0	7–9	2–7	0	1–2
ProTA	NS(PD)	Present	Present	Present	Present	Present	Present	Present	Present	Present
	AD	0	3–4	1–2	3–5	0	2	2–4	0	1–2
	AV	0	0	0	2–3	0	0	0	0	0
	PD	0	0	0	0	0	1–2	0	0	0
	PV	0	0	0	0	0	0	0	0	0
	Range	0	3–4	1–2	5–8	0	3–4	2–4	0	1–2
MesoCO	D	6–7	4–6	6–7	5–7	8–9	18–23	7–12	8–16	11–15
	A	1–2	0–1	1–2	4–7	4–8	14–18	6–11	4–6	3–9
	V	0	0	0	0	0	13–18	0	0–1	0–1
	Range	7–9	4–6	7–9	11–12	12–17	48–55	13–22	14–25	15–24

MesoTR	Pr	0–1	0–1	0–1	1–2	1–2	10–16	4–5	1–2	2–4
	Di	0	0	0	0	0	4–7	0	0	0
	Range	0–1	0–1	0–1	1–2	1–2	17–20	4–5	1–2	2–4
MesoFE	AD	4–5	5–7	3–5	4–5	4	9–25	5–8	3–4	2–3
	AV	15–17	11–16	12–14	11–15	16–19	22–26	21–31	8–14	18
	PD	0	0	0	0	0	6–10	0	0	0
	PV	9–11	7–10	6–10	5–7	11–13	9–23	13–17	7–8	8–11
	Range	30–33	25–30	21–28	14–17	31–36	61–78	42–54	20–25	28–31
MesoTI	NS(PD)	Present	Present	Present	Present	Present	Present	Present	Present	Present
	AD	0	3–6	4–5	5–6	0	5–8	4–6	0	3–4
	AV	1–2	8–10	3–4	7–9	1–2	4–8	6–13	1	3–5
	PD	0	0	0	0	0	4–8	0	0	0
	PV	0	0–2	0	1–2	0	0	0–2	0	0
	Range	1–2	12–18	7–9	14–17	1–2	15–20	10–20	1	7–9
MesoTA	NS(PD)	Present	Present	Present	Present	Present	Present	Present	Present	Present
	AD	0	4–5	3–4	4–6	0	3–5	3–6	0	3
	AV	0	3–6	0	5–9	0	2–4	5–7	0	0–1
	PD	0	0	0	0	0	0	0	0	0
	PV	0	0	0	0	0	0	0	0	0
	Range	0	8–11	3–4	9–14	0	5–9	8–12	0	3–4
MetaCO	D	5–6	3–5	5–7	4–7	6–8	24	7–9	11–14	12–17
	A	0–1	0–3	1–2	4–8	3–6	18	4–9	4–9	7–11
	V	0	0	0	0	0	23	0	0	0
	Range	5–7	3–8	6–9	10–14	11–12	65	13–16	15–23	19–26
MetaTR	Pr	0–2	0–1	0–1	1–2	1–4	11	4–8	1–2	2–5
	Di	0	0	0	0	0	6	0	0–1	0
	Range	0–2	0–1	0–1	1–2	1–4	17	4–8	1–2	2–5
MetaFE	AD	4–5	6–9	2–6	6–7	4–5	25	7–11	3–4	4–5
	AV	12–14	12–16	11–16	10–13	15–16	32	26–28	7–12	16–18
	PD	0	0	0	0	0	8	0	0	0
	PV	11–13	5–11	8–10	7–10	10–17	26	9–12	7–10	9–11
	Range	27–31	25–34	23–31	24–30	30–36	91	43–50	19–25	31–33

TABLE 4 (*concluded*).

Segment*	Sensillar series†	Instar II				Instar III				
		Ldel (n = 4)	*Llan* (n = 6)	*Lsub* (n = 4)	*Lang* (n = 4)	*Ldel* (n = 4)	*Lfla* (n = 3)‡	*Llan* (n = 5)	*Lnig* (n = 5)	*Lsub* (n = 4)
MetaTI	NS(PD)	Present	Present	Present	Present	Present	Present	Present	Present	Present
	AD	0	5–8	6–7	7–8	0	8	7–9	0	4–6
	AV	1–2	9–13	5–6	9–11	1	10	15–17	1	6–7
	PD	0	0	0	0	0	4	0	0	0
	PV	0	0–1	0	1–2	0	0	0–1	0	0
	Range	1–2	14–20	11–12	18–21	1	22	23–26	1	11–12
MetaTA	NS(PD)	Present	Present	Present	Present	Present	Present	Present	Present	Present
	AD	0	4–8	3–7	5–8	0	5	6–8	0	5–7
	AV	0	6–10	2–5	9–10	0	7	9–12	0	2–4
	PD	0	0	0	0	0	1	0	0	0
	PV	0	0	0	0	0	2	0	0	0
	Range	0	10–18	7–12	14–17	0	15	15–20	0	9–10

NOTE: *Lang, L. angusticollis*; *Ldel, L. delkeskampi*; *Lfla, L. flavoscutatus*; *Llan, L. lanceolatus*; *Lnig, L. nigriceps*; *Lsub, L. subseriatus*. Range is the total number of secondary setae on segment.

* Leg segments: CO, coxa; FE, femur; TA, tarsus; TI, tibia; TR, trochanter.

† Sensillar series: A, anterior; AD, anterodorsal; AV, anteroventral; D, dorsal; Di, distal; NS, natatory setae; PD, posterodorsal; Pr, proximal; PV, posteroventral; V, ventral.

‡ Except for metathoracic leg for which only one specimen was available.

FCL = 0.47 mm (n = 1); HL/HW = 1.12. **Antenna:** length of antenna/HW = 1.04. **Maxilla:** length of antenna/length of maxillary palpus = 1.79. **Labium:** palpomere 2 is 1.45 as long as palpomere 1. **LEGS** (Figs. 13–16). Metathoracic leg about 3.80 times as long as HW; position and number of additional setae (Table 3). **ABDOMEN.** LLAS = 0.44 mm, (n = 1); LLAS/HW = 0.52. **UROGOMPHUS** (Fig. 20). Total length of urogomphus = 2.38 mm (n = 1), 5.39 times as long as LLAS, 2.82 times as long as HW.

Instar II

No specimen was available for study.

Instar III

COLOR. Head capsule: predominantly brown, with an irrorate yellowish pattern on frontoclypeus and parietals; **head appendages:** creamy white to pale yellow except A4 infuscate; **thorax:** terga brown; **legs:** yellow; **abdomen:** terga brown; **urogomphus:** brown, paler apically. **HEAD. Head capsule:** HL = 2.15–2.25 mm (mean = 2.20 mm, n = 4); HW = 1.89–1.92 mm (mean = 1.90 mm, n = 4); FCL = 0.88–0.91 mm (mean = 0.89 mm, n = 4); HL/HW = 1.13–1.19. **Antenna:** length of antenna/HW = 0.68–0.72. **Maxilla:** length of antenna/length of maxillary palpus = 1.71–1.75. **Labium:** palpomere 2 is 0.89–0.99 as long as palpomere 1. **LEGS.** Metathoracic leg about 3.60 times as long as HW; position and number of secondary setae (Table 4). **ABDOMEN.** LLAS = 1.32–1.36 mm (mean = 1.34 mm, n = 4); LLAS/HW = 0.69–0.72. **UROGOMPHUS.** Total length of urogomphus = 5.70–6.15 mm (mean = 5.91 mm, n = 4), 4.20–4.57 times as long as LLAS, 2.96–3.25 times as long as HW.

Distribution

This species probably has the most southerly distribution of any Dytiscidae; it has been recorded several times from the extreme south of Chile and from South Georgia (Enderlein 1912; Holdhaus 1932; Schweiger 1958; Říha 1961; Moroni 1973; Bachmann and Trémouilles 1981).

Remarks

Study of the larval morphology of the genus *Lancetes* involves the issue of the number of larval instars for that genus. Members of the family Dytiscidae are characterized by three larval instars. Unexpectedly, however, Nicolai and Droste (1984) postulated four larval instars in *L. angusticollis*. We believe that Nicolai and Droste (1984) artificially created an additional larval instar by subdividing instar II into two groupings (*i.e.*, instars II and III). Indeed, the measures of head capsule provided in their paper for their instars II and III clearly overlap and the range of variation of the measures of head capsule for their instar IV is wider than the variation of measures of instars II and III together. It is noteworthy that no emphasis was put in their study on the unusual presence of an additional larval instar in that species and that the authors neglected to refer to larval exuviae to support their finding. Similarly, the recent study of Arnold and Convey (1998) on the life history of *L. angusticollis* cannot be used to support the four-instar thesis of Nicolai and Droste (1984) because the determination of larval instars in their study was based on *a priori* measures of head capsules provided by Nicolai and Droste (1984). Accordingly, in absence of unambiguous arguments, we postulate that only three larval instars should occur in *L. angusticollis*.

As instar I, *L. angusticollis* can readily be distinguished from either *L. delkeskampi* or *L. subseriatus* (the only two other species of the genus *Lancetes* known as instar I)

by (*i*) the presence of an additional pore on the dorsal surface of the mentum and (*ii*) the terminal position of the primary seta UR8 (Fig. 20). See also under *L. delkeskampi* and *L. subseriatus*.

The instars I and III of *L. angusticollis* were first described by Mjöberg (1906) (as *Anisomera claussi* Müller), Beier (1928), Gressitt (1970) (as *Lancetes claussi*), and Brinck (1945). Brancucci and Ruhnau (1985) described its pupa.

In South Georgia, *L. angusticollis* has been collected in lakes, pools, and shallow slow-flowing streams. The life history of this species has been studied in detail by Nicolai and Droste (1984) [as *Lancetes claussi* (Müller)] and Arnold and Convey (1998). Based on the measures of head capsule provided in this paper, our instar III should correspond to the instar IV of Nicolai and Droste (1984) and of Arnold and Convey (1998).

Larvae of *Lancetes lanceolatus* (Clark)

Source of material

The larvae studied (six instar II and five instar III) were collected in association with adults at the following localities: **Australia,** 5 km W Casterton, Vic, 24.ix.1998; 10 km N Coonarra, SA, 26.ix.1998; 8 km N Forreston, SA, 08.viii.1999; 10 km S Forreston, SA, 17.ix.1996; Gifford RES, SA, 07.v.1997; 1km S Drik Drik, Vic, 24.ix.1998. The identification is firm, as *L. lanceolatus* is the only species of the genus *Lancetes* found in Australia.

Diagnostic combination (instar III)

Profemur lacking a submarginal PV keel with elongate spinulae; metathoracic leg about 3.50 times HW; coxae with <26 secondary setae; trochanter with <8 secondary setae; protibia and tarsi with secondary spiniform setae; protarsus lacking secondary ventral setae; larger species, HL >2.50 mm.

Redescription

Instar I

No specimen was available for study.

Instar II

COLOR. Head capsule: predominantly brown with an irrorate yellowish pattern and a latero-distal macula on each side; **head appendages:** predominantly pale brown except A4, MX3, and apical half of LB2 piceous; **legs:** predominantly creamy white, distal articles slightly darker; **abdomen:** terga predominantly brown, LAS paler; **urogomphi:** dark brown, paler apically. **HEAD. Head capsule:** HL = 1.62–1.73 mm (mean = 1.69 mm, n = 6); HW = 1.54–1.61 mm (mean = 1.58 mm, n = 6); FCL = 0.74–0.77 mm (mean = 0.75 mm, n = 6); HL/HW = 1.04–1.13. **Antenna:** length of antenna/HW = 1.15–1.24. **Maxilla:** length of antenna/length of maxillary palpus = 1.89–1.98. **Labium:** palpomere 2 is 0.79–0.95 as long as palpomere 1. **LEGS.** Metathoracic leg about 3.60 times as long as HW; position and number of secondary setae (Table 4). **ABDOMEN.** LLAS = 0.94–1.05 mm (mean = 0.99 mm, n = 5); LLAS/HW = 0.59–0.66. **UROGOMPHUS.** Total length of urogomphus = 3.90–4.65 mm (mean = 4.42 mm, n = 4), 3.94–4.84 times as long as LLAS, 2.54–3.01 times as long as HW.

Instar III

COLOR. Head capsule: frontoclypeus predominantly creamy white with a brownish pattern macula mesally; parietals brownish with an irrorate creamy white pattern; **head appendages:** creamy white to pale yellow except A4, and apex of MX3 and LB2 infuscate; **thorax:** terga brownish mesally, creamy white to pale yellow laterally; **legs:** predominantly creamy white; **abdomen:** terga pale brown to brown; **urogomphus:** yellow. **HEAD. Head capsule:** HL = 2.78–2.83 mm (mean = 2.82 mm, n = 5); HW = 2.60–2.75 mm (mean = 2.66 mm, n = 5); FCL = 1.08–1.18 mm (mean = 1.13 mm, n = 3); HL/HW = 1.05–1.07. **Antenna:** length of antenna/HW = 0.89–0.92. **Maxilla:** length of antenna/length of maxillary palpus = 1.87–1.91. **Labium:** palpomere 2 is 0.69–0.76 as long as palpomere 1. **LEGS.** Metathoracic leg about 3.40 times as long as HW; position and number of secondary setae (Table 4). **ABDOMEN.** LLAS = 1.95–2.08 mm (mean = 2.00 mm, n = 3). LLAS/HW = 0.71–0.78. **UROGOMPHUS.** Total length of urogomphus = 6.03–6.78 mm (mean = 6.51 mm, n = 5), 3.20–3.47 times as long as LLAS, 2.32–2.56 times as long as HW.

Distribution

Australia, Tasmania, and New Zealand (Ríha 1961).

Remarks

In Australia, *L. lanceolatus* is widespread in small creeks and ponds but seemingly in relatively low density in any one locality (Ordish 1966; Watts 1998).

Larvae of *L. lanceolatus* were first described by Watts (1963).

Larvae of *Lancetes flavoscutatus* Enderlein

(Figs. 24, 25, 28, 29, 32)

Source of material

The larvae studied (two instar III) were collected in association with adults at **Falkands Islands** (see under *L. subseriatus*).

Diagnostic combination (instar III)

Profemur with a submarginal PV keel bearing elongate comb-like spinulae (Fig. 32); metathoracic leg about 3.50 times HW; coxae with >40 secondary setae; trochanter with >10 secondary setae; protibia and tarsi with secondary spiniform setae (Figs. 28, 29); protarsus lacking secondary ventral setae (Figs. 28, 29); larger species, HL >2.50 mm.

Redescription

Instar I

No specimen was available for study.

Instar II

No specimen was available for study.

Instar III

COLOR. Not described because of the poor state of preservation of the specimens studied. **HEAD. Head capsule:** HL = 2.63–2.85 mm (mean = 2.74 mm, n = 2); HW = 2.38–2.50 mm (mean = 2.44 mm, n = 2); FCL = 1.13–1.38 mm (mean = 1.25 mm, n = 2); HL/HW = 1.11–1.14. **Antenna:** length of antenna/HW = not determined. **Maxilla:** length of antenna/length of maxillary palpus = not determined. **Labium:** length of palpomere 2/length of palpomere 1 = not determined. **LEGS** (Figs. 24, 25, 28, 29, 32). Metathoracic leg about 3.50 times HW; position and number of secondary setae (Table 4). **ABDOMEN.** LLAS = 1.55–1.58 mm (mean = 1.56 mm, n = 2); LLAS/HW = 0.63–0.65. **UROGOMPHUS.** Total length of urogomphus is not determined (broken).

Distribution

Argentina, Falkland Islands, South Georgia, and Chile (Cekalovic and Spano 1981).

Remarks

Instar III of *L. flavoscutatus* are unique among the species studied by the presence of a submarginal PV keel with elongate spinulae on profemur (visible under a dissecting microscope) (Fig. 32) and by the presence of a significantly larger number of secondary setae on legs (Table 4).

The mature larva and pupa of *L. flavoscutatus* were first described by Cekalovic and Spano (1981).

Larvae of *Lancetes nigriceps* (Erichson)

(Fig. 33)

Source of material

The larvae studied (instars III) were collected in association with adults at the following locality: **Argentina**, San Juan prov. Ischigualasto State Park, Río Salado.

Diagnostic combination (instar III)

Profemur lacking a submarginal PV keel with elongate spinulae; metathoracic leg about 3.10 times HW; coxae with <26 secondary setae; trochanter with <8 secondary setae; protibia and tarsi lacking secondary spiniform setae; protarsus with secondary ventral setae; smaller species, HL <2.50 mm.

Redescription

Instar I

No specimen was available for study.

Instar II

No specimen was available for study.

Instar III

COLOR. Head capsule: dorsal surface yellow with a reticulate brown pattern; **head appendages:** predominantly pale brown, most articles infuscate proximally and distally; **thoracic and abdominal terga:** predominantly brown; **legs:** yellow to pale brown; **urogomphus:** pale brown, darker proximally for a short distance. **HEAD. Head capsule:** HL = 2.23–2.40 mm (mean = 2.31 mm, n = 5); HW = 2.05–2.08 mm (mean = 2.07 mm, n = 5); FCL = 0.88–0.93 mm (mean = 0.91 mm, n = 5); HL/HW = 1.07–1.17. **Antenna:** length of antenna/HW = 0.68–0.70. **Maxilla:** length of antenna/length of maxillary palpus = 1.61–1.65. **Labium:** palpomere 2 is 0.68–0.75 as long as palpomere 1. **LEGS.** Metathoracic leg about 3.10 times as long as HW; position and number of secondary setae (Table 4). **ABDOMEN** (Fig. 33). LLAS = 1.02–1.20 mm (mean = 1.13 mm, n = 5); LLAS/HW = 0.49–0.59. **UROGOMPHUS.** Total length of urogomphus is not measured (broken).

Distribution

South America (Argentina, Bolivia, and Chile) (Ríha 1961; Bachmann and Trémouilles 1981).

Remarks

The instar III of *L. nigriceps* was first described by Brinck (1948) from specimens collected in Peru. According to Brinck (1948), larvae of *L. nigriceps* are characterized by the presence of ventral secondary setae on coxae. Secondary V setae are lacking on coxae of the specimens we studied.

Discussion

Analysis of the data matrix (Table 2) in the parsimony software program NONA gave one shortest tree of length 107 (Fig. 34) (CI = 0.48 and RI = 0.83), which supports the monophyly of the genus *Lancetes* with the Dytiscinae with respect to the chosen outgroup. The only unambiguous synapomorphy in support of this hypothesis is the secondary subdivision of the cephalic appendages (character 55). Other putative synapomorphies are the proximal articulation of the primary seta CO7 both on meso- and meta-coxa (character 25, Fig. 13) (homoplastic in the genera *Laccophilus*, *Neptosternus* Sharp, and *Australphilus*), and to a lesser extent, the presence of additional primary setae on ventral margin of tibiae (character 34, Figs. 15, 16; homoplastic in *Rhantus* Dejean and *Neoscutopterus* Balfour-Browne).

Within this clade, the genus *Lancetes* is treated as monophyletic based on presence of multifragmented urogomphi, a unique feature within the Dytiscidae (character 56, Figs. 20–21). Other synapomorphies include presence of only two lamellae clypeales in instar I (character 5, Figs. 1, 3, 4; homoplastic in the Laccophilinae), absence of an occipital suture (character 15; homoplastic in Laccophilinae + Agabini), primary seta FE1 articulated distally (character 32, Fig. 13; homoplastic in the Agabini), and by the elongate aspect of the primary seta TI7 (character 37, Fig. 16; homoplastic in the Colymbetini and the genus *Hydaticus*).

Both the dataset provided in this study and the one proposed by Miller (2001) that was based on adult morphology give similar phylogenetic information. This result suggests that a broad combined phylogenetic study of adult and larval features (only possible when more larval taxa are known) would likely improve resolution, based on larval and adult data independently, and accordingly, more strongly support the hypothesis of

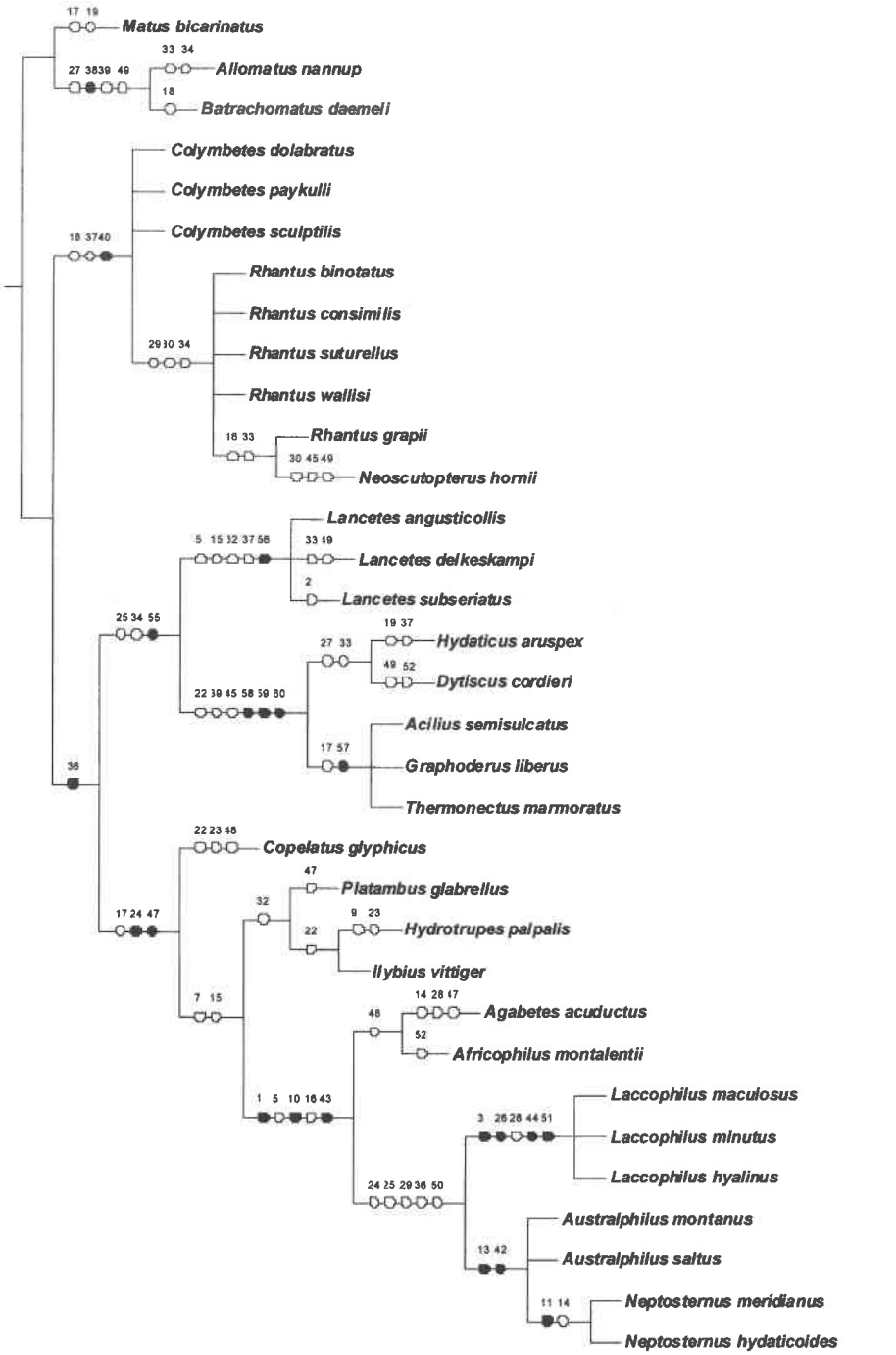


FIGURE 34. Single shortest tree found from cladistic analysis of the matrix in Table 4 after removal of nine uninformative characters and exclusion 19 species of Agabinae with the same combination of character states as *Ilybius vittiger*. Tree length 107 (CI = 0.48 and RI = 0.83). Character codes (as in Table 4) above branches refer to unique character-state transformations (●) or homoplasious character-state transformations (○). Tree produced in WINCLADA using unambiguous optimization (Nixon 1999).

sister-group relationship between the genus *Lancetes* and members of the subfamily Dytiscinae.

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Appendix A

Taxa examined for cladistic analysis. Taxa are arranged alphabetically by subfamily following Nilsson (2001).

Subfamily AGABINAE
- *Agabus* Leach
  - *A. anthracinus* Mannerheim
  - *A. arcticus* (Paykull)
  - *A. bifarius* (Kirby)
  - *A. confinis* (Gyllenhal)
  - *A. discolor* (Harris)
  - *A. elongatus* (Gyllenhal)
  - *A. falli* (Zimmermann)
  - *A. phaeopterus* (Kirby)
  - *A. semipunctatus* (Kirby)
  - *A. strigulosus* (Crotch)
  - *A. subfuscatus* Sharp
- *Hydrotrupes* Sharp
  - *H. palpalis* Sharp
- *Ilybiosoma* Crotch
  - *I. bjorkmanae* (Hatch)
  - *I. roguus* (Larson)
  - *I. seriatum* (Say)
- *Ilybius* Erichson
  - *I. angustior* (Gyllenhal)
  - *I. biguttulus* (Germar)
  - *I. picipes* (Kirby)
  - *I. subaeneus* (Erichson)
  - *I. vittiger* (Gyllenhal)
  - *I. wasastjernae* (CR Sahlberg)
- *Platambus* Thompson
  - *P. glabrellus* (Motschulsky)

Subfamily COLYMBETINAE
- *Colymbetes* Clairville
  - *C. dolabratus* Clairville
  - *C. paykulli* Erichson
  - *C. sculptilis* Harris
- *Rhantus* Dejean
  - *R. grapii* (Gyllenhal)
  - *R. binotatus* (Harris)
  - *R. consimilis* Motschulsky
  - *R. suturellus* Harris
  - *R. wallisi* Hatch

Subfamily COPELATINAE
- *Copelatus* Erichson
  - *C. sp.*

Subfamily DYTISCINAE
- *Acilius* Leach
  - *A. semisulcatus* Aubé
- *Graphoderus* Dejean
  - *G. liberus* (Say)
- *Thermonectus* Dejean
  - *T. marmoratus* (Gray)
- *Dytiscus* Linnaeus
  - *D. cordieri* Aubé
- *Hydaticus* Leach
  - *H. aruspex* Clark

Subfamily LACCOPHILINAE
- *Africophilus* Guignot
  - *A. montalentii* Sanfilippo and Franciscolo
- *Australphilus* Watts
  - *A. montanus* Watts
  - *A. saltus* Watts
- *Laccophilus* Leach
  - *L. hyalinus* (De Geer)
  - *L. maculosus* Say
  - *L. minutus* (Linnaeus)
- *Neptosternus* Sharp
  - *N. hydaticoides* (Régimbart)
  - *N. meridianus* Omer-Cooper

Subfamily LANCETINAE
- *Lancetes* Sharp
  - *L. angusticollis* (Curtis)
  - *L. delkeskampi* Riha
  - *L.subseriatus* Zimermann

Subfamily MATINAE
- *Allomatus* Mouchamps
  - *A. nannup* Watts
- *Batrachomatus* Clark
  - *B. daemeli* (Sharp)
- *Matus* Aubé
  - *M. bicarinatus* (Say)