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Descriptions of bamboo-inhabiting larvae and puparia of Oriental soldier flies *Ptecticus brunettii* and *P. flavifemoratus* (Diptera: Stratiomyidae: Sarginae) with observations on their biology

RUDOLF ROZKOŠNÝ and DAMIR KOVAC

Department of Zoology and Ecology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic; e-mail: rozk@sci.muni.cz

Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; e-mail: dkovac@sng.uni-frankfurt.de

Stratiomyidae, Sarginae, *Ptecticus*, larvae, puparia, mouth parts, developmental cycle, territoriality, spatial segregation, diapause, plastron, bamboo, phytotelmata, Malaysia

Abstract. The first detailed description of larvae of *Ptecticus* Loew is presented for *P. brunettii* and *P. flavifemoratus* from West Malaysia. There are pronounced morphological and behavioural differences between the last larval instar, inside whose cast cuticle the pupa remains, and earlier instars. The larval mouthparts are similar to those of other known Stratiomyidae larvae but may display a set of autapomorphic characters. The structure of the mandibular-maxillary complex suggests that larvae of *Ptecticus* are micropantophagous scavengers that feed chiefly upon microorganisms. The larvae of both species are associated with decaying bamboo shoots; *P. brunettii* inhabits the space between the culm sheaths and *P. flavifemoratus* lives in water-filled shoot stumps. This is the first record of aquatic Sarginae larvae and egg plastron in the Stratiomyidae. The life cycle and behaviour of *P. brunettii* and *P. flavifemoratus* is described and the resource partitioning of stratiomyids and xylomyids associated with bamboo is discussed.

INTRODUCTION

Stratiomyidae and Xylomyidae are the only families among the lower Brachycera (Orthorrapha) in which the pupae are formed within the hardened skin of the last larval instar (overview see McFadden, 1967; Rozkošný, 1982; Smith, 1989). In most subfamilies of the Stratiomyidae, the last larval instar does not differ substantially from the penultimate instar and is fully able to move about and feed. The puparial period can only be detected by the loss of locomotory ability (subfamily Stratiomyinae), and the presence of inconspicuous, short, rod-like, dorsolateral pupal respiratory horns on abdominal segments 1–6 (Beridinae, Pachygasterinae) or 2–5 (Clitellariinae). Puparia of some Clitellarinae (*Oxycera*) are characterized by elongated, laterally projecting anterior spiracles.

However, in the Sarginae and Hermetiinae, the puparial period can occupy virtually the whole ultimate larval instar and the penultimate and ultimate instars often differ remarkably (McFadden, 1967; Rozkošný, 1982). Larvae of the penultimate instar possess a well-developed mandibular-maxillary complex, while in the last larval instar the head is unusually flat and the mouthparts are degenerate and apparently non-functional.

The immature stages of *P. brunettii* and *P. flavifemoratus* described herein were found during an ongoing study of insects associated with bamboo in Peninsular Malaysia (Kovac & Azarae, 1994; Kovac & Streit, 1996). The 15 species of Stratiomyidae and Xylomyidae that have been found inhabiting bamboo belong to the genera *Microchrysa* (in prep.), *Ptecticus* (Kovac & Rozkošný, 1995; Rozkošný & Kovac, 1994a, 1996a, 1997), *Odontomyia* (Rozkošný & Kovac, 1994b), *Camptopteromyia* (Rozkošný & Kovac, 1991), *Pachygaster* (in prep.) and *Solva* (Xylomyidae; Rozkošný & Kovac, 1996b). Of these genera, *Ptecticus* showed particularly high diversity, with five species occurring regularly in bamboo shoots. In order to first gain an understanding of resource partitioning among this diverse group of shoot-inhabiting stratiomyids and xylomyids we collected as much information regarding habitat and general biological data as possible.

MATERIAL AND METHODS

The study was conducted in West Malaysia during the bamboo sprouting season (c. August through November) during 1993–1995. The study site was located at the Ulu Gombak Field Studies Centre (University of Malaya) which is situated on the western slopes of the Main Range (altitude c. 250 m, see also Kovac & Streit, 1996). Stratiomyid larvae were reared on indigenous bamboo species *Gigantochloa scortechinii* Gamble. This is the dominant bamboo species that occurs within the Main Range (height: 16–20 m, diameter of basal internodes: 8–10 cm).

Larvae were collected from shoots that were damaged by animals, falling tree branches or bamboo shoot collectors. Later in the study, when the habitat requirements of the larvae were known, larval habitats were created artificially. To promote colonization by *P. flavifemoratus* and its aquatic larvae, young shoots, 30–40 cm high, were broken or cut in such a way that an above ground cavity was formed that would accumulate water (Fig. 36).

Larvae of *P. brunettii* develop between the culm sheaths of apical 1–1.5 m of the shoot where the internodes are still short and completely covered by several layers of sheaths. To attract *Ptecticus brunettii*, the apical part of shoots c. 2 m high were cut off and left lying on the ground. Then, several additional cuts were made through the culm sheaths to attract the flies faster and to create additional oviposition opportunities for *P. brunettii*, since the eggs of this species are inserted between the culm sheaths.

After cutting or breaking the shoots, females of both *Ptecticus* spp. were observed flying to the shoots and ovipositing. Some of the eggs were moved to the laboratory for rearing and the others remained at the field site, at least initially. After 2–3 weeks, older larvae were collected from the same field sites and reared to the adult stage along with the laboratory-hatched larvae.

RESULTS

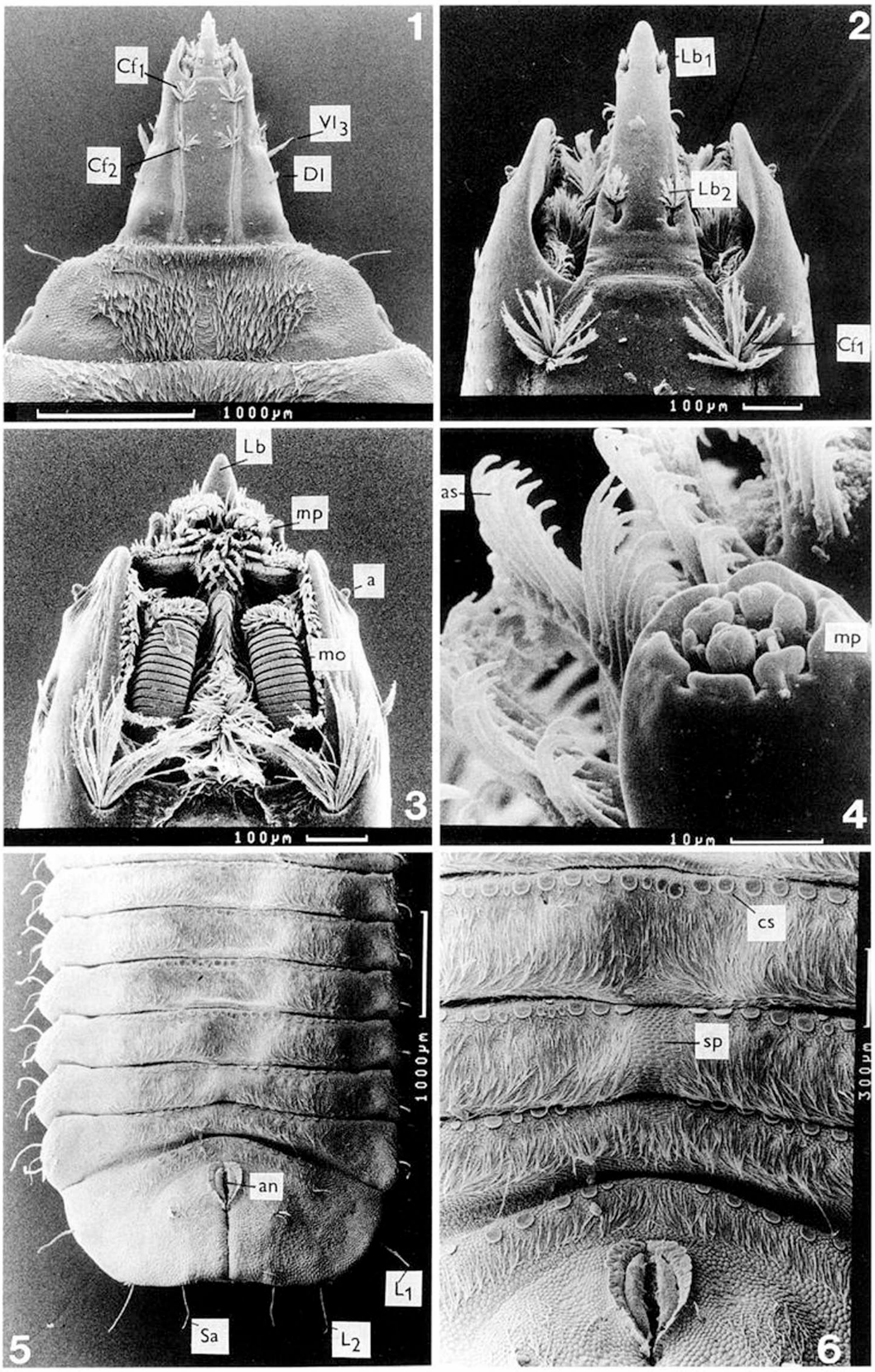
Descriptions of larvae and puparia

Ptecticus brunettii Rozkošný & Kovac, 1996
(Figs 1–12; 25–28)

Larva (of penultimate instar)

SHAPE AND COLOUR. Elongate oval, flattened dorsoventrally, head prominent anteriorly (Fig. 1) and anal segment rounded posteriorly (Fig. 5). Pale brown; head somewhat darkened in anterior half; body surface predominantly mat but head shining. Integument with fine honeycomb reticulation. More or less distinct ornamentation consisting of darker and larger cuticular plates scattered in transverse oval sublateral depressions of abdominal

Figs 1–6. *Ptecticus brunettii*, larva (penultimate instar). 1 – head and first thoracic segment, dorsal view; 2 – apical one-third of head, dorsal view; 3 – apical one-third of head, ventral view; 4 – right maxillary palpus and apical maxillary setae; 5 – abdominal segments, ventral view; 6 – middle part of abdominal segments 5–8, ventral view. a – antenna, an – anal slit, as – apical maxillary setae, Cf – clypeofrontal setae, cs – cuticular scales, Dl – dorsolateral seta, L – lateral setae, Lb – labrum, mo – molar area, mp – maxillary palpus, Sa – subapical seta, sp – sternal patch, Vl – ventrolateral seta.


1
Cf_1
Vl_3
Cf_2
Dl
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2
Lb_1
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mo
3
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4
10µm
1000µm
an
L_1
Sa
L_2
5
cs
sp
300µm
6

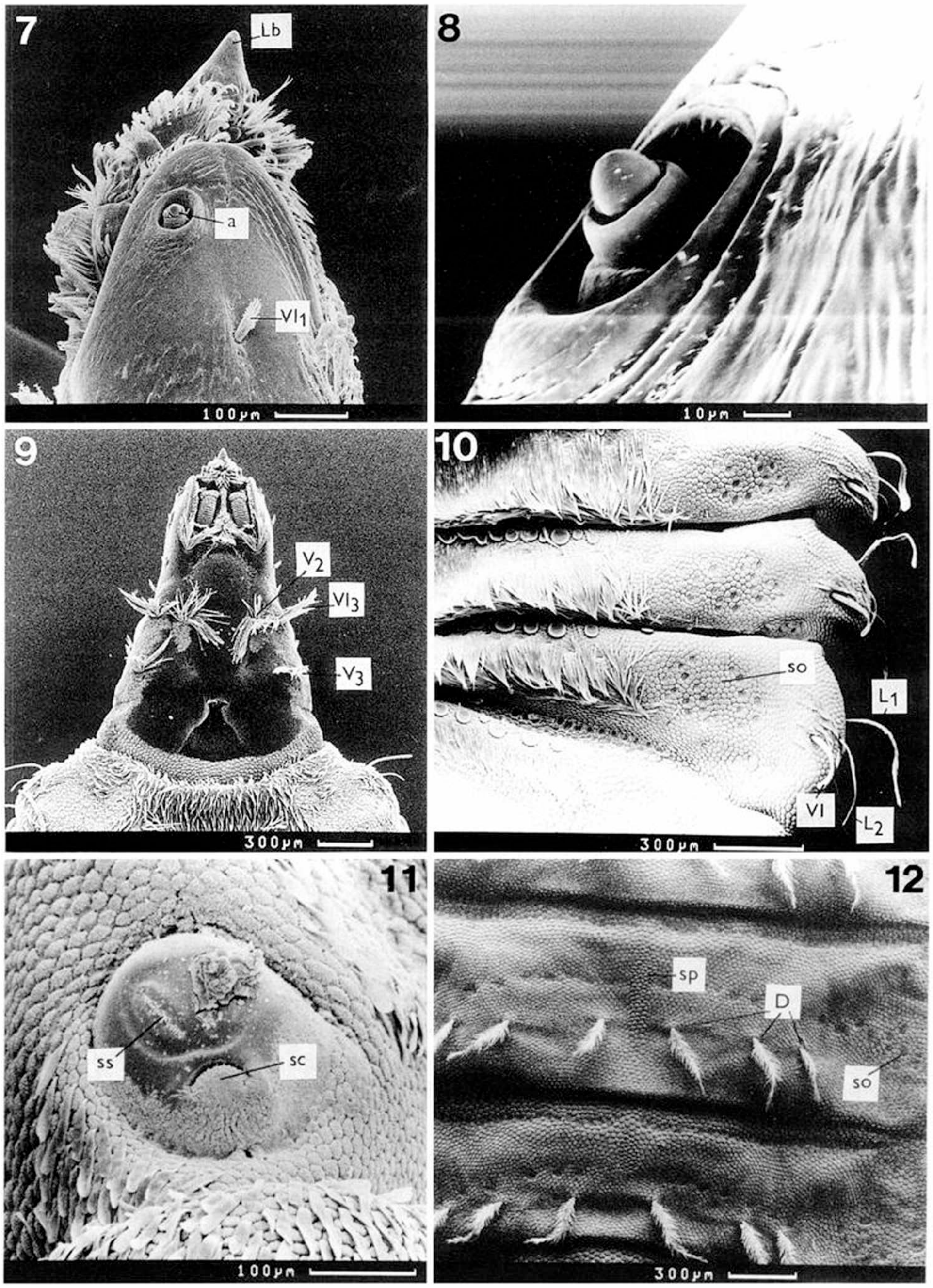
segments (Fig. 10) and several symmetrical areas on both sides of anal segment. Some transverse oval cuticular plates also visible in central part of mid-line between sublateral depression and middle of each segment. Dense rows of flat and rounded scales distinct along anterior margin of abdominal segments dorsally and ventrally.

HEAD. Antennae small, placed subapically in anterolateral corners of head capsule, two-segmented, apical segment rounded (Figs 7–8). Labrum oriented anteriorly, pointed, much longer than genal lobes (Figs 1–2). Eyes barely prominent, somewhat paler than surrounding areas. Ventral labrum ventrally with cascade of symmetrical hair tufts. Each mandibular-maxillary complex with apical set of fans consisting of dense, distally-bent setae (Fig. 3). Maxillary palpus cylindrical, with usual group of apical sensilla (Fig. 4). Subpalpal area covered with several semicircularly arranged bunches of flat setae. Molar area semicylindrical, transversely ridged. Inner margin of genal lobes with dense growth of short hairs, labial projection with a tuft of long hairs.

BODY SEGMENTS. Larval body consisting of three thoracic and eight externally visible abdominal segments. Hairs on body segments golden brown and mostly adpressed. Haired areas less extensive than in *P. flavifemoratus*. Dorsally, hair patches on thoracic segment 1 confined to two subtriangular areas leaving longitudinal medial stripe bare (Fig. 1). Following body segments with hairy area occupying medial 1/3 to 1/2, sublateral and lateral parts of segments bare (except for constant setae). Extent of hairs on ventral side similar to dorsal side, but sternal patch bare. Anal segment bare dorsally and haired along anterior margin ventrally. Rounded scales dorsally in 1–3 rows, ventrally well-developed along anterior margin of all abdominal segments (including anal segment; these mostly larger and only in 1 row) (Figs 5–6). Transverse rows particularly extensive on anterior segments (up to 28 scales), sparser (12–16 scales) and medially interrupted on last 3 segments. Midsternal patch in form of middle stripe on abdominal segment 6 and a pale area at posteromedial margin of segment 5, consisting of 5–6 irregular longitudinal rows of transversely enlarged cuticular cells (Fig. 6). Anal segment comparatively short with remarkably rounded posterolateral corners; slightly emarginate posteromedially. Both dorsal and ventral sides have a low semicircular elevation beyond anterior margin. Anal slit located on median of ventral side of anal segment, bordered by a flat and broad double rim (Fig. 6).

RESPIRATORY SYSTEM. Anterior spiracles on sides of 1st thoracic segment. Each formed by a low cuticular plate bearing anterior circular stigmatic area with two spiracular slits and a smaller posterior circle with stigmatic scar (Fig. 11). Very small and indistinct, possibly non-functional, mostly circular vestiges of dorsolateral spiracles found on thoracic segment 3 and abdominal segments 1–7. Posterior spiracular opening placed dorsally beyond transverse subapical fold of anal segment. Both dorsal and ventral lips of this opening lead to a spiracular chamber bordered by relatively short, flat and pinnate setae.

CHAETOTAXY. All characteristic setae of the head are present, 2 pairs of clypeofrontals, 2 labrals, 1 dorsolateral, 1 lateral, 3 ventrolaterals and 3 ventrals. Clypeofrontals, 3rd ventrolateral and ventrals are particularly bushlike with long branches; other setae less conspicuous, shorter and pubescent (Figs 2–3, 9). Constant setae on body segments usually stronger than hairs and distinctly pubescent. Thus, 2 pairs of anterodorsals and 3 dorsals distinguishable on thoracic segment 1, and 3 dorsals on each following thoracic segment. Ventrally, 1 pair of doubled ventral setae is visible on each thoracic segment (inner pair



Figs 7–12. *Ptecticus brunettii*, larva (penultimate instar) (7–11) and puparium (larval skin of last instar) (12). 7 – apical part of head, lateral view; 8 – right antenna; 9 – head, ventral view; 10 – abdominal segments 5–7, left half, ventral view; 11 – right anterior spiracle; 12 – middle part of abdominal segments 6–7 (puparium). a – antenna, D – dorsal setae, L – lateral setae, Lb – labrum, V – ventral setae, Vl – ventrolateral setae, sc – stigmatic scar, so – sternal ornamentation, sp – sternal patch, ss – stigmatic slit.

indistinct). In addition, dorsolateral and ventrolateral setae are present on lateral wall of each thoracic segment. Normally, abdominal segments with transverse rows of 3 pairs of dorsal and 3 pairs of ventral setae but both barely distinguishable among hairs. Setae on lateral wall of abdominal segments usually clearly visible; 4 total: 1 dorsolateral, 1 ventrolateral and 2 lateral on each side (Figs 5, 10). Anal segment with a pair of strong and isolated dorsal setae. Five pairs of ventral setae on anal segment in usual position, more or less distinct (inner anterior seta often less distinct, inner posterior seta long and smooth). Lateral setae of anal segment reach length of preceding abdominal segment; subapical setae of same length as dorsals and apical setae much smaller (Fig. 5).

MEASUREMENTS. Length 5.2–13.0 mm, maximum width: 2.6–6.6 mm.

Puparium (larval skin of last instar)

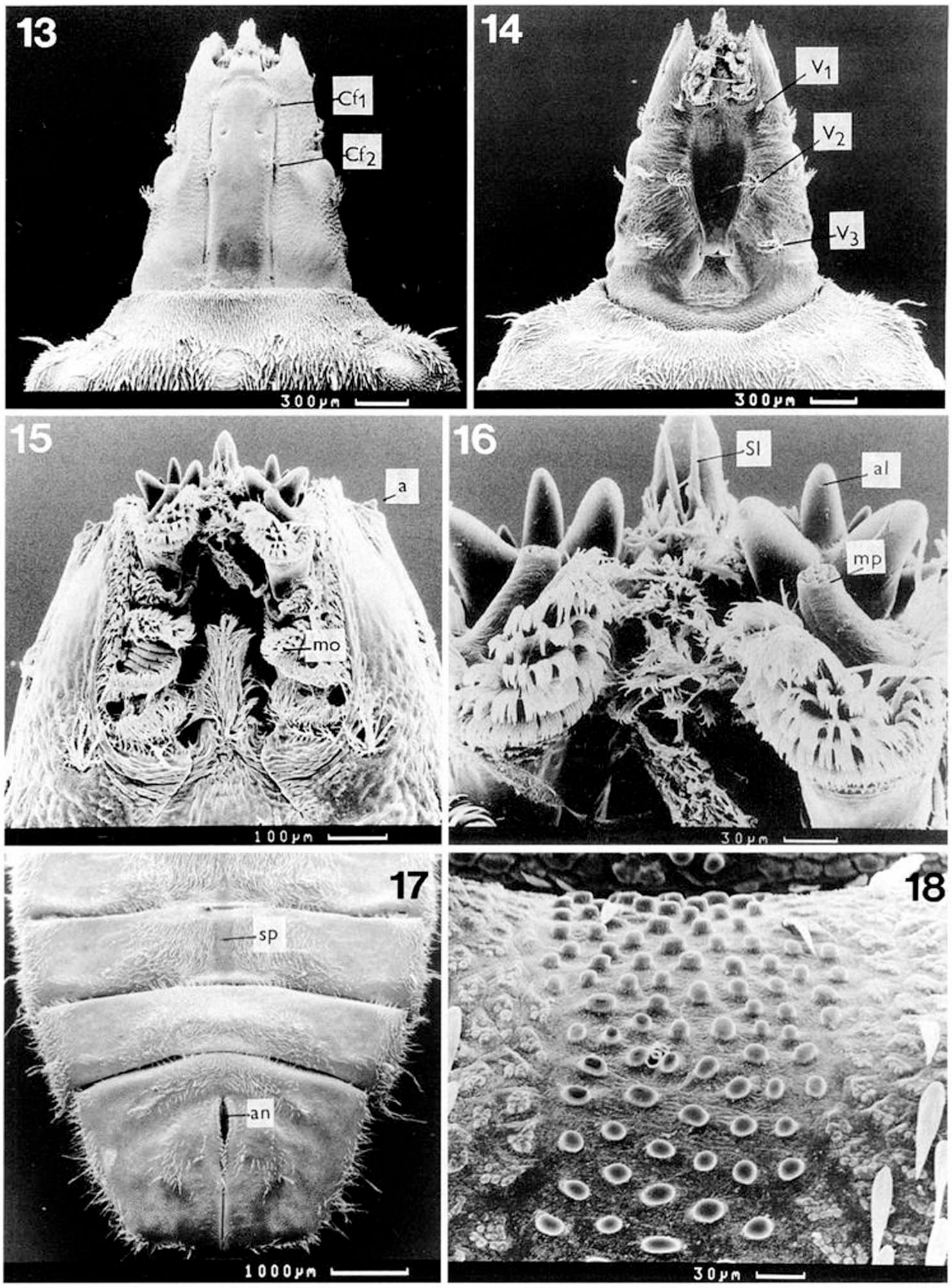
SHAPE AND COLOUR. Elongate suboval, remarkably dorsoventrally flattened. Integument rough, reticulate surface structure well retained, head smooth. Body segments without hairs but with constant conspicuous setae. Reddish brown but central part of body segments (beginning from thoracic segment 3) dark brown; anal segment with dark anteromedial patch. Ornamentation less distinct than in larva, relevant cuticular plates distinctly larger but barely darker than others (Fig. 12).

HEAD. Head flattened, anteriorly rounded, abruptly broadened below protuberant eye prominences. Postocular lobes not prominent in dorsal view but deeply emarginate in ventral view (Figs 25–26). Mouth opening completely reduced, superimposed by a central cuticular plate. Mandibular-maxillary complexes dried, hardened and coalescent with genal lobes. Only vestiges of molar area distinct.

BODY SEGMENTS. Body segments without anterior row of rounded scales. Only transverse row of dark small circular plates more or less distinct on boundary of segments (Fig. 12). Mid-sternal patch on abdominal segment 6 relatively short, not reaching margins of segment; consists of 3–6 longitudinal rows of pale cells (Fig. 28). Abdominal sternum 5 without sternal patch. Anal segment of same shape as in larva description, i.e. unusually short, posterolaterally rounded and posteromedianly emarginate (Figs 27–28). Dorsal side of anal segment with middle circular elevation; ventral side with semicircular elevation beyond anterior margin and two symmetrical ridges in posteromedial position. Anal slit relatively short, without marginal rim.

RESPIRATORY SYSTEM. Anterior spiracles are the same shape and position as in larva, found on sides of thoracic segment 1 but almost circular. Vestiges of segmental spiracles on metathorax and abdominal segment 1–7 positioned laying dorsolaterally as small, oblique oval plates, sometimes barely distinct. Posterior opening of spiracular chamber shifted to posterior margin of anal segment and almost terminal. Rest of marginal fringe more or less retained. Very short but distinct, rodlike pupal respiratory horns developed as new cuticular structures in dorsolateral position on abdominal segments 2–5.

CHAETOTAXY. Configuration of constant setae corresponds to that of all Sarginae and to preceding larval stage. Setae on head simple with very short pubescence (Figs 25–26), setae on body segments regularly strong, pubescent, many in posterior half of body almost plumate (Figs 27–28). All 3 pairs of dorsal and ventral setae on abdominal segments well-developed and of about same length, with long pubescence (Fig. 12). Two lateral setae developed (in addition to usual dorsolateral and ventrolateral seta) on lateral wall of abdominal segments 1, 6 and 7; one lateral seta on abdominal segments 4 and 5. Anal segment



Figs 13–18. *Ptecticus flavifemoratus*, larva (penultimate instar). 13 – head, dorsal view; 14 – head, ventral view; 15 – mouthparts, ventral view; 16 – anterior part of mandibular-maxillary complexes; 17 – abdominal segments 5–8, ventral view; 18 – mid-part of abdominal segment 6, part of sternal patch. a – antenna, al – apical maxillary lobes, an – anal slit, mo – molar area, mp – maxillary palpus, sp – sternal patch, V – ventral setae.

with one pair of dorsal setae and 5 pairs of ventral setae. Subapical setae of anal segment about as long as lateral setae; apical setae distinctly shorter (Fig. 28).

MEASUREMENTS. Length 12.0–15.0 mm, maximum width: 3.8–4.0 mm.

MATERIAL EXAMINED. 6 larvae and 1 larval exuvia from West Malaysia, Ulu Gombak Field Studies Centre, decaying bamboo shoots of *Gigantochloa scortechinii*, between the culm sheats, 4.xi.1993 and 12.ix.1995, D. Kovac leg.; 1 puparium and 3 puparial exuviae, larvae collected on 4.xi.1993 (see above) and 1 puparium on 13.x.1995 from the same locality, 2♀ eclosed on 25.xi.1993 and 1♂ eclosed on 18.x.1995.

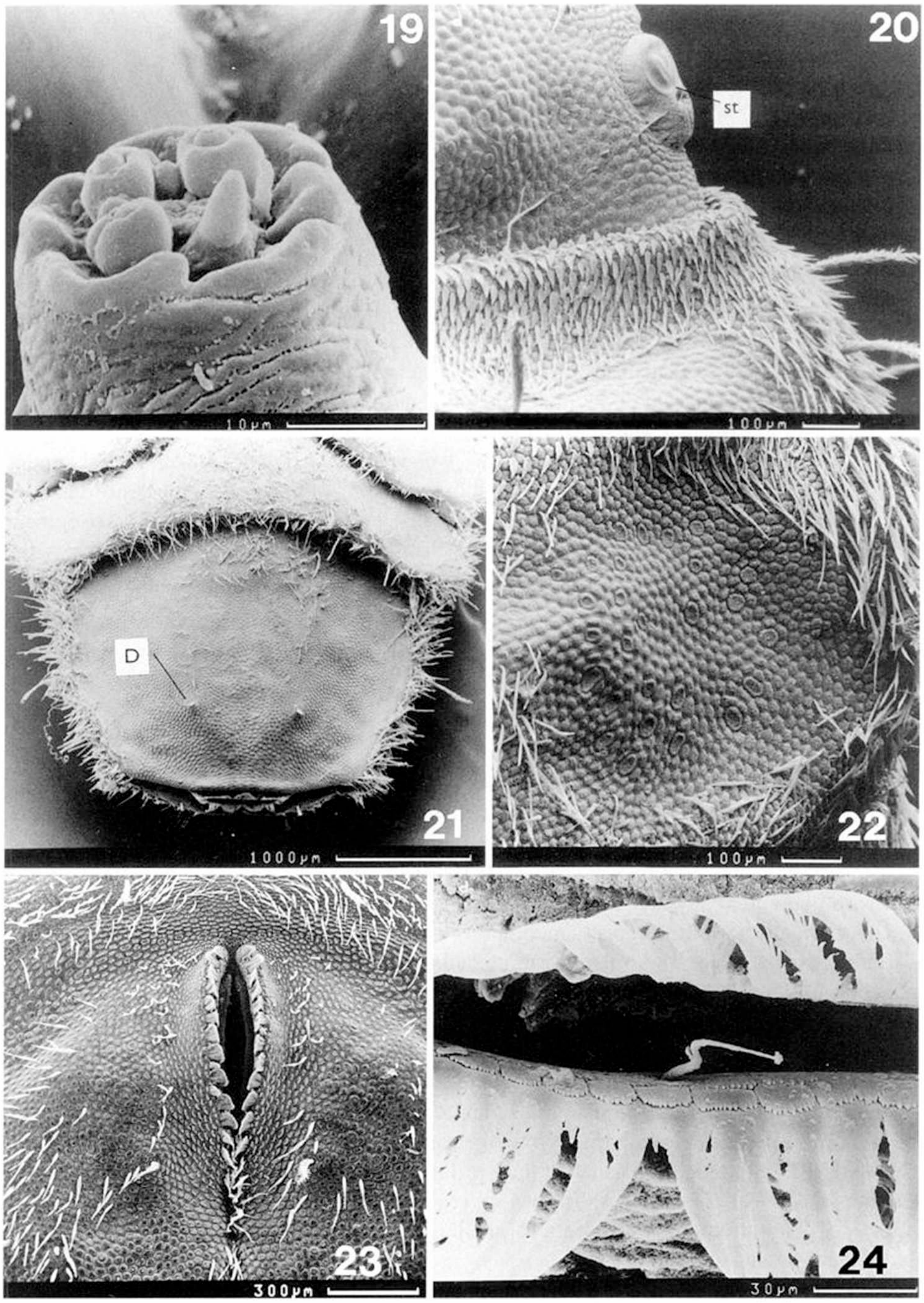
Ptecticus flavifemoratus Rozkošný & Kovac, 1996
(Figs 13–25; 29–32)

Larva (of penultimate instar)

SHAPE AND COLOUR. Elongate oval to subcylindrical, consists of anteriorly prominent head, three thoracic and eight visible abdominal segments. Pale brown to sandy yellow, without conspicuous darker pattern. Head mostly mat and predominantly smooth, clypeofrons conspicuously shiny. Integument of body segments leathery with fine honeycomb appearance. Relatively large, circular to oval cuticular plates form ornamentation in sublateral depressions that is similar to preceding species description but configuration of cuticular plates is more circular (Fig. 22). Longitudinal ornamentation on both sides of anal segment is distinct. Transverse row of oval plates is more or less distinct along anterior margin of each body segment.

HEAD. Small, two-segmented antennae in anterolateral corners of head capsule. Labrum pointed in dorsal view with curved apex, not remarkably longer than genal lobes (Figs 13–14). Eye prominences light, barely protuberant. Labrum with a tuft of pinnate setae on ventral side, pair of long, slender, sublabral setae distinct (Figs 15–16). Distal part of each mandibular-maxillary complex with a remarkable group of 5 conical appendages of differing sizes: three are stout and long (reaching length of maxillary palpus) and the two distal appendages are small (Fig. 16). Relatively slender maxillary palpus with distal group of 1 conical and 3 sphaerical sensilla (Fig. 19). Molar area (Fig. 3, mo) semicylindrical, transversely ridged; each ridge with a rim of short flat setae. Each molar area partially superimposed by slightly spiralled garlands of fine setae (Fig. 15). Ventral labial projection visible with several tufts of long hairs in the middle.

BODY SEGMENTS. Body segments covered with dense pubescence but sublateral longitudinal stripes on dorsal and ventral side virtually bare. Presence of hair interrupted in middle of thoracic segment 1, in the vicinity of the sternal patch, and along the dorsal and ventral posterior margins of thoracic segments. Hair mostly golden brown, predominantly adpressed on thoracic and two first abdominal segments; much longer, sparser and mostly erect on the remaining abdominal segments. Ventral side of abdominal segments 1–6 with a transverse row of flat, scalelike spines along anterior margin. Number of spines gradually decreases from about 22 (on abdominal segment 1) to about 8 (on abdominal segment 6). Sternal patch in middle of abdominal segment 6 (consists of 8–10 irregular longitudinal rows of cells) and abdominal segment 5 (consists of 5–6 longitudinal rows of cells) bandshaped and occupies nearly the whole length of segment 6 and more than half of segment 5 (Fig. 17). Cuticular cells of sternal patch with characteristic papillae (Fig. 18). Anal segment subquadrate, slightly tapered towards posterior margin (Fig. 21). Anal slit situated in



Figs 19–24. *Ptecticus flavifemoratus*, larva (penultimate instar). 19 – right maxillary palpus; 20 – anterior spiracle; 21 – anal segment; 22 – abdominal segment 6, submarginal ornamentation; 23 – anal slit; 24 – pinnate setae on lips of posterior spiracular opening. D – dorsal seta, st – anterior spiracle.

middle of ventral side, occupying about one third the length of the anal segment and bordered by dull marginal teeth (Fig. 23).

RESPIRATORY SYSTEM. Virtually the same as that described for larva of *P. brunettii* including very small and indistinct circular vestiges of dorsolateral spiracles on thoracic segment 3 and abdominal segments 1–7. Posterior spiracular opening placed, as a rule, beyond transverse subapical fold of anal segment (Fig. 21). Both lips of opening bordered by flat and pinnate setae (Fig. 24).

CHAETOTAXY. All characteristic setae present as described in preceding species. Clypeofrontals, dorsolateral, labrals, ventrolaterals and ventrals bushlike but relatively small (Figs 13–14). Third ventral placed much more posteroventrally than in *P. brunettii*. Two pairs of anterodorsals and three dorsals distinguishable on thoracic segment 1, and 3 dorsals on each following thoracic segment. Ventrally, 1 pair of doubled ventral setae is visible on each thoracic segment. Dorsolateral and ventrolateral seta present on lateral wall of each thoracic segment. On abdominal segments, normally 3 pairs of dorsal and 3 pairs of ventral setae are present but these are barely visible among long hairs. Setae on lateral wall of abdominal segments 1–2 are mostly well visible: 1 dorsolateral, 2 laterals and 1 ventrolateral. Lateral wall of following abdominal segments mostly with dense hairs so that lateral setae are virtually indistinguishable. A pair of dorsal setae of anal segment complemented by a longitudinal row of hairs in front of each. Five pairs of ventral setae on anal segment are more or less distinct. Subapical and apical setae of anal segment distinct; both are short and of equal length.

MEASUREMENTS. Length 9.6–15.7 mm, maximum width: 3.2–4.8 mm.

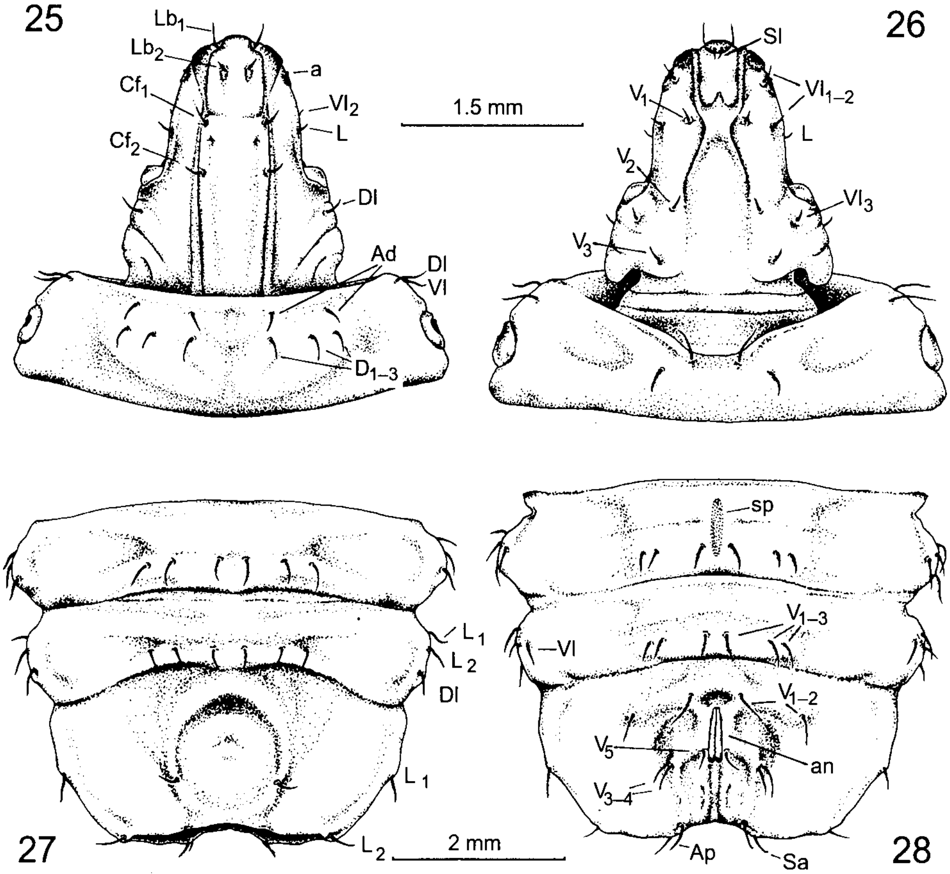
Puparium (larval skin of last instar)

SHAPE AND COLOUR. Elongate, subcylindrical, somewhat flattened dorsoventrally. Integument rough and rigid, retains cuticular structures developed in preceding larval instar. In contrast to the preceding larval instar, smooth and without hairs (except for constant setae). Reddish brown; central part of body segments usually darker. Ornamentation formed by cuticular plates in sublateral depressions and in middle and along anterior margin of body segments, but often barely visible. Head suboblong and flat; lateral eye prominences well-protuberant, postocular lobes very low (Figs 29–30).

HEAD. Head capsule compact, mouthparts coalescent, remainder of molar areas only partially distinct. Labrum turned down; mandibular-maxillary complexes dried and tightly attached to genal lobes of head capsule; mouth opening covered by a complete cuticular plate. Remainders of antennae distinct but very small.

BODY SEGMENTS. Body segments smooth; integument with mozaic appearance. Anal segment subquadrate as described for larva, posteriorly somewhat narrowed with horseshoe elevation in middle of dorsal side and semicircular transverse ridge on ventral side and 2 pairs of longitudinal ventral ridges (along anal slit and in distal mediolateral position) (Figs 31–32). Sternal patch smaller than in larva; does not reach margins of abdominal segment 6, almost circular or short oval on segment 5. Its larger part (on segment 6) consists of 1–7 longitudinal cell rows, and smaller part (on segment 5) formed by 6–12 cells. Inner teeth of anal slit barely visible.

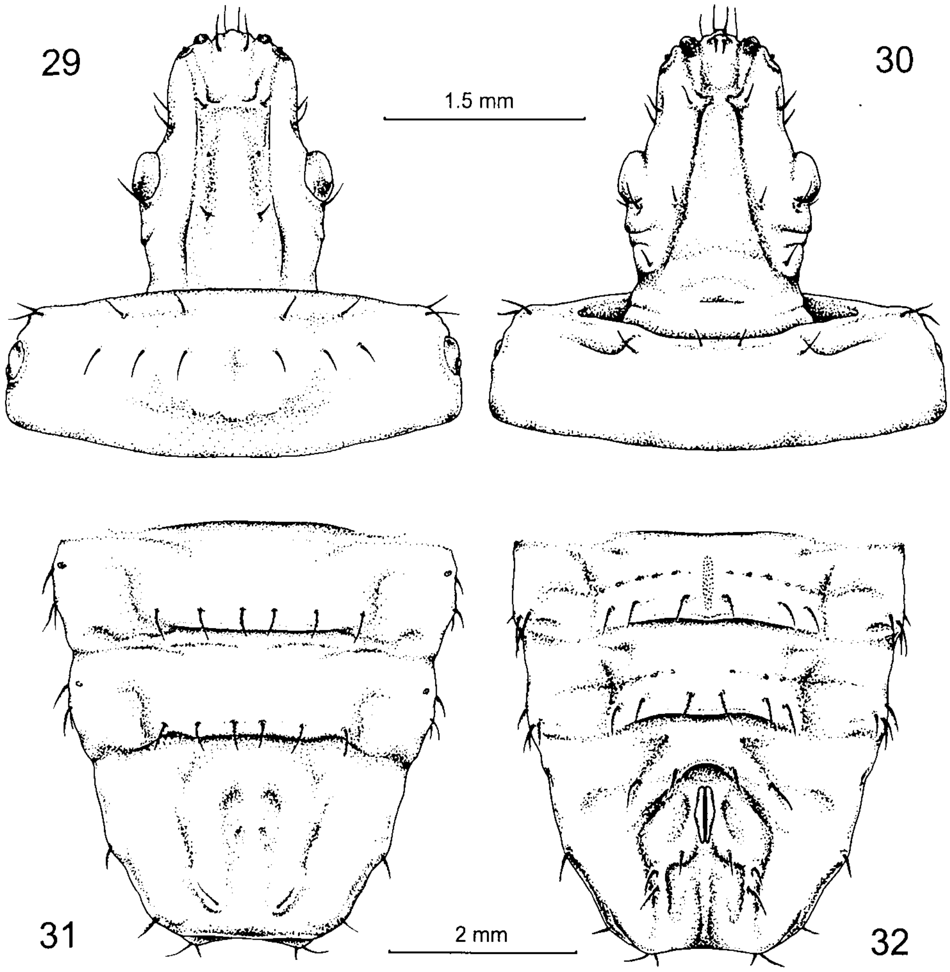
RESPIRATORY SYSTEM. Anterior spiracles of same shape and position as in larva but elongate-oval rather than circular. Vestiges of segmental spiracles on metathorax and abdominal segments 1–7 and posterior opening of spiracular chamber nearly identical to



Figs 25–28. *Ptecticus brunettii*, puparium. 25–26 – head and thoracic segment, dorsal and ventral view. 27–28 – last three abdominal segments, dorsal and ventral view. a – antenna, Ad – anterodorsal setae, an – anal slit, Ap – apical seta, Cf – clypeofrontal setae, D – dorsal setae, Dl – dorsolateral seta, L – lateral setae, Lb – labral setae, Sa – subapical seta, Sl – sublateral setae, sp – sternal patch, Vl – ventrolateral setae, V – ventral setae.

puparium of *P. brunettii*. Very small but distinct pupal respiratory horns are even less distinct than in *P. brunettii*; located in small pale areas dorsolaterally on abdominal segments 2–5.

Chaetotaxy. Setae on head simple and smooth (or nearly so); setae on body segments rather short but distinctly pinnate. Head setae in same position as in larva. All 3 pairs of dorsal and also ventral setae on abdominal segments well-developed and strong. Anal segment with only one pair of dorsal setae and 5 pairs of ventral setae. Subapical and apical setae of anal segment are approximately the same length as lateral setae. Two lateral setae (in addition to usual dorsolateral and ventrolateral setae) developed on each lateral wall of abdominal segments 1, 6 and 7 and reduced on segments where pupal respiratory horns occur (i.e. 2–5).



Figs 29–32. *Ptecticus flavifemoratus*, puparium. 29–30 – head and thoracic segment 1, dorsal and ventral view. 31–32 – last three abdominal segments, dorsal and ventral view.

MEASUREMENTS. Length 12.6–19.9 mm, maximum width: 3.8–4.0 mm.

MATERIAL EXAMINED. 5 larvae from West Malaysia, Ulu Gombak Field Studies Centre, bamboo stump (*Gigantochloa scortechinii*) filled with water, 3.viii.1993 and 24.viii.1994, D. Kovac leg; 2 puparia and 5 puparial exuviae reared from larvae collected on 3.viii. and 24.viii.1994.

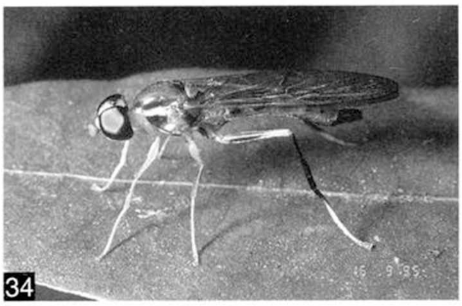
Biology of *Ptecticus brunettii* and *P. flavifemoratus*

P. brunettii. The larvae of *P. brunettii* inhabit the spaces between the culm sheaths of dead bamboo shoots that lie on the ground. During our investigations, only the apical sections of the shoots, which are completely enclosed by several layers of culm sheaths, were colonized. This region extends approximately 1.5 m from the apex of the shoot. Below this zone, the internodes are long, hard and only partially covered by a culm sheat. To facilitate investigation of *P. brunettii*, shoot tips were cut off and laid on the ground (Fig. 33). Usually, after only a few minutes, the first *P. brunettii* came flying toward the shoots. Territorial males rested on leaves and other projectiles (Fig. 34) and occasionally undertook patrol flights among the shoots. Other males were attacked in the air and chased away. Copulation with females, which are smaller, took place in mid-air.

During oviposition, the females push individual eggs, which are white, beneath culm sheaths. The larvae stay in very narrow, damp spaces between the sheaths or between the innermost sheath and the culm wall. Pupation also occurs in larval habitat. In adaptation to their environment, both larvae and puparia possess a strongly flattened body. Puparia are easily distinguished from light-coloured larvae by their dark-brown colour and coarse skin (Fig. 35). When culm sheaths are experimentally removed, the originally immobile larvae of the last instar start to crawl about in search of a place to hide.

Complete decomposition of the bamboo shoots takes about 4–6 weeks, after which only the durable culm sheaths remain. *P. brunettii* completes its entire development during this time. In the case of one investigated shoot, the time elapsed between the felling of the bamboo and emergence of the adult flies (n = 37, 18♂ and 19♀) was 40–52 days. In other cases, a female emerged after 35 days and a male after 61 days. Pupation of one male larva occurred just 30 days after the bamboo was felled.

P. flavifemoratus. So far, the larvae of *P. flavifemoratus* have been found exclusively in water-filled stumps of young bamboo shoots (Fig. 36). These habitats are created when bamboo shoots are



Figs 33–35. *Ptecticus brunettii*, habitat, adult and puparium. 33 – a stand of the bamboo *G. scortechinii* in Ulu Gombak, West Malaysia; larvae develop in the apical region of decaying bamboo shoots lying on the ground (arrow; length c. 1.5 m). 34 – adult male perching on a leaf and guarding a decaying shoot (length c. 11 mm). 35 – puparium (ventral view; length c. 14 mm). The upper culm sheaths have been removed to expose the puparium.

damaged due to storms (e.g., because of falling tree limbs), of animal activity (e.g., wild pig), or gathering by humans (for food). Unless the point of breakage is not very close to an internodal septum or the culm sheaths continue to envelop the culm tightly, the shoot stump may fill with water (pH 6 to over 7) within a few hours and a phytotelma is created. Apparently, this contains both rainwater accumulated in the stump and bamboo sap, because in some cases the stumps were filled with liquid even though no rain had fallen after the culm was broken.

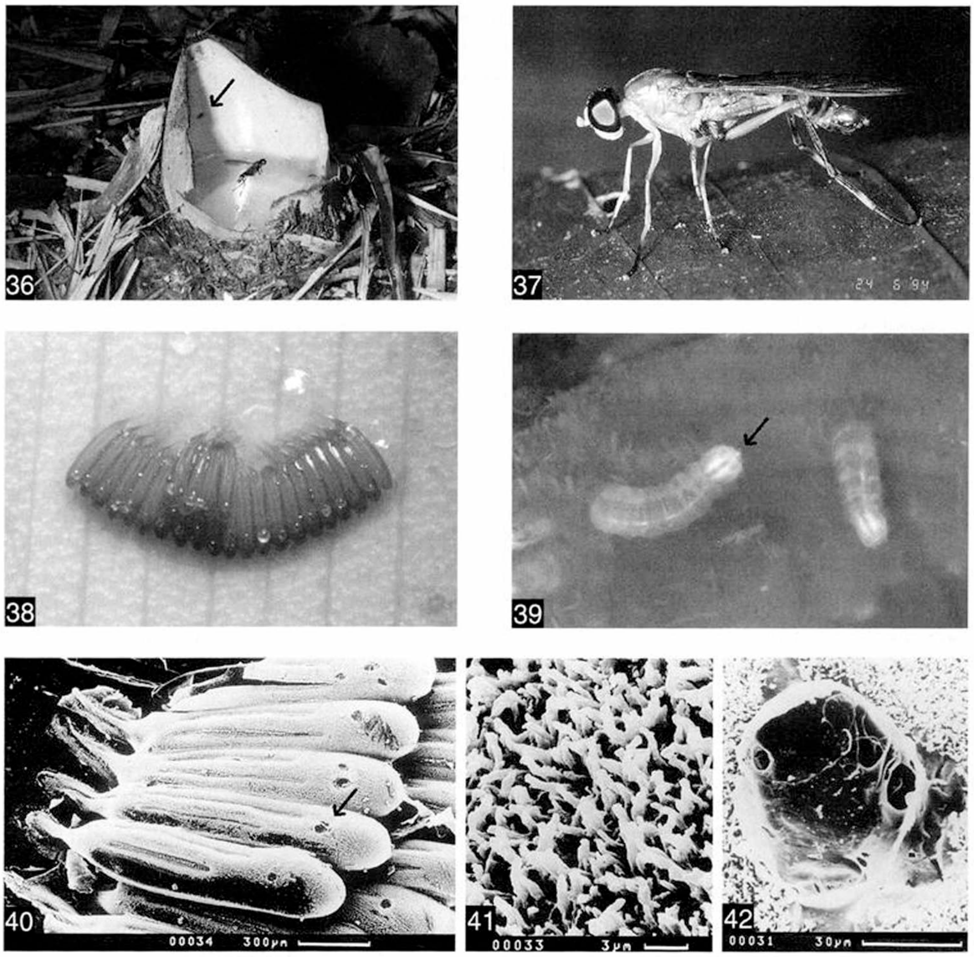
The first *P. flavifemoratus* sometimes appeared within a few minutes after the shoot was broken. Usually, a male that was resting on nearby leaves or other raised objects appeared first (Fig. 37). From time to time, the individual flew to the bamboo stump and hovered above the water trapped in the stump (Fig. 36). Then, in most cases, the fly returned to its original perch. Other males were ignored as long as they remained calm on a resting object. However, if they flew toward the bamboo stump, they were attacked in the air by the first male and forced to retreat. Copulation with females took place during flight.

Females deposited their mass of eggs, which are brownish, only on the first or second day after the shoots were broken. Eggs were deposited on the insides of the sheaths (Figs 36, 38) or, in cases where the sheaths had fallen off, on the bamboo wall. First, a large number of eggs were deposited next to each other in a semicircle, with the apical projections of each egg pointing toward the inside of the semicircle (or, in relation to the sheath, upwards). Then, up to three additional layers of eggs were deposited immediately above and partially covering the first layer. Each new layer of eggs was shifted toward the inside of the semicircle and contained less eggs than the preceding layer. Eggs were glued together with a secretion and attached to the substratum.

The eggs of *P. flavifemoratus* are elongately-oval. The basal part is somewhat broader, whereas the apical part ends in two projections (Fig. 40). The average length of eggs observed in this study was approximately 1.5 mm (length of apical projections approximately 0.5 mm), the largest width was 0.28 mm. A SEM-investigation showed that the upper side of the eggs is covered with very fine pubescence (length 2–3 µm), whereas the sides bordering adjacent eggs are hairless (Fig. 40). Additional conspicuous structures on the egg surface are two long grooves (also pubescent) and 1–2 circular hairless regions at the basal end of the egg surface (Figs 40, 42). Openings that lead into the interior of the egg exist in the hairsless regions. Under field conditions, a water droplet was present on each hairless region (Fig. 38). Smaller droplets also occurred at the borders between eggs if the lateral hairless parts of the eggs happened to point upwards.

The eggs of three egg masses were counted: the first mass contained 34 eggs (18 eggs in the first row, 13 in the second, and 3 in the third); the second mass, 25 eggs (21 in the first row and 4 in the second, see Fig. 38), and the third mass, 56 eggs (23 in the first row, 16 in the second, 12 in the third, and 5 in the fourth). There were up to 7 egg masses within single bamboo stump. Low shoot stumps (Fig. 36) were preferred for oviposition. Of the 20 experimentally-created shoot stumps, 10 were used for oviposition by *P. flavifemoratus*. Eggs were deposited on only one out of 30 high bamboo stumps (height c. 1.5 m) and no larvae were later found on these stumps.

Larvae hatched after 2–3 days (n = 3 egg masses) and then crept into the water. Larvae were buoyant and maintained contact with the water surface by use of their posterior



Figs 36–42. *Ptecticus flavifemoratus*, habitat, adult, larvae and eggs. 36 – a water-filled bamboo shoot stump of *G. scortechinii* (diameter c. 10 cm), one day after the apical part of the shoot was broken off. A male is hovering above the water surface. Note the egg mass on the culm sheath (arrow). 37 – male resting on a leaf and guarding the bamboo stump (length c. 12.5 mm). 38 – egg mass on the inner surface of a culm sheath (length of eggs c. 1.5 mm). Note the water droplets in the basal region of the eggs. 39 – larvae feeding in bamboo stump (length c. 10 mm). They are submerged and have an air bubble at the tip of the abdomen (arrow). 40 – eggs (SEM-photo). dorsal surface is covered with minute hydrofuge plastron hairs; note the circular hairless region at the basal part of the egg (arrow) and the absence of hairs on the sides of the eggs. 41 – enlarged plastron hairs from the apical part of the egg. 42 – enlarged circular hairless region with pores. In the field, this region is usually covered by a water droplet (see Fig. 38).

spiracles. They were also able to crawl to the bottom of the internode, while carrying an air bubble on their posterior end (Fig. 39). Their mouthparts were constantly in motion, taking up food particles from the bamboo wall, open water, and the water surface. During daytime the larvae always stayed in the water. At night, only one larva was observed leaving the water and remaining within the moist region of the bamboo wall. Development, from oviposition to emergence of mature larva from the water, took 12–13 days (n = 3).

Mature larvae left the bamboo stump to pupate probably in soil or leaf litter. Developmental time, from pupa to the adult, was highly variable. In one case it took 19 days (♀); in another, 42 days (♂). Only some pupae, however, completed development in relatively short time. For example, on 24 August approximately 20 almost full-grown larvae were collected from the field; they pupated very soon thereafter. A few individuals developed rather quickly to the adult stage, but the overwhelming majority had still not eclosed 3 months later. Therefore they were taken to Frankfurt and kept for several months at room temperature (c. 22–24°C during daytime) and moistened from time to time. In the following year, they were taken back to Malaysia. Only on 13 July, 1995, i.e., almost one year after pupation, did the last remaining individual eclose.

Bamboo shoot tissue is a rich food resource exploited by larvae of various fly families (Tephritidae, Muscidae, Drosophilidae, etc.), and the bamboo wall is quickly broken down by their feeding activities. Consequently, the accumulated water may leak out of the shoot containers within a few days, especially if the culm sheaths do not firmly enclose the stump. When the shoot stump is dry, both Stratiomyidae larvae and other aquatic inhabitants, e.g., mosquito larvae, are captured by ants (*Pheidole*, *Crematogaster*, and others). In the case mentioned earlier in which 10 of 20 shoot stumps were colonized, four of the colonized shoot stumps were dry within a few days, and the *Ptecticus*-larvae were carried off by ants. Other enemies of *P. flavifemoratus* include larvae and adults of various beetle species of the family Staphylinidae. They hunt just above the water surface for mosquito larvae and other aquatic insects that come to the surface to replenish their air supply. On two occasions, capture of young *P. flavifemoratus* larvae by staphylinids was observed; in one such case capture was accomplished by an adult, however, in the other case by a beetle larva.

DISCUSSION

Both larvae described herein can be distinguished by the shape of the head capsule and anal segment, select cuticular structures, the extent of pubescence, and arrangement of the mandibular-maxillary complexes. The larva of *P. brunettii* is characterized by rounded scales along the anterior margin of abdominal segments, reduced hair patches and specific structure of the anal segment. Characteristic features of the *P. flavifemoratus* larva are the unique apical groups of conical lobes on the maxillary mouthparts and the absence of rounded cuticular scales. Additionally, ventral scales are replaced by rows of flat elongate-triangular spines and the subquadrate anal segment is very distinct.

The puparia (last instar larvae) of both species maintain the larval shape of the anal segment and exhibit differences in the structure of the head capsule and the configuration of setae on the lateral wall of abdominal segments. Scales, spines and the hair covering found in earlier larvae are absent. Specific puparial characters are the flat head with degenerated mouthparts and the 4 pairs of pupal respiratory horns on anal segments 2–5.

This is the first detailed description of the penultimate instar larva of *Ptecticus*. A short note concerning the "antepenultimate instar" of *P. trivittatus* (Say) from North America was found in McFadden (1967) ("body setae short, partially hidden by fine pubescence that covers body; anal spines present"). The puparium of the same species is also briefly described under the description of "mature larva". Other notes concerning larvae of South American *P. testaceus* Fabricius (see Lindner, 1928) and African *P. posticus*

(Wiedemann) (see Engel & Cuthbertson, 1939) apparently also refer to puparia. Only the puparia of *P. longipennis* (Wiedemann) and *P. malayensis* Rozkošný & Kovac (also originating from Malaysia) have been described in sufficient detail (Rozkošný & Kovac, 1994a). Both of these puparia may be distinguished by a dark pattern that consists of undulating longitudinal bands and patches. The puparium of *P. longipennis* has a bipartite postocular lobe on the head and that of *P. malayensis* bears a distinct narrow middle incision on the posterior margin of the anal segment.

The structure of mouthparts in examined *Ptecticus* larvae is basically the same as those found in other members of the subfamily Sarginae (see Vaillant & Delhom, 1956; Roberts, 1969; Rozkošný, 1982) and are even similar to groups of Stratiomyidae that are relatively ecologically and systematically distant (Bischoff, 1925; Cook, 1949; Schremmer, 1951; McFadden, 1967; Faucheaux, 1978; Rozkošný, 1982). A remarkably complicated mandibular-maxillary complex confirms that stratiomyid larvae represent a distinct exception among larvae of the lower Brachycera in regards to their feeding habits. Whereas the majority of larvae of primitive Brachycera are parasites or predators, all known Stratiomyidae larvae appear to be scavengers. Their mandibular-maxillary complexes only allow motion in a vertical plane and are the result of strong specialisation. Typical biting mouthparts have thus been altered to form a sweeping apparatus. McFadden (1967) described the feeding habits of stratiomyid larvae as micropantophagous, but, in certain groups, there are also tendencies towards saprophagy, coprophagy or even phytophagy. Terrestrial larvae feed upon decaying plant and animal material in moist soil, rotten wood, under the bark of trees, and in other organic materials. Larvae of *Ptecticus* have often been found under such conditions, as have many arboreal larvae of Pachygasterinae that live under the bark of trees. According to Teskey (1976), such larvae apparently feed on fermenting sap, fungus spores or decomposer microorganisms.

P. flavifemoratus is the first species of the subfamily Sarginae that is known to have truly aquatic larvae, although the larvae of *P. tricolor* (and perhaps larvae of other *Ptecticus* species) are able to stay in a nearly liquid decaying substrate for considerable stretches of time. The adaptations to aquatic habitat are not as extreme as in the exclusively aquatic species of *Stratiomys* and *Odontomya* (Stratiomyinae) which possess a terminal segment that is greatly elongated. However, last abdominal segment of *P. flavifemoratus* is distinctly longer than that of *P. brunettii*. Likewise, the marginal hair fringes on the body segments (Fig. 17) may represent a specific ecological adaptation.

The eggs of *P. flavifemoratus* are unusual because they have an egg plastron. When an egg mass of this species is submerged in the water, it remains enclosed in a thin layer of air because of the fine water-repellent pubescence on the egg surface that acts as plastron hairs. The presence of egg-plastron has been previously documented in various fly families, but not in Stratiomyidae (Hinton 1961, 1981). The plastron serves as protection against rain and, in the case of *P. flavifemoratus*, probably also acts as a safeguard in case of rising water levels in the bamboo stump or the accumulation of liquid secreted by the sheaths. Eggs of the three other investigated *Ptecticus* species do not possess a plastron. They lie well-protected beneath the bamboo culm sheaths (*P. brunettii*, *P. tricolor*) or are attached to the exterior surface of the culm sheaths and are enclosed in a gelatinous mass (*P. malayensis*). Droplets of liquid that accumulate on the naked, pore-bearing regions of the egg (Fig. 38) are particularly remarkable. It is unknown whether this liquid is produced by the egg or is collected from an extraneous source. Perhaps the droplets play a significant role in osmoregulation of the eggs.

Bamboo shoots are a very nutrient-rich but short-lived habitat that is broken down completely within just a few weeks. Decay occurs even faster in water-filled bamboo shoot stumps. When the culm sheaths no longer tightly envelop the stump, rapid decomposition of the internode wall causes water to dissipate within only a few days. Therefore, *P. flavifemoratus* larvae must race against time. This may have led to the evolution of the females' ability to quickly locate suitable larval habitats and achieve fast oviposition. This also may have led to short larval development time. Rapid larval development is probably encouraged by the very nutritious, submerged internode wall tissue. In *P. flavifemoratus* larval development takes only 10 days, approximately one-third of the time required by *P. brunettii* larvae, although the larvae of *P. flavifemoratus* grow larger (up to 2 cm long).

Water-filled bamboo shoots, suitable for the development of *P. flavifemoratus*, are not only short-lived, but also are available only during a brief period of the year. Bamboo shoots of *G. scortechinii* occur at the research location from July through January, but toward the end of the year only tall shoots (height c. 16–20 m) are found. The young shoots, suitable for colonization by *P. flavifemoratus*, occur only during the first few months of the shoot growing season, usually from the end of July through September. Since *P. flavifemoratus* is adapted for water-filled bamboo shoot stumps, it is likely that the animals have to go through a period of quiescence until the next shoot-growing season. This prediction is corroborated by our observations that, indeed, only a small percentage of the pupae immediately develop into adults (possibly at the beginning of the shoot growing season), while the majority apparently remain in diapause until the next shoot growing season. An internal clock might play a role here, because one of the pupae taken to Frankfurt and exposed to environmental conditions that differed from those in their natural habitat (differing day and night lengths and temperatures as low as 15°C), nevertheless, eclosed at the usual time, which is the middle of the shoot growing season.

During the present investigations of bamboo inhabitants, 14 stratiomyids and one xylomyid (*Solva*) were reared in bamboo. Except for *Odontomyia latitibia* Rozkošný & Kovac, an aquatic stratiomyid from Sabah (Rozkošný & Kovac, 1994b), all species were found in the immediate vicinity of the Ulu Gombak Field Studies Centre. Although knowledge on the biology of the Stratiomyidae and Xylomyidae remains fragmentary, several conclusions may be drawn concerning their resource partitioning.

Of the 14 stratiomyid and xylomyid species found in Ulu Gombak, 10 were regularly encountered in decaying bamboo shoots. Two of these, *Camptopteromyia fractipennis* de Meijere and *Pachygaster* n. sp., were also found in fully grown, decaying bamboo culms. *Ptecticus brunettii*, *Ptecticus minimus* (Rozkošný & Kovac, 1997) and *Ptecticus tricolor* van der Wulp all were found in shoot tips lying on the ground; *P. brunettii* between the culm sheaths, *P. minimus* in the internode wall, and *P. tricolor* in the internode cavity. *P. tricolor* also colonizes internode cavities in the apical region of upright, young shoots killed by weevil larvae *Cyrtotrachelus* sp. (Rozkošný & Kovac, 1994a, Kovac & Azarae, 1994). *Ptecticus malayensis* is confined to *Cyrtotrachelus* shoots and inhabits the internode cavities of both lower and higher shoots tips (several meters high). *P. flavifemoratus* occurs only in water-filled bamboo shoot stumps.

The larvae of *Microchrysa* n. sp. occurred under or between the culm sheaths of both the apical and the basal shoot regions. *Microchrysa* n. sp. was the only species able to go through its whole larval development in rolled-up culm sheaths lying on the ground. This suggests that the species is specialized on culm sheaths. *Solva completa* de Meijere also occurred under or between culm sheaths, whereas *C. fractipennis* and *Pachygaster* n. sp. only occurred in the basal, more ligneous part of the culm under the culm sheaths. Additionally, the latter three species also colonized the basal internode cavities when there was an opening in the wall.

The four remaining species were single captures. *Ptecticus proximus* Rozkošný & Kovac was found in the apical region of the internode cavity of a shoot that had been damaged by *Cyrtotrachelus*, *Ptecticus longipennis* in the internode cavity of an old, decaying bamboo culm (other collections from prematurely fallen *Artocarpus* fruits and a tapioca root, both of which had fairly hard consistence) and *Hermetia inflata* (Walker) in the internode cavity of upright, fully grown bamboo culm that contained an abandoned stingless bee nest (of a Melliponini species not confined to bamboo). The larvae of *Hermetia illucens* (L.) were reared from eggs laid by a female in an unused rearing container that contained decaying bamboo shoot material. The larvae developed comparatively slowly and the resulting adults were considerably smaller than the normal size for this species. This species was not found within bamboo in the field. In Gombak, this pantropical species was frequently found in rotting fruit (banana, durian) or in cadavers (dead dogs).

The above survey shows that microhabitats of the species that regularly inhabit bamboo shoots do not overlap totally. Only *C. fractipennis* and the rarer *Pachygaster* sp. n. inhabit exactly the same habitat. It is necessary to confirm, however, whether *Pachygaster* sp. n. sometimes occurs under the bark of trees as do other *Pachygaster* spp. The spatial segregation between closely related species of the genus *Ptecticus* is particularly striking. The only *Ptecticus* spp. with an overlap zone are *P. tricolor* and *P. malayensis*. Both species are able to colonize internodes of young shoots damaged by *Cyrtotrachelus*, but so far they have not been found together in the same shoot. Furthermore, the two species do not compete for the same colonization zones (*P. tricolor* colonizes shoots lying on the ground; *P. malayensis* colonizes tall *Cyrtotrachelus*-infested shoots).

Co-occurrence in the same microhabitat is more frequently the case for the species that are less phylogenetically related. *Microchrysa* sp. *P. flaviventris*, *P. brunettii* and *S. completa*, for example, are found together between the sheaths in the upper part of a shoot. In the lower part of a shoot, *S. completa*, *Microchrysa* sp., *C. fractipennis*, or *Pachygaster* sp. may co-occur with one or two other species under a sheath, and *C. fractipennis* and *Pachygaster* sp. may share the same internode cavity in older fallen bamboo culms.

These overlaps mainly concern species that occur on shoot parts of fairly hard consistency or fully grown bamboo culms; this includes all except the *Ptecticus* spp., which colonize the shoots only later and have a longer developmental time. It is likely that these species, which belong to different genera or subfamilies, possess feeding specializations that lead to reduced competition for resources. In terms of competition, it is important to consider that not every suitable bamboo shoot is colonized by all species simultaneously and the number of individuals in a habitat is often small. To enable a detailed analysis of resource partitioning of stationyids and xylomyids associated with bamboo, additional quantitative investigations are necessary regarding life cycles, food acquisition, geographic distribution, and other biological factors.

CONCLUSIONS

1. Larvae of both examined species are associated with decaying bamboo shoots. The larvae of *P. brunettii* inhabit the space between the culm sheaths in the apical portion of a shoot, whereas the larvae of *P. flavifemoratus* are aquatic and inhabit water-filled bamboo shoot stumps.

2. Although puparia of *Ptecticus* (like those of other Sarginae) maintain at least some specific features that are characters of the preceding larval instar, many larval characters are considerably reduced (mouthparts, transverse rows of cuticular structures, hair patches, and setae on the lateral wall of some abdominal segements). The differences between earlier larvae and puparia of *Ptecticus* are much more pronounced than those described for the European genera of the same subfamily.

3. The majority of earlier descriptions of Sarginae larvae actually refer to their puparia. These are distinguishable, particularly by the shape of the head and anal segment, colour, and chaetotaxy.

4. A detailed study of the mouthparts of both examined larvae demonstrated that even the mandibular-maxillary complex, the groundplan of which appears to be virtually the same throughout the family, may show valuable species-specific characters.

5. The mandibles and maxillae of the larvae are modified into a specialized sweeping apparatus (paired mandibular-maxillary complex). The structure of the apparatus confirms that *Ptecticus* larvae are micropantophagous scavengers that feed mostly upon microorganisms that develop in decaying plant tissues.

6. *P. flavifemoratus* adaptations for aquatic habitats were documented. For the first time, an egg plastron was recorded for the family Stratiomyidae and aquatic larvae were recorded for the subfamily Sarginae.

7. *P. flavifemoratus* puparia either develop into the adult stage immediately, or the development is arrested in the puparial stage until the next shoot-growing season.

8. Males of both *P. brunettii* and *P. flavifemoratus* are larger than females and are territorial.

9. Comparison with other stratiomyids and xylomyids that occur in decaying bamboo shoots revealed that spatial segregation is very pronounced, especially in closely related *Ptecticus* spp.

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