Zootaxa 3750 (5): 450–464
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3750.5.2
http://zoobank.org/urn:lsid:zoobank.org:pub:06F7524F-2ABB-412B-A9FA-91B8A059196E

Redescription and lectotype designation of the endemic South African mayfly *Lestagella penicillata* (Barnard, 1932) (Ephemeroptera: Teloganodidae)

LYNDALL L. PEREIRA-DA-CONCEICOA[1] & HELEN M. BARBER-JAMES[1,2]

[1]*Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140. E-mail: lyndall.pereira@gmail.com*
[2]*Department of Freshwater Invertebrates, Albany Museum, Grahamstown, 6140*

Abstract

The imago and nymph of *Lestagella penicillata* are redescribed based on historic specimens and new material from Table Mountain slopes (Skeleton Gorge and Window Stream), Western Cape, South Africa. A male from Barnard's syntype series is designated as the lectotype. Wear-and-tear of mouthparts, particularly the mandibles, has led to errors in identification of diagnostic characters for the nymphs in earlier publications. Previous descriptions of the mandibles being atrophied, in terms of dentition, are erroneous. The generic diagnosis of *Lestagella* is modified to account for these errors and intraspecific variability. Adults are distinguished from other Teloganodidae by the combination of a short, detached iMP vein on the forewing, three caudal filaments and gill socket vestiges on segments II - IV. Nymphs are distinguished from other Teloganodidae by a conspicuous head fringe, lamellate gills on abdominal segments II–IV and a dorso-ventrally flattened body.

Key words: South Africa, Western Cape, acid streams, worn mouthparts, mouthpart regeneration

Introduction

Teloganodidae (Ephemeroptera) are pannote mayflies (McCafferty & Edmunds 1979, McCafferty & Wang 2000) placed in the superfamily Ephemerelloidea Demoulin, along with ten other families (Jacobus & McCafferty 2006). Originally assigned to Ephemerellidae, they were elelvated to family level ranking (McCafferty & Wang 1997). Teloganodidae can be distinguished from all other sister groups by shared derived characteristics of the abdominal gills (McCafferty & Wang 1997; 2000). Jacobus & McCafferty (2006) included that the stout and spatulate setae found on the margins of the coxal projections of the nymphs are apomorphic and characteristic of the family.

The relationships between teloganodid genera are still uncertain and have differed between studies depending on the use and treatment of various characters utilised in the morphological analyses. McCafferty & Benstead (2002) used the characters and cladogram from McCafferty & Wang (1997) to produce a cladogram including the Madagascan genus *Manohyphella* Allen, 1973. In a later study, Jacobus & McCafferty (2006) published a larger study on Pannota (including the Teloganodidae genera), using more characters including egg morphology. Any autapomorphies and characters considered to be ambiguous, prone to convergence or highly variable were excluded from the analysis (Jacobus & McCafferty 2006).

Teloganodidae have a disjunct distribution throughout the southern Afrotropical and Oriental regions (Sartori *et al.* 2008). Currently, there are 22 species in eight genera of Teloganodidae described globally (Sartori *et al.* 2008), with five species in four genera from continental Africa (McCafferty & Wang 1997, 2000): *Lestagella penicillata* (Barnard, 1940) (discussed in this paper); *Ephemerellina barnardi* Lestage, 1924; *Lithogloea harrisoni* Barnard, 1932 and *Nadinetella* McCafferty & Wang, 1998, with two species *N. brincki* (Demoulin, 1970) and *N. crassi* (Allen & Edmunds, 1963).

The African Teloganodidae are endemic to pristine mountain streams found in the southern and western Cape of South Africa, with only one genus known to extend to the Amathole Mountains (Eastern Cape). They commonly occur on stones and vegetation, usually in swiftly flowing currents including waterfalls (McCafferty & Wang

 Accepted by F. Salles: 20 Nov. 2013; published: 23 Dec. 2013

1997). Harrison & Agnew (1962) noted that certain South African Teloganodidae are restricted to acidic waters found only in the southern and Western Cape regions due to the heath-like vegetation type (fynbos) in combination with the geology (Table Mountain Sandstone). Currently, *Lestagella* Demoulin, 1970 is the only African genus of Teloganodidae recorded from pH neutral rivers in the Amathole Mountains and in the Wit River, a tributary of the Gamtoos River, Eastern Cape. The recorded distribution of *Lestagella* (Fig. 1) shows a range extending from the Cederberg area (Western Cape) through to the Amatole Mountains (Eastern Cape), with the exception of the Kogelberg region, where no *L. penicillata* were found in any of the rivers despite extensive sampling.

Early instars of *Lestagella penicillata* from Table Mountain slopes (Western Cape) were originally misdiagnosed and described as *Lithogloea harrisoni* Barnard (1932). This was later corrected by Barnard (1940), and a second species of the genus *Lithogloea*, *Lithogloea penicillata* Barnard (1940) was described. However, no type specimen was allocated. Demoulin (1970) erected a new genus, *Lestagella*, and removed *L. penicillata* from *Lithogloea*, placing it within the newly erected genus as the only described species. No imagos of *L. penicillata* had been adequately described, but Barnard (1940) indicated that the female subimago and male imago of *L. penicillata* are very similar to those described for *Lithogloea harrisoni*.

The generic diagnosis has been modified from Demoulin (1970), McCafferty & Wang (1997) and Jacobus & McCafferty (2006), as some of the diagnostic characters are seen to be variable between individuals within a population of the same species. Wear-and-tear of mouthparts has also led to errors in identification where diagnostic characters of the nymphs are previously described as atrophied. For the purposes of this study and to avoid ambiguities, the term "atrophy" refers to a part or organ that is reduced or undeveloped, not worn down.
In this study, a male adult of *Lestagella penicillata* is designated and described from the original syntype series from the Iziko Museum, Cape Town, South Africa. Detailed descriptions of the nymphal stage are presented using material from the original syntype series from the Iziko Museum and the Natural History Museum in London, England and from fresh material housed at the Albany Museum, Grahamstown, South Africa, with mention of the effects of wear-and-tear of mouthparts on species identification.

Material and methods

Specimens of *Lestagella penicillata* were examined from the original syntype series collected by Barnard in 1932 from both the Iziko Museum collection, Cape Town [SAMC] and the Natural History Museum, London [BMNH], as well as freshly collected material held at the Albany Museum, Grahamstown [AMGS]. One male imago from the Keppel Harcourt Barnard (K.H.B) material from the SAMC material, collected from the slopes of Table Mountain (Fig. 1, represented as a cross on map), was slide mounted for descriptive purposes and is here designated as the lectotype for *Lestagella penicillata*. This study also examines and describes the nymphal stage from the paralectotype material. Fresh specimens of nymphs, subimagos and imagos from the lectotype locality were collected to aid in descriptions and for comparative purposes. Fresh imagos collected for this study were positively associated with nymphs by comparing a section of the *Cytochrome oxidase subunit 1* [*COI*] gene for both stages, using primers LCO1490 and HCO2198 (Folmer et al. 1994). The fresh material was then compared to the historical material and positively identified; also Barnard (1940) noted that *Lithogloea harrisioni* (the only other teloganodid that could be confused with *Lestagella penicillata*) was not collected from the Table Mountain slopes, which further supports the association between nymph and imago.

Euparal was used for all slide mounts with the exception of wings, which were slide mounted in ethanol to accentuate the wing venation, and once the ethanol was dry, the corners of the coverslip were glued in place with clear nail varnish. Wing venation follows the notation of Kluge (2004). Slide mounting can result in dissected specimen parts becoming fixed at skewed angles resulting in distortion and must be taken into careful consideration when describing species. Whole specimens of nymphs and imagos from the lectotype locality are presented as photographs (Fig. 2), and line illustrations are used for more detailed structures (Figs. 3–15). The lectotype and paralectotypes described here belong to the SAMC collection, with additional paralectotypes from the same series held at BMNH.

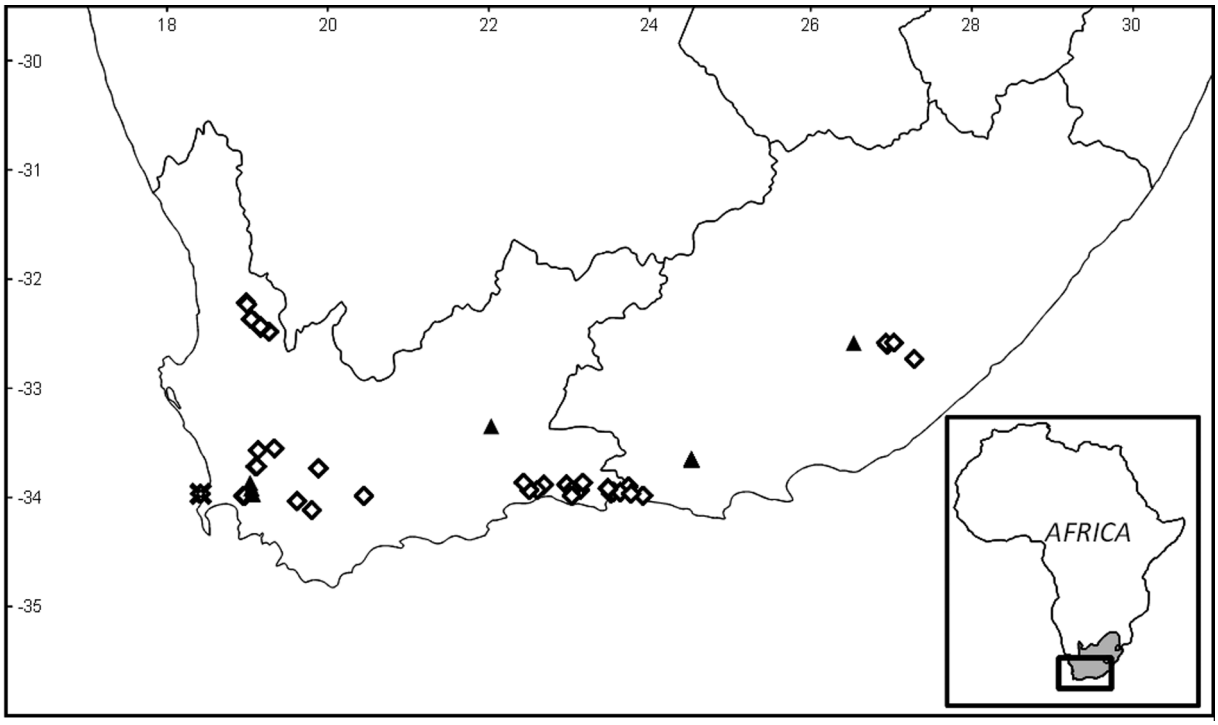

FIGURE 1. Map of recorded and sampled localities of the genus *Lestagella*. Diamonds represent sampled localities, triangles are previously recorded localities obtained from the Albany Museum (AMGS) database, and the cross ("**X**") denotes the lectotype locality from Table Mountain slopes.

Lestagella Demoulin, 1970

Lestagella Demoulin 1970: 130, Figure 15 (a–r); McCafferty & Wang 1997: 403–405, Figures 7, 16, 25, 34, 43, 52, 61, 68, 72, 86.
Type species: *Lithogloea penicillata* by original designation

Diagnosis. *Nymph*. *Lestagella* nymphs can be distinguished from other Teloganodidae by the following combination of characters: a well-developed marginal fringe of setae on the head (Fig. 2c–e), spatulate setae on margin of prothorax, simple filamentous gills present on abdominal segment I, lamellate gills on segments II–IV with fully operculate gill on segment II, tibia lined with a single row of setae on the antero-dorsal surface, tarsal claw with well-developed subapical denticle, other denticles small. Abdominal segments with moderately developed posterolateral processes that are slightly separated from the base of the following segment, three caudal filaments with lateral, hair-like setae and a subequal median caudal filament.

Imago. *Lestagella* adults can be distinguished from other Teloganodidae by the combination of the following characters: three caudal filaments, forewings with a relatively short, detached iMP and the presence of gill socket vestiges on abdominal segments II–IV.

Lestagella penicillata (Barnard, 1940)

Lithogloea harrisoni Barnard, 1932: 253, *pro parte* young nymphs, Fig. 43 a–c
Lithogloea penicillata Barnard, 1940: 637
Ephemerellina penicillata Allen & Edmunds, 1963: 12
Lestagella penicillata Demoulin, 1970: 130

Material examined. SOUTH AFRICA: Lectotype, ♂ imago, Table Mt. slopes, XI-1932, K.H.B., approximately 33°58′S, 18°25′E. Condition: head, thorax and abdomen mostly disintegrated (kept in ethanol with syntype series). Slide preparations (EPH-A000411): genitalia, wings, mid- and hindlegs (forelegs missing), SAMC.

Paralectotypes. 5 ♀ nymphs, slide preparations of 3 ♀ nymphs (EPH-A000411): Gills (Slide 27), mouthparts (Slide 23, Slide 25, Slide 27) and legs (Slide 27), Table Mt. slopes, XI-1932, K.H.B., SAMC. 1 ♀ subimago, 1 ♂ subimago, 1 ♀ imago, 19 nymphs, (EPH-A000411), Table Mt. slopes, XI-1932, K.H.B., SAMC; 3 ♂ adults (BMNH(E) 1201855–BMNH(E) 1201857), 3 ♀ adults (BMNH(E) 1201858–BMNH(E) 1201860), 1 ♂ subimago (BMNH(E) 1201861), 29 nymphs (BMNH(E) 1201862–BMNH(E) 1201866; BMNH(E) 1201872–BMNH(E) 1201891; BMNH(E) 1239038–BMNH(E) 1239041), Table Mt. slopes, XI-1932, K.H. Barnard, BMNH.

Other material examined. 3 ♂ adult, 1 ♀ adult, (BMNH(E) 1201851–BMNH(E) 1201854) Orange Kloof Table Mt, 28-XI-1934, K.H.B. 2 ♀ nymphs, whole specimen photographed (HMJ 181A), slide preparations: HMJ 60A, whole specimen. 1 ♂ nymph, slide preparations: HMJ 60A, whole specimen. 2 ♂ imagos, slide preparations: genitalia, wings and legs (HMJ 181A), genitalia and wings (HMJ 181A), Table Mt. slopes, Window Stream 18-II-2012, 14-XII-2012, AMGS. 2 ♂ nymphs, slide preparations: gills (HMJ 118A) and mouthparts (HMJ 118A), Table Mt. slopes, Skeleton Ravine, 29-X-2012, AMGS.

FIGURE 2. Paralectotypes of *Lestagella penicillata*. (a) Lateral view of adult female; (b) lateral view of adult male. Dorsal views of (c) female nymph and (d) male nymph, arrow showing foreleg regeneration where one foreleg is noticeably smaller than the other and without various types of setae. (e) Ventral view of male nymph. Scale bars = 1 mm.

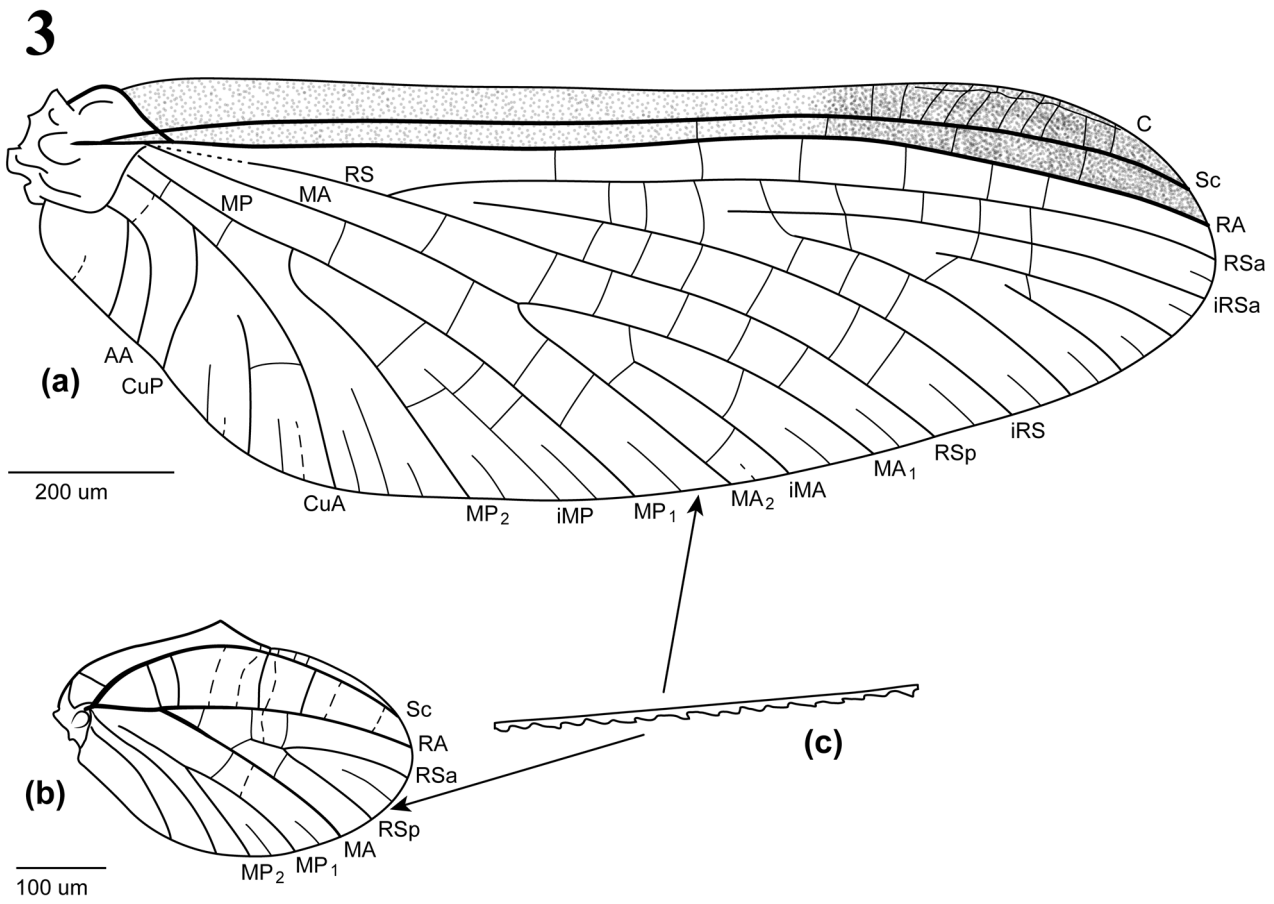

FIGURE 3. Lectotype male imago of *Lestagella penicillata*. (a) Forewing with dotted line showing basally faint RS vein, dashed lines show variations in intercalaries seen in other specimens, intercalaries always absent between RA and RSa; (b) hindwing ovoid in shape with costal elevation and slight medial depression as depicted, variations in venation are shown as dashed lines; (c) Ventral margins of both fore- and hindwings showing jagged edge possibly as a result of shedding of subimaginal falcate microtrichia.

Male Imago (Lectotype and paralectotypes). *Head* (Fig. 2b). Antennae length half the width of the head capsule; dorsal portion of compound eyes large, reddish-brown and spherical; compound eyes only slightly separated dorsally (Fig. 2b).

Thorax. Forewings (Fig. 3a) narrow with distinct pterostigma present with 8–10 crossveins, variations in intercalaries denoted by dashed lines. RS basally faint. Marginal intercalaries present, sometimes paired, but not present between RA and RSa. Hindwings (Fig. 3b) ovoid with costal elevation and slight medial depression in costal margin. Ventral margins of both fore- and hindwings jagged, possibly as a result of shedding of subimaginal falcate microtrichia.

Forelegs (Fig. 4a–d) with tibiae just over twice the length of femora and slightly longer than tarsi, segments I and II of tarsi subequal, segment III half-length of segment II and segment IV is ca. one third length of segment III. Femora with subtriangular, scale-like projections and few scattered setae (Fig. 4b). Tibiae and tarsi with smaller scale-like protrusions and scattered setae (Fig. 4c). Claws modified into two pad-like lobes with flat scale-like dorsal surface and smooth, slightly grooved ventral surface (Fig. 4d). Mid- and hindlegs (Fig. 4e) with tibiae ca. 0.8 times femora length, few setae scattered on tibia becoming slightly more frequent nearer the tarsi (Fig. 4f). Tarsi one third the length of tibiae, tarsal segments I–III subequal in length with many short simple setae, segment IV twice the length of segment III. Distal end of tibia and tarsal segments I–III with distinct spike on ventral surface (Fig. 4g). Claws with one pad-like lobe and one hook, dorsal surface with flat scales as in foreleg.

Abdomen with gill socket vestiges present on segments II - IV. Male abdomen ca. two thirds thickness of female abdomen. Male genitalia (lectotype (Fig. 5a–c)), genital forceps three-segmented, segment I more broad than other segments and ca. two-thirds the length of segment II (Fig. 5a). Segment III reduced, bending inwardly,

nearly forming a right angle, inner lateral margin of genital forceps with ovoid scale-like processes on all three segments (Fig. 5a). The ventral, dorsal and outer margin surfaces of segment I and II covered with few simple setae scattered and small subtriangular scales (Fig. 5b) while the third segment has many larger, slightly more elongate subtriangular scale-like processes (Fig. 5c). Penis lobes elongated but shorter than genital forceps, fused with a small medial notch or indentation, slightly broadened distally, longitudinal groove vestigial. Styliger plate distinctly convex. Three caudal filaments ca. subequal in length and one third longer than body length, few setae scattered all over caudal filament surface.

Female Imago. *Head* (Fig. 2a). Antennae as in male; without dorsal portion of compound eye, compound eyes relatively small and laterally situated.

Thorax. Forewings as in male; fore-, mid- and hindlegs similar in structure to mid- and hindlegs of male.

Abdomen with gill socket vestiges present. Caudal filaments as in male.

Nymph. Colouration of immature nymphs pale, straw-coloured and slightly darker as nymphs mature with darker abdominal markings (Fig. 2c–d). Body dorso-ventrally flattened.

Head with well-developed marginal fringe of setae extending to lateral margin of head with setae longer anteriorly and shorter laterally (Fig. 2 c–d). Male nymphs show developing dorsal compound eyes (Fig. 2d).

Labrum (Fig. 6) width 3 times length. Lateral margins rounded, anterior with slight emargination. Basal margin with elongated, squared notch medially. One third of apico-dorsal margin with densely clustered, feathered setae; similar feathered setae scattered along lateral margin (Fig. 6a). Dorso-medial transverse row of setae 3–4 times larger than apico-dorsal setae and not feathery and possible remnant setal bases situated towards dorso-basal margin (Fig. 6b). Dorso-lateral margin with single cluster of setae 1.5 times length of dorso-medial transverse setae (Fig. 6c).

Hypopharynx (Fig. 7), lingua and superlinguae of similar size, both rounded apically, narrowing towards the base. Lingua with variable distomedial notch, ranging from deep indentation to none (Fig. 7d). Dorsal surface with tuft of fine setae antero-laterally; very short brush setae covering dorsal to ventral anterior surface and a small cluster of larger setae postero-laterally (Fig. 7e). Superlinguae with long, feathery setae on outer antero-lateral margin (Fig. 7f) becoming shorter and non-feathery on outer lateral margin closest to base. Small, short setae sparsely covering inner antero-lateral surface extending from antero-dorsal to inner latero-ventral surface, covering two thirds toward base.

Labium (Fig. 8) with partly divided glossae and paraglossae. Paraglossae slightly falciform, larger than glossae which are rounded apically. Apical surfaces of glossae and paraglossae with short-feathered setae (Fig. 8g). Lateral outer surface of paraglossae with long, thin-feathered setae 2 times the length of apical setae (Fig. 8h). Dorsal surface of paraglossae and glossae with short, scattered setae and 2 rows of longer setae situated obliquely from paraglossal base towards base of glossae (Fig. 8i). Labial palps three-segmented, segment I as long as segment II and III combined. Articulation between segment II and III distinct. Segment II narrows slightly distally, segment III small with slight medial constriction and tapered distally. Lateral surfaces of segment II and III with scattered setae. Prementum and postmentum as seen in Fig. 8; postmentum covered with sparsely scattered simple setae and disc-shaped sensory pits or setal bases.

Mandibles (Fig. 9–11) elongate, length almost 4 times width. Few long socketed-setae (< 10) from middle of outer lateral margin towards the base. Incisors single, prominent, with small tuft of very fine setae on outer edge of incisor near distal end (Fig. 10–11a). Ventral surface of mandibles (Fig. 9) with many disc-shaped sensory pits or setal bases, medio-transverse groove with small triangular scales or sclerotized projections (Fig. 9b). Left mandible (Fig. 10) with prostheca close to incisor, well-developed into long sclerotized setae with the longest seta feathered or brush-like (Fig. 10c). Molar region prominent with 2–3 long thin setae below mola. Right mandible (Fig. 11) with prostheca well-developed, with branched sclerotized setae, with a single feathery or brush-like seta protruding out towards the mola (Fig. 11d); molar region with 3 sclerotized seta-like projections distally (Fig. 11e) and an elongated, thumb-like proximal ridge (Fig. 11f); row of setae (< 10) below mola.

Maxillae (Fig. 12–13) uniform with maxillary palp absent. Canines fused into a single elongate canine, with a depression along inner margin containing a single seta (Fig. 12g). Cluster of long, thin setae at base of canine on outer face. Apex of galea-lacinia with two dentisetae (Fig. 12h, 13h) and 6–7 long socketed setae. Proximal dentiseta slightly serrated on the inner margin. One large seta present on inner dorso-lateral surface below galea-lacinia apex and 5 thin simple setae on inner lateral surface below large single seta as seen in Fig. 12. A few large and thin, simple setae present on lower, outer lateral margin.

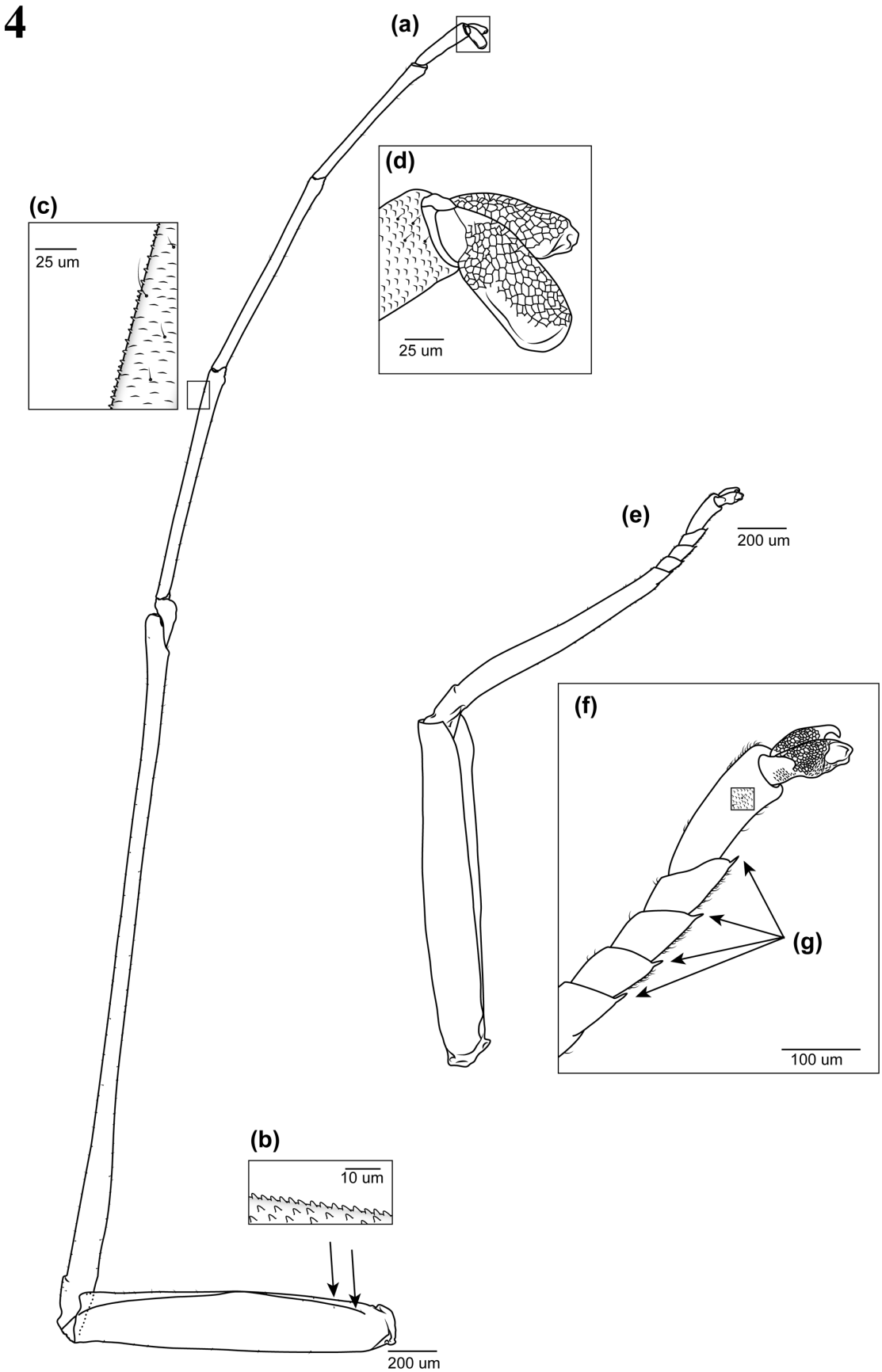

FIGURE 4. Paralectotype male imago of *Lestagella penicillata*. (a) Foreleg showing details of (b) femora; (c) tarsus and (d) tarsal claw. (e) Hindleg showing (f) details of the tarsi and claw and (g) spine-like processes of tarsi (female imago fore-, mid- and hindlegs similar to male hindleg).

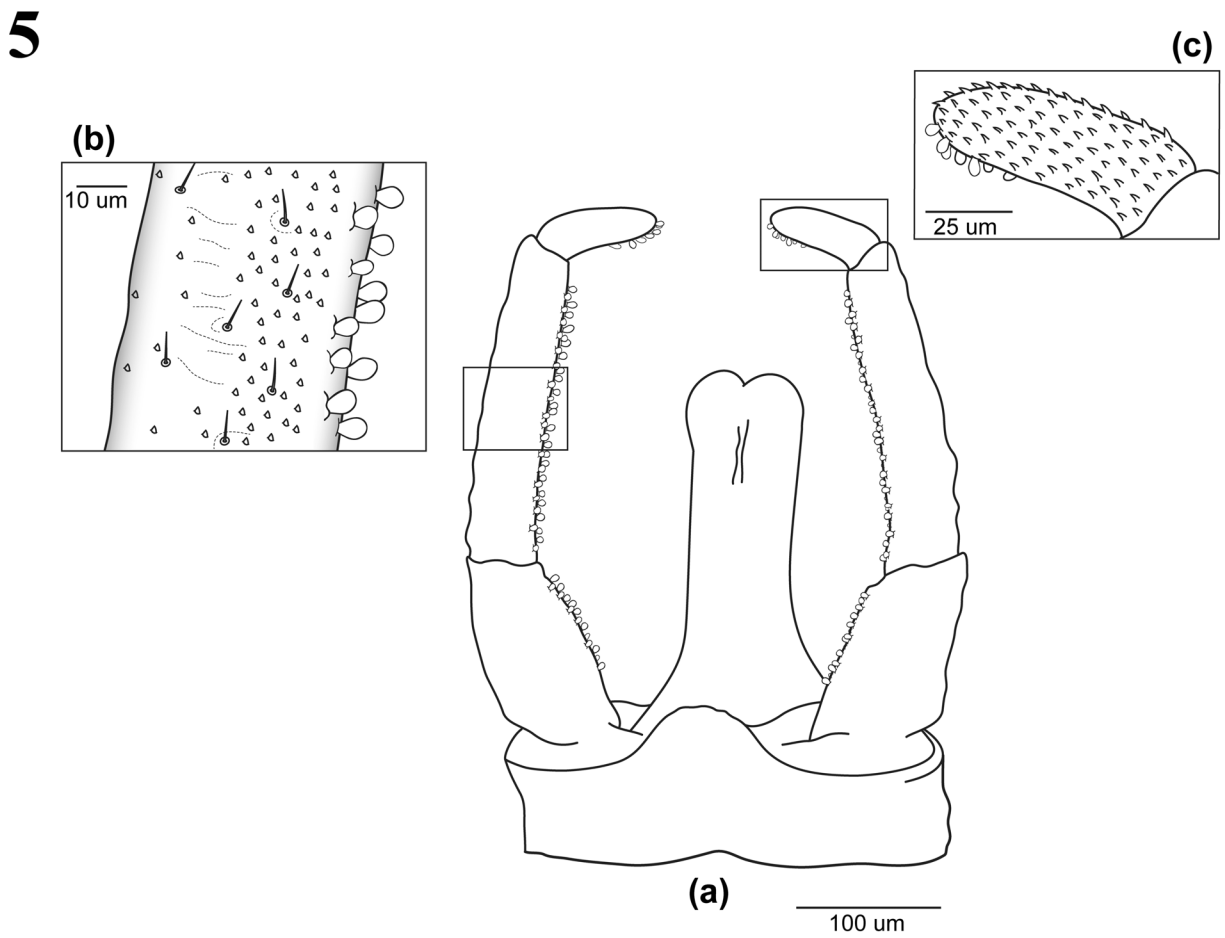

FIGURE 5. Lectotype male (a) genitalia of *Lestagella penicillata* showing details of genital forceps (b) segment II and (c) segment III.

Thorax. Outer edges of prothorax lined with spatulate setae similar to spatulate setae shown in Figure 14a on forefemur. Foreleg (Fig. 14), femur subequal to tibia in length, medially broadened, narrowing toward distal and proximal ends. Medio-transverse spatulate setae (Fig. 14a) present along transverse ridge on dorsal surface of forefemur; size of medial gap between transverse ridges of spatulate setae variable (Fig. 14b). This ridge extends distally along the postero-lateral margin where the setae become longer (over 3 times length of spatulate setae). Short spatulate and lanceolate setae are present along antero-lateral margin with few long setae scattered near proximal base. Dorsal surface of tibia with single row of long, perpendicular setae, lateral margins interspersed with small, simple setae. Tarsus ca. half the length of tibia, entire surface interspersed with small, simple setae. Tarsal claw (Fig. 14c) elongate with a single row of 4–6 variably sized smaller denticles followed by one large apical tooth. A single row of 4 small, subapical setae present apicolaterally on each side of claw. Ventral base of tarsal claw with small sparsely scattered setae. Mid- and hindlegs as seen in Fig. 2c–e, femora slightly more elongate and without transverse ridge of stout setae, antero-lateral margins with long setae and postero-lateral margins with spatulate or stout setae. Tibia, tarsi and claws similar to foreleg.

Abdomen with many fine setae covering the ventral surface, becoming more hirsute closer to the lateral margins. Abdominal segments with series of dark spots dorso-laterally, largest occurring on segment II (Fig. 2c–d). Postero-lateral processes subtriangular, moderately developed and slightly separated from base of following segment, processes with single row of long setae. Filamentous gill I (Fig. 15a) present on abdominal segment I; three-segmented with long, thin, fine setae scattered around segment III. Lamellate gills present on segments II to IV. Gill II (Fig. 15b) fully operculate, upper lamella ovoid with thin setae present starting ca. two thirds from base, setae longer anteriorly and shorter laterally; lower lamella bifid and highly lobed. Gill III (Fig. 15c) upper lamella more circular in shape with thin setae present starting ca. three quarters from base, setae longer anteriorly and shorter laterally, lower lamella not bifid, singular and highly lobed. Gill IV (Fig. 15d) almost semicircular, lower lamella absent, thin setae present along lateral margin to apex, setae longer anteriorly and shorter laterally. All three

caudal filaments banded at base, sparsely setose with setae becoming slightly longer distally, medial caudal filament well-developed, cerci ca. two thirds length of body.

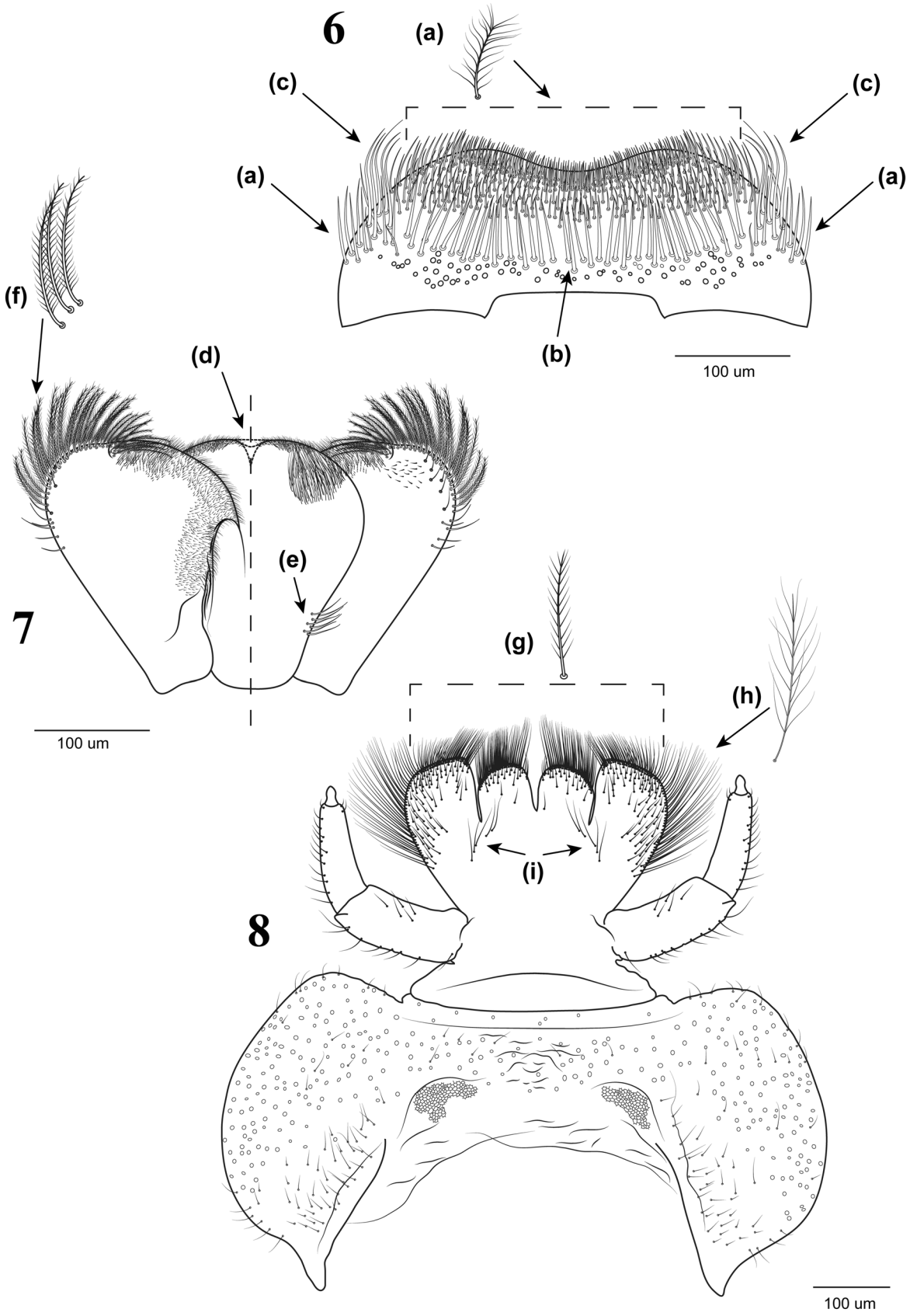

FIGURE 6–8. Paralectotype nymph of *Lestagella penicillata*. Fig. 6. Labrum showing (a) feathered setae; (b) remnant setal bases; (c) long, smooth setae (not feathered); Fig. 7. Hypopharynx, dorsal view (right) and ventral view (left); Fig. 8. Labium.

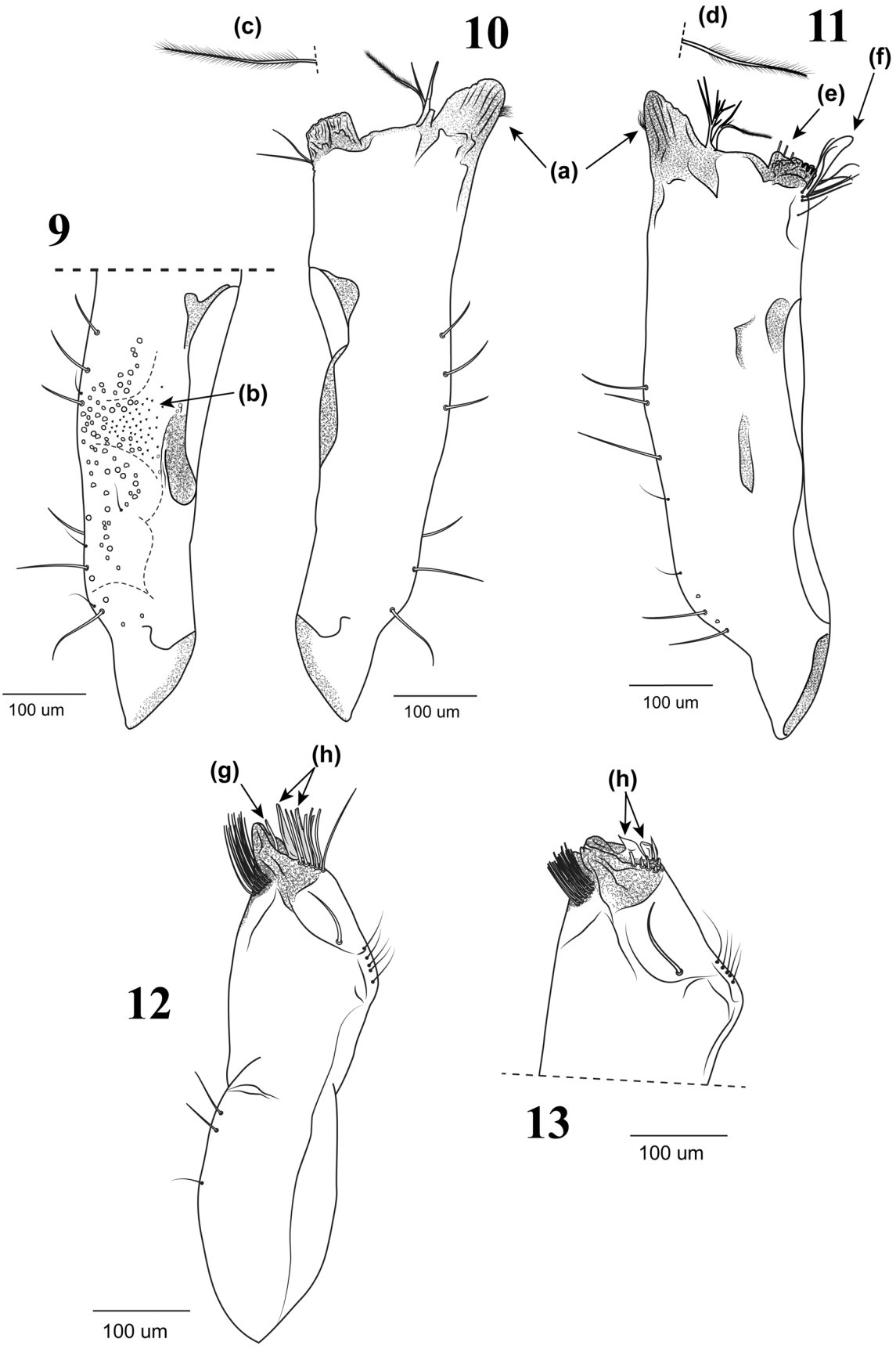

FIGURE 9–13. Paralectotype nymph of *Lestagella penicillata*. Fig. 9. Ventral surface of mandibles; Fig. 10. Left mandible; Fig. 11. Right mandible; Fig. 12. Right maxilla; Fig. 13. Worn maxilla from a mature nymph.

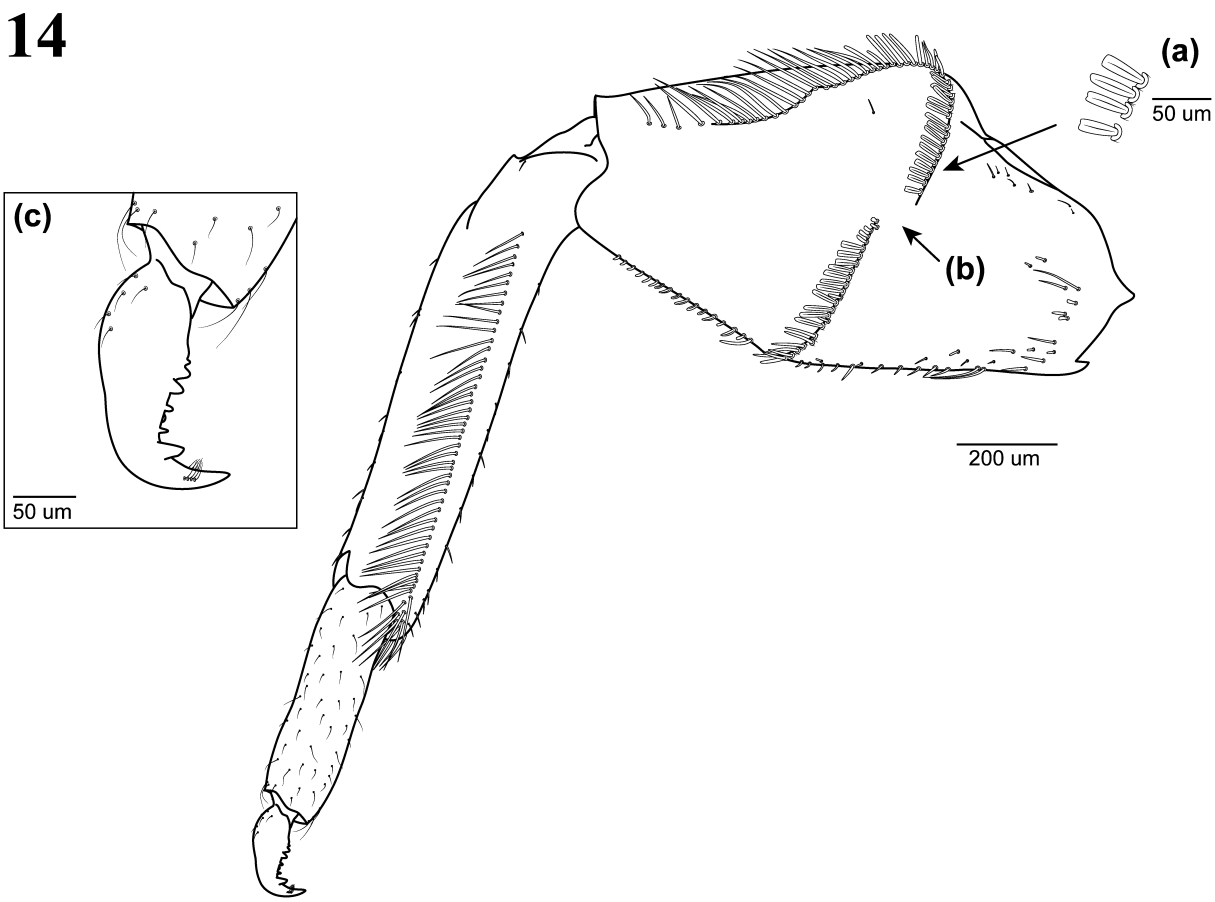

FIGURE 14. Paralectotype nymph foreleg of *Lestagella penicillata* showing (a) spatulate setae; (b) variable medio-transverse gap on femur; (c) tarsal claw showing denticles and subapical setae.

Discussion

L. penicillata shows a high degree of variability in the lingual medial notch of the hypopharynx (Fig. 7), other factors such as wear-and-tear of mouthparts (Fig. 16), regeneration of limbs (Fig. 2d, arrowed) and different moulting stages can affect the interpretation of morphological characters and identification of the species. However, the imago stage is less variable than the nymphal stage and differences have been seen in the adult stages of potential new and undescribed species of *Lestagella*. Edmunds (1959) attributed the differences in distinctiveness between life stages to different rates of evolution between the nymphs and short-lived adults and emphasised the importance of knowing the adult and nymphal stages when recognising genera and species groups (Edmunds 1962).

McCafferty & Wang (1997) stated that the presence of a medial notch on the lingua of the hypopharynx was diagnostic of the genus. However, in the material examined for the species *L. penicillata* alone the hypopharynx was found to be variable and not a suitable character for generic or species diagnosis.

Demoulin (1970) and McCafferty & Wang (1997) both described the mandibles of *L. penicillata* as being atrophied. The use of the term "atrophy" in both studies is ambiguous and unclear. Demoulin (1970) noted that the nymphal mandibular and maxillary canines underwent "progressive atrophy" with age. McCafferty & Wang (1997) suggested that the mandibles are apically atrophied while the maxillae have modified apices, which could refer to either the dentition being reduced, or the thickness and width of the mandibles. In this particular case, it is assumed that McCafferty & Wang (1997) were referring to the reduction in dentition, as the width of the mandibles were already mentioned as being narrow, and both left and right mandibles clearly show worn-down dentition in the illustrations.

Demoulin (1970) examined two nymphs at a younger and older stage, and it is by chance that the younger nymph had moulted more recently than the older nymph, therefore having less worn-down mandibular and maxillary canines, thus making it appear that there is a process of "progressive atrophy" in these mouthparts. It is therefore important to ensure that freshly moulted specimens are used for slide mounting when used for identification purposes, as stressed in other taxonomic studies (e.g. Kluge 2004, Sartori *et al.* 2008).

By the aforementioned definition of atrophy in the introduction section, neither of these reported "atrophies" are true for *Lestagella*; this "atrophy" is due to wear-and-tear and is seen and well-documented in various other groups [Baetidae (Muller-Liebenau 1973); Ephemeroidea (Elpers 1997); and other stream animals such as Plecoptera, Coleoptera, Diptera, an isopod and snail (Arens 1990)]. When the *Lestagella* nymph approaches the next moult, the mouthparts are well worn down (appearing atrophied), but the new mouthparts are evident (Fig. 16). As McCafferty & Wang (1997) only described the ultimate nymphal stage, it is most likely that the nymphal mouthparts were worn down and they would not be replaced due to final nymphal moult to the subimaginal stage.

Figure 16(a–f) shows the mouthparts of a *L. penicillata* nymph approaching the next moult. New, well-developed incisors and molars are evident in the left and right mandibles (Fig. 16a and b respectively, arrowed), which appear to be initially distinctly separated; new setae and molar projections are arrowed. The maxilla (Fig. 16c) regrowth shows a very well-developed, fused incisor and the dentisetae and other setae are clearly visible (see arrows). Newly developed mouthparts can also be seen for the hypopharynx, labium and labrum as seen in Figure 16(d–f) respectively.

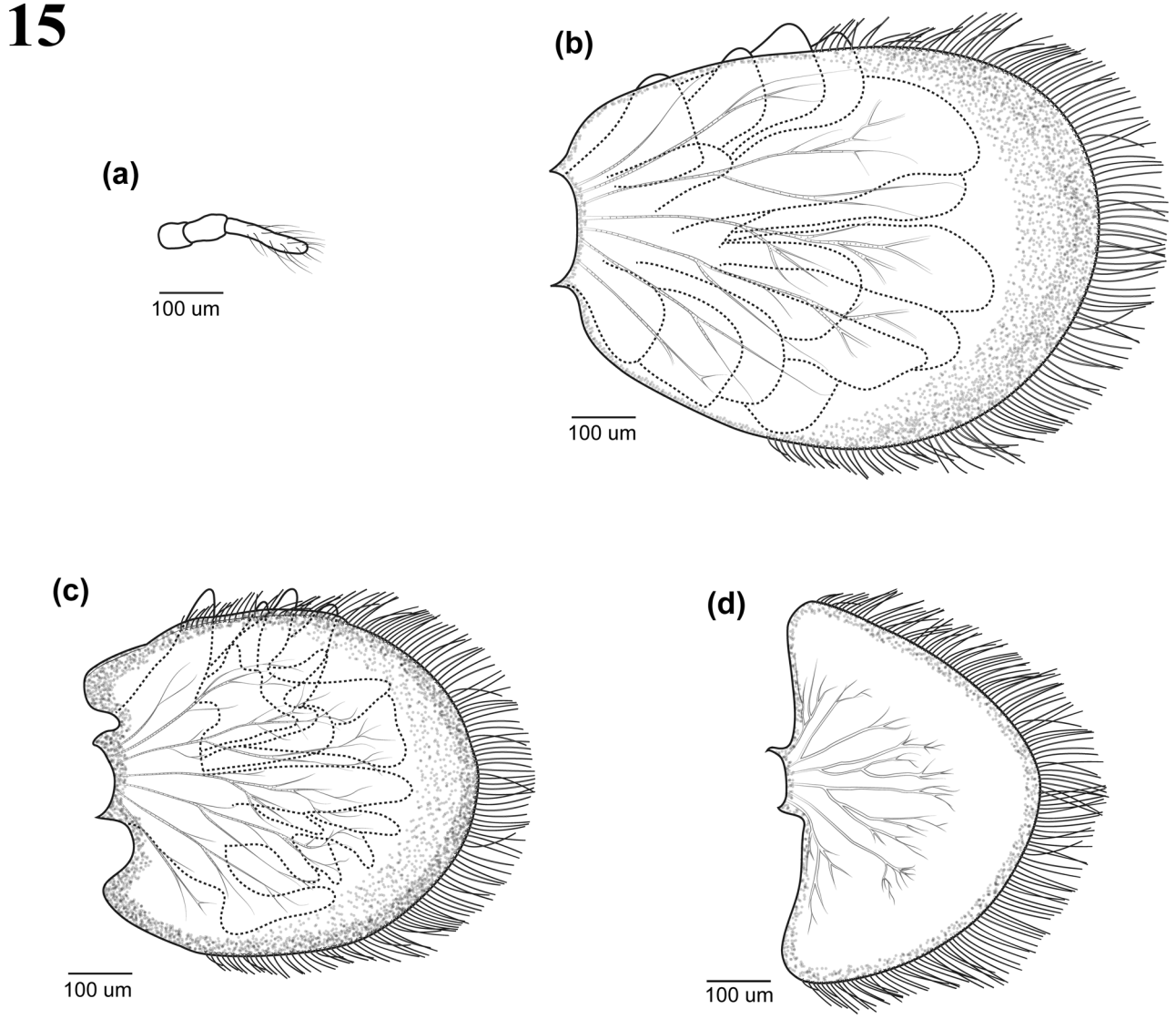

FIGURE 15. Paralectotype nymph gills of *Lestagella penicillata*. (a) Filamentous first gill I on abdominal segment I; (b) operculate lamellate gill II found on abdominal segment II; (c) lamellate gill III; (d) lamellate gill IV.

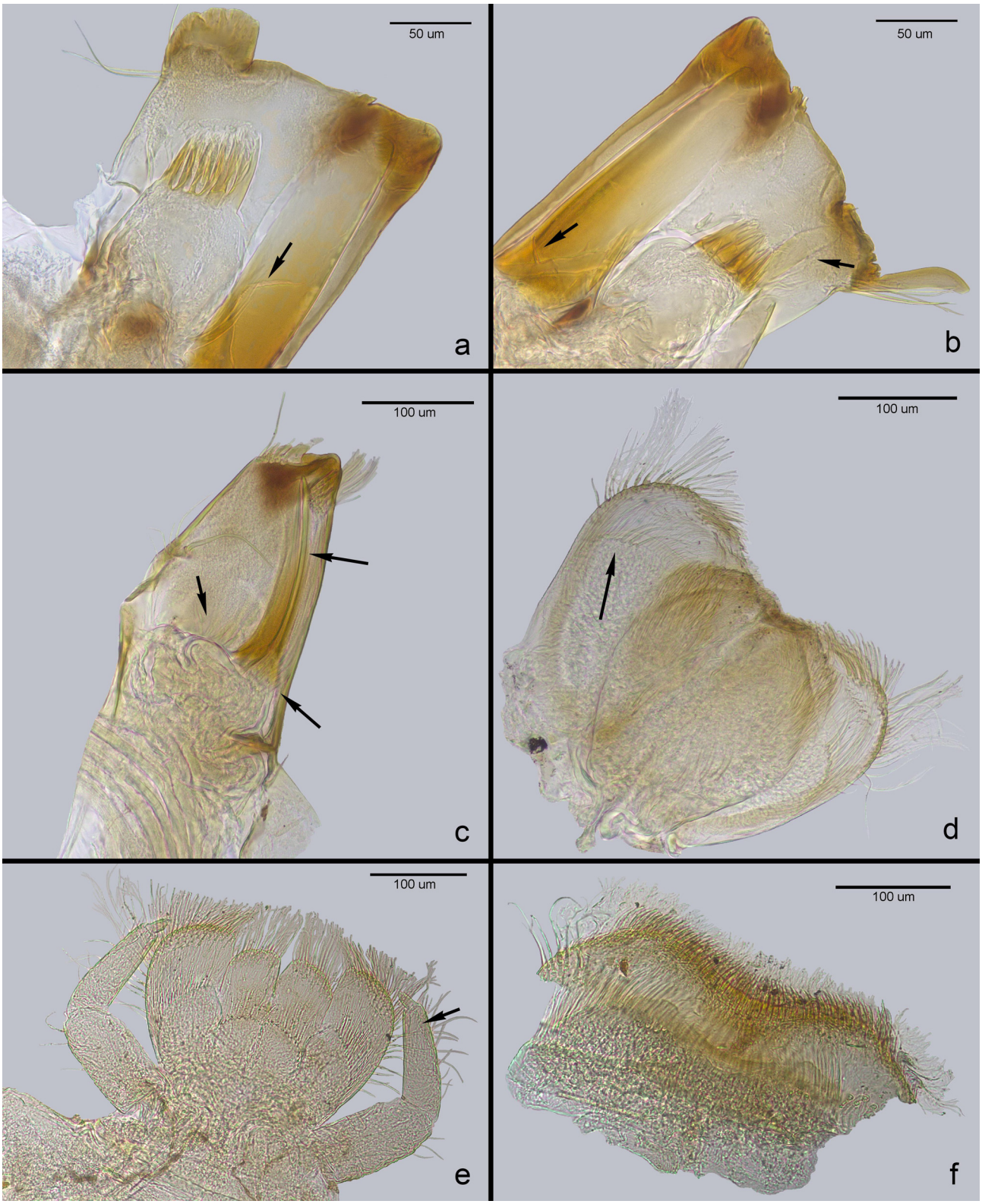

FIGURE 16. Regrowth of mouthparts of *Lestagella penicillata*. (a) Left mandible; (b) right mandible; (c) maxilla; (d) hypopharynx; (f) labium and (f) labrum.

Concluding remarks

This comprehensive account of *Lestagella penicillata*, including descriptions of all life stages, and the importance of choosing freshly moulted penultimate nymphs with unworn mouthparts for species diagnosis, sets a benchmark for all further studies of not only new species of *Lestagella*, but of all Afrotropical Teloganodidae.

Acknowledgements

Many thanks go to Vere Ross-Gillespie for accompanying us on field trips to the lectotype locality, Carolyn Bruton for accommodating us during field work for this paper. Grateful thanks to Jocelyn, Julian and James Pereira da Conceicoa for providing transport, accommodation and assistance in the field. Thanks too to Luke Jacobus and Michel Sartori for constructive criticism of the manuscript. The National Research Foundation (NRF) of South Africa (Grant: 78791) and Rhodes University Research Council Grant 31170 for the financial support which enabled this research. LLPdC gratefully acknowledges a NRF Innovations Scholarship and an Ernst and Ethel Eriksen Trust bursary. The Department of Sport Recreation, Arts and Culture, South Africa, is acknowledged for supporting the Albany Museum, where this research was carried out. Any opinion, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Research Foundation or the Ernst and Ethel Eriksen Trust. Material collected under permit Nr. AAA007-00382-0035.

References

Allen, R.K. & Edmunds, G.F. (1963) New and little known Ephemerellidae from southern Asia , Africa and Madagascar (Ephemeroptera). *Pacific Insects*, 5, 11–22.

Arens, W. (1990) Wear and tear of mouthparts: a critical problem in stream animals feeding on epilithic algae. *Canadian Journal of Zoology*, 68, 1896–1914.
http://dx.doi.org/10.1139/z90-269

Barnard, K.H. (1932) South African may-flies (Ephemeroptera). *Transactions of the Royal Society of South Africa*, 20, 201–259.
http://dx.doi.org/10.1080/00359193209518858

Barnard, K.H. (1940) Additional records, and descriptions of new species, of South African alder-flies (Megaloptera), may-flies (Ephemeroptera), caddisflies (Trichoptera), stone-flies (Perlaria), and dragon-flies (Odonata). *Annals of the South African Museum*, 32, 609–661.

Demoulin, G. (1970) Ephemeroptera: des faunes ethiopienne et malgache. *South African Animal Life*, 14, 24–170.

Edmunds, G.F. (1959) Subgeneric groups within the mayfly genus Ephemerella (Ephemeroptera: Ephemerellidae). *Annals of the Entomological Society of America*, 52, 543–547.

Edmunds, G.F. (1962) The principles applied in determining the hierarchic level of the higher categories of Ephemeroptera. *Systematic Zoology*, 11, 22–31.
http://dx.doi.org/10.2307/2411446

Elpers, C. (1997) Comparative morphology of the mandibles of seven genera of Ephemeroidea (Ephemeroptera). *In*: Landolt, P. & Sartori, M. (Eds.), *Ephemeroptera & Plecoptera: Biology-Ecology-Systematics*. Mauron + Tinguely & Lachat, Fribourg, pp. 311–316.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Harrison, A.D. & Agnew, J.D. (1962) The distribution of invertebrates endemic to acid streams in the western and southern Cape Province. *Annals of the Cape Provincial Museums*, 2, 273–291.

Jacobus, L.M. & McCafferty, W.P. (2006) Reevaluation of the phylogeny of the Ephemereoptera Infraorder Pannota (Furcatergalia), with adjustments to higher classification. *Transactions of the American Entomological Society*, 132, 81–90.

Kluge, N.J. (2004) *The Phylogenetic System of Ephemeroptera*. Kluwer Academic Publishers, Dordrecht/ Boston/ London, 456 pp.

Lestage, J.A. (1924) Les Ephémères de l'Afrique du Sud. Catalogue critique & systématique des espèces connues et description de trois genres nouveaux et de sept espèces nouvelles. *Revue Zoologique Africaine*, 12, 316–352.

McCafferty, W.P. & Edmunds, G.F. (1979) The higher classification of the Ephemeroptera and its evolutionary basis. *Annals of the Entomological Society of America*, 72, 5–12.
McCafferty, W.P. & Wang, T.Q. (1997) Phylogenetic systematics of the family Teloganodidae (Ephemeroptera: Pannota). *Annals of the Cape Provincial Museums*, 19, 387–437.
McCaffetry, W.P. & Wang, T.Q. (1998) New name for a generic homonym in Teloganodidae (Ephemeroptera). *Entomological News*, 109, 344.
McCafferty, W.P. & Wang, T.Q. (2000) Phylogenetic systematics of the major lineages of pannote mayflies (Ephemeroptera: Pannota). *Transactions of the American Entomological Society*, 126, 9–101.
McCafferty, W.P. & Benstead, J.P. (2002) Cladistic resolution and ecology of the Madagascar genus *Manohyphella* Allen (Ephemeroptera: Teloganodidae). *Annales de Limnologie*, 38, 41–52.
http://dx.doi.org/10.1051/limn/2002005
Müller-Liebenau, I. (1973) Morphological characters used in revising the European species of the genus Baetis Leach. *In*: Peters, W.L. & Peters, J.G. (Eds.), *Proceedings of the First International Conference on Ephemeroptera*. E. J. Brill, Leiden, pp. 182–198.
Sartori, M., Peters, J.G. & Hubbard, M.D. (2008) A revision of Oriental Teloganodidae (Insecta, Ephemeroptera, Ephemerelloidea). *Zootaxa*, 51, 1–51.