BIOLOGY AND DESCRIPTION OF THE THIRD INSTAR LARVA AND PUPARIUM OF *ICHNEUMONOPSIS BURMENSIS* HARDY (DIPTERA: TEPHRITIDAE: DACINAE: GASTROZONINI), A BAMBOO-BREEDING FRUIT FLY FROM THE ORIENTAL REGION

Damir Kovac
Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany
Email: damir.kovac@senckenberg.de

Amnon Freidberg
Department of Zoology, The George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel
Email: afdipter@post.tau.ac.il

Gary J. Steck
Florida State Collection of Arthropods, Florida Department of Agriculture & Consumer Services
Gainesville, FL 32614-7100, U.S.A.
Email: Gary.Steck@freshfromflorida.com

ABSTRACT. — The biology of *Ichneumonopsis burmensis* was studied in north Thailand. The larvae developed in the pith of living bamboo shoots of *Melocalamus compactiflorus*. *M. compactiflorus* has two shoot-growing periods per year, in April–June and September–November. Adults of *I. burmensis* were collected in March–May and October–November. Larvae pupariating in November remained dormant during the hot season (February–April). Usually only one internode of a particular bamboo shoot was infested by *I. burmensis*, and this internode was inhabited by a single larva. The feeding activities of the larva caused the 5–6 apical internodes located above the infested internode to fall off, resulting in a typical damage pattern. In contrast to other Gastrozonini, *I. burmensis* larvae did not skip, and they constructed a puparial chamber inside the bamboo internode. Remarkable morphological characters of *I. burmensis* larvae include the large and strongly ramified anterior spiracles consisting of more than 100 papillae, a labial lobe covered by strong, outward oriented spines, a labial sense organ and a facial mask consisting mainly of accessory plates. These morphological characters are interpreted as an adaptation to the specific bamboo microhabitat utilised by *I. burmensis*. The association of *I. burmensis* with bamboo indicates that *Ichneumonopsis* belongs to the primarily bamboo-inhabiting tribe Gastrozonini. However, the strong differences between the larval characters of *I. burmensis* and other Gastrozonini suggests that this genus has an isolated position within this group.

KEY WORDS. — *Ichneumonopsis*, biology, new record, bamboo, Thailand

INTRODUCTION

Ichneumonopsis burmensis Hardy, 1973 (Fig. 1) is a rarely collected, wasp-like tephritid fly with hitherto unknown biology. The type locality of *I. burmensis* is Chin Hills, Myanmar (Hardy, 1973: 132). Additional specimens were collected in India (Meghalaya; Radhakrishnan, 2000) and, in the present study, in NW Thailand.

Ichneumonopsis is a monotypic genus of uncertain affinities, as indicated by the evolving opinions on the systematic position of *I. burmensis*. Hardy (1973: 132) placed it in the Adramini, subfamily Trypetinae. Hancock (1986) considered *Ichneumonopsis* the most primitive genus of the subfamily

Dacinae and erected a new tribe, Ichneumonopsidini, with *Ichneumonopsis* as its type genus. Norrbom et al. (1998: 21) tentatively placed *Ichneumonopsis* in the Gastrozonina (Dacinae), which were later given a higher rank (= Gastrozonini) by Korneyev (2000). Kovac et al. (2006) included *Ichneumonopsis* in their catalogue of the Gastrozonini.

Gastrozonini are the only Tephritidae breeding in grass (Poaceae), except for some Acanthonevrini genera (Phytalmiinae). The majority of the Gastrozonini species occur in the Oriental Region, but some are also present in the adjacent southeastern Palaearctic and Australasian Regions. In addition, three genera are known from the Afrotropical

Region. Asian species with known larval habitats breed in bamboo shoots (Allwood et al. 1999; Hancock & Drew, 1999). Afrotropical species of the genus *Bistrispinaria* were reared from grasses other than bamboo, such as *Panicum maximum* Jacq. (Copeland, 2007).

D. Kovac has discovered the larvae of *Ichneumonopsis* in bamboo shoots of *Melocalamus compactiflorus* during an ongoing study of tephritids breeding in bamboo. In the present study we report on the rearing and biology of *Ichneumonopsis burmensis*, characterise the bamboo damage patterns caused by the larvae, describe the third instar larva and puparium, compare the larval characters with those of other Gastrozonini and discuss their adaptive significance.

MATERIAL AND METHODS

Field observations of *I. burmensis* were conducted in NW Thailand, district Pangmapha, Province Mae Hong Son (approximate georeferences for the main study site: 19°28,189' 98°17,741'). The study was carried out between 2008 and 2011, covering all months except January and February. The mountainous Pangmapha district is primarily covered with dipterocarp monsoon forests, however, bamboo forests are common in disturbed areas. In Pangmapha the rainy season begins in April or May and ends in October, with the highest amounts of rainfall occurring in July and August. In the cool season (December until February) the night temperatures may fall to about 10°C. In the hot season (February until April) the temperature may rise to 40°C, and fires are frequent.

Bamboo shoot internodes suspected to contain *I. burmensis* larvae were cut off, placed in plastic bags and transferred to the laboratory. In the laboratory the internodes were opened and inspected for *I. burmensis*. For rearing, internodes containing larvae were wrapped with moist tissue at the cut end and placed in plastic boxes. Puparia were removed from the internodes, transferred to clean plastic boxes and placed between sheets of moist tissue.

Puparia and larvae were preserved in 70% ethanol. All larvae collected had already reached the third instar stage. Larvae were boiled for 2–3 minutes prior to preservation. The adults were either pinned or preserved in 70% ethanol. For the study of the cephalopharyngeal skeleton, larvae were treated overnight in 10% KOH following Steck & Wharton (1986) and Steck et al. (1990). Subsequently, the cephalopharyngeal skeleton and anterior and posterior spiracles were dissected and slide-mounted.

For scanning electron microscopy (SEM) two larvae and two puparia were dehydrated in a graded series of ethanol solutions and dried in hexamethyldisilazane (HMDS; Nation, 1983). After two soaks of 1 hour, HMDS containing the specimens was poured into a small dish and allowed to evaporate under a fume hood (Brown, 1993). Dried specimens were mounted on stubs, coated with palladium gold and observed under a Hitachi scanning electron microscope (CamScan CS24).

Terminology follows White & Elson-Harris (1992), White et al. (1999), and Frias et al. (2006, 2009). The terms pseudocephalon, labial lobe and labial organ are used according to Courtney et al. (2000). In the present study we have coined the term "pad organ" for paired lobes or pads equipped with a tiny sensillum located in a cuticular pit in the middle of the pad (Figs. 22, 26). These sensilla were previously recorded from other tephritids, for example, *Aciurina thoracica* ("two distinct lobes lie laterally and ventrolaterally on gnathocephalon, each bearing smaller, dome-shaped, smooth, verrucate papilla with central pore": Headrick & Goeden, 1993: 70), *Anastrepha ludens* ("pit"; Carrol & Wharton, 1989), and *Ceratitis rosa* ("pit sensilla"; Carrol, 1998). The pad organ, i.e., sensillum in combination with the pad-like lobe, may be homologous with the "cheek organ" described by Szpila & Pape (2008) in a sarcophagid larva. In tephritids, pad organs occur in various locations of the pseudocephalon, not just in the cheek area.

Specimens examined are deposited at the Senckenberg Museum, Frankfurt am Main, Germany and at Tel Aviv University, Israel.

RESULTS

BIOLOGY

Habitat and food plant. — In the Pangmapha district we have detected about 15 bamboo species and about 25 species of Gastrozonini. *Ichneumonopsis* larvae occurred only in bamboo shoots of *Melocalamus compactiflorus* (Kurz) Bentham. Other bamboo species examined by us included *Dendrocalamus* (*D. giganteus* Munro, *D. hamiltonii* Nees & Arnott ex Munro, *D. strictus* (Roxburgh) Nees, *D.* sp.), *Bambusa* (*B. polymorpha* Munro, *B. tuldoides* Munro), *Cephalostachyum* (*C. pergracile*), *Thyrsostachys* (*T. siamensis* Gamble) and several unidentified species.

In Pangmapha *M. compactiflorus* occurred in river valleys from 600–1200 m. It grew in open clearings, at the edges of fields (Fig. 2) or in secondary forest. The culms were up to 3 cm wide at base. They were arching over the ground, if not supported by surrounding vegetation. Side branches were sometimes about as thick as the main culm and often replaced it (Fig. 2). Older bamboo clumps formed dense thickets, which could reach a height of more than 10 m.

Bamboo shoots of *M. compactiflorus* appeared twice a year. A first set of bamboo shoots started to grow right after the beginning of the rainy season (end of April). Numerous bamboo shoots were present around May–June. At the end of June most shoots already possessed side branches with leaves.
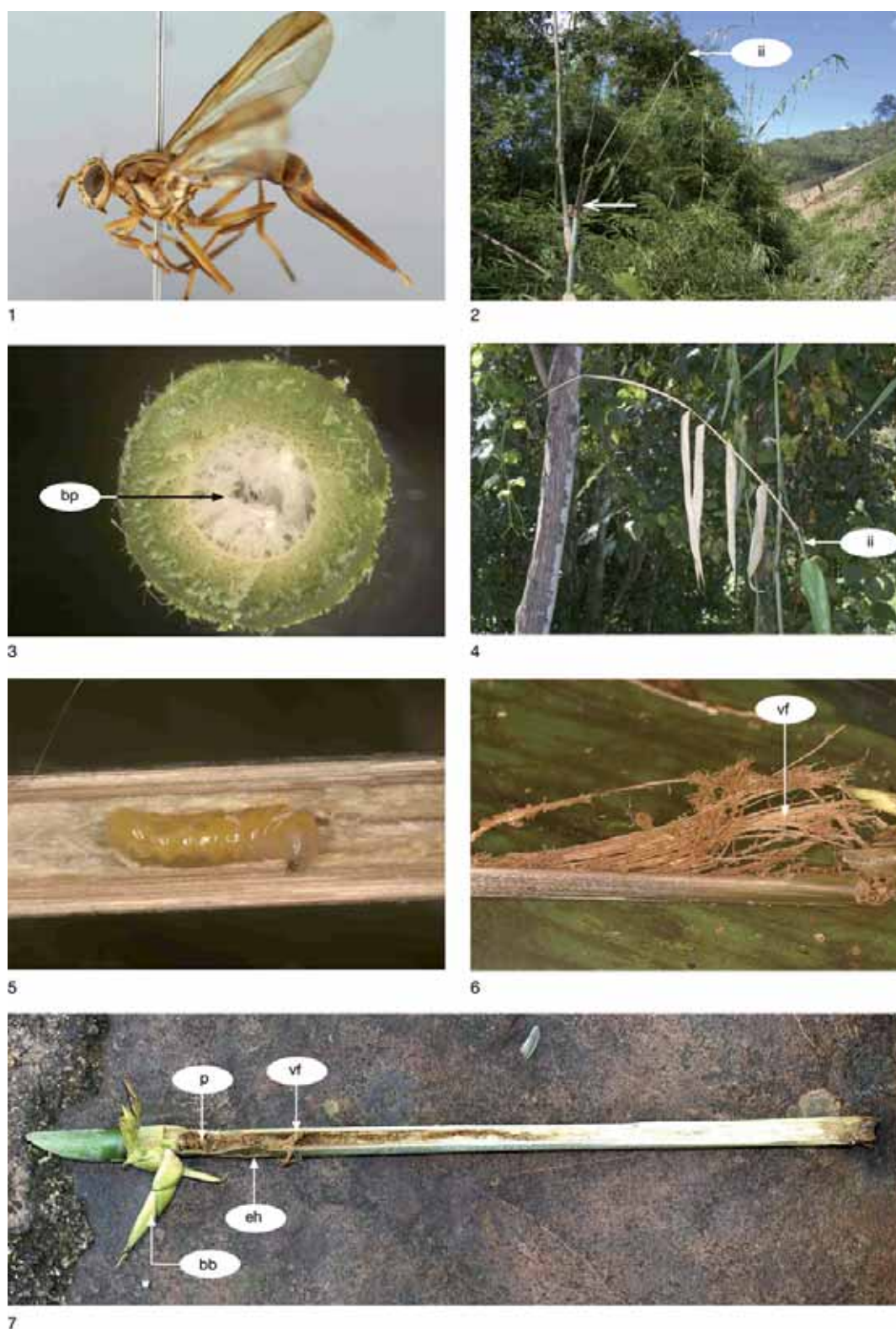
Figs. 1–7. Adults, habitat and development of *I. burmensis*-larvae. 1, Habitus of *I. burmensis* female. 2, Bamboo stand of *M. compactiflorus* in north Thailand at the edge of a field in November. The bamboo shoot in the front was damaged by a larva of the weevil *Cyrtotrachelus* sp. and the apical part of the main stem has dropped to the ground (large arrow points to the stump of the main stem). One of the resulting side branches of the main stem is infested by an *I. burmensis* larva (ii). The large side branch on the left has taken over the function of the main stem. 3, Cross-section through an *M. compactiflorus* internode near the apex of the bamboo shoot (diameter: 7 mm). The internode cavity contains white pith. 4, Apical part of an infested bamboo shoot of *M. compactiflorus*. The arrow points to the internode containing an *I. burmensis* larva. The upper internodes are dead but still attached to the bamboo shoot. 5, *I. burmensis* larva feeding on the white pith inside a bamboo internode (diameter of the internode cavity: 3–4 mm). 6, Bamboo fibres, ca. 5–7 cm long, recently torn off by the larva. 7, Lateral cut through an *I. burmensis*-internode (base of the internode on the left). The larva has eaten up about half of the white pith in the basal part the internode cavity and has freshly pupated at the base of the internode. Note the thin bamboo wall at the level of the exit hole. Most of the torn off vascular fibres have been removed in order to show the puparium. They filled the cavity bween the puparium and the "vf" arrow. eh = exit hole; bp = bamboo pith; bb = branch bud; ii = *I. burmensis*-internode; p = puparium; vf = vascular fibres.

A second set of shoots started to grow in August, with most of the new shoots appearing between September and November. During the first growth period the bamboo shoots were mostly thin and emerged from the ground, whereas during the second growth period the shoots were generally thicker and emerged from the ground as well as from the nodes of older bamboo culms.

The shoots of *M. compactiflorus* were solid in the lower part of the stem. In the apical part of the bamboo shoot, in which the larvae of *I. burmensis* developed, the internodes possessed cavities filled with white pith (Fig. 3).

Larval development. — The infested bamboo shoots were 2–5 m tall and up to 2 cm wide at base. *I. burmensis* attacked only one or rarely two internodes of a particular bamboo shoot. If two internodes were colonised, they were always located next to each other. The infested internode was always the 4th to 6th internode below the apex of a bamboo shoot (Figs. 4, 16). In general, it was the first internode below the apex, which was not entirely enveloped by the protective culm sheath. The distance from the tip of the bamboo shoot to the base of an *I. burmensis*-internode was about 40–50 cm. Internodes colonised by *I. burmensis* were 70–295 mm long (median = 150 mm; n = 37) and 3.5–12 mm wide (median = 5.5 mm; n = 37).

Larvae of *I. burmensis* (Figs. 5, 33) developed in the main stem of the bamboo shoots, but also in side branches of the appropriate size. New side branches appeared when the tip of the bamboo shoot was damaged, for example, by the larvae of the large weevil *Cyrtotrachelus* sp. (Fig. 2), by other insects or by humans.

Every *I. burmensis*-internode contained only one larva. The yellowish larvae (Fig. 5) were sluggish and were never observed to skip. They fed on the bamboo pith inside the internode cavities. The bamboo walls were not eaten, but they were partly damaged in the basal part of the internode. During their development the larvae ate about 1/3 – 2/3 of the bamboo pith filling the internode cavity, depending on the size of the internode (Fig. 7).

Bamboo damage patterns. — The first sign of *I. burmensis* infestation was the limp leaves of the 4–6 apical internodes located on top of the infested bamboo shoot (Figs. 4, 16; an uninfested bamboo shoot is shown in Fig. 15). At that stage the larvae were already mature (third instar) and some had started to tear off vascular bundles from the bamboo wall (see under "Pupariation"). Subsequently, these apical internodes turned brown and died off. They broke off at the predetermined breaking point and dropped down to the ground. The predetermined breaking point (pbp) is an area of weakness (special morphological structure), where the dead bamboo breaks.

Internodes infested by *I. burmensis* also died and turned brown, but remained attached to the bamboo shoot (Figs. 9, 10, 17, 18). However, a narrow area at the base of the internode infested by *I. burmensis*, where the culm sheath and the branch bud were attached, remained green and alive (= zone of intercalary growth, after Wong, 1995: 15; Figs. 8, 17). After the infested internode had died off, the branch bud would start to grow and the emerging branches would push away the dry culm sheath from the bamboo stem (Fig. 9). If two adjacent internodes were infested by *I. burmensis*, the upper internode died off entirely, i.e., the side branches appeared only at the base of the lower internode. Puparia were found in the infested internodes only after the side branches had started to grow.

After several weeks or months the internode infested by *I. burmensis*, which was still attached to the bamboo shoot, would break at the level of the exit hole (Figs. 11, 19). The upper part of the cracked internode would come to rest upon the side branches (Figs. 11, 19), then dangle at the tip of the shoot for a while and subsequently fall down to the ground.
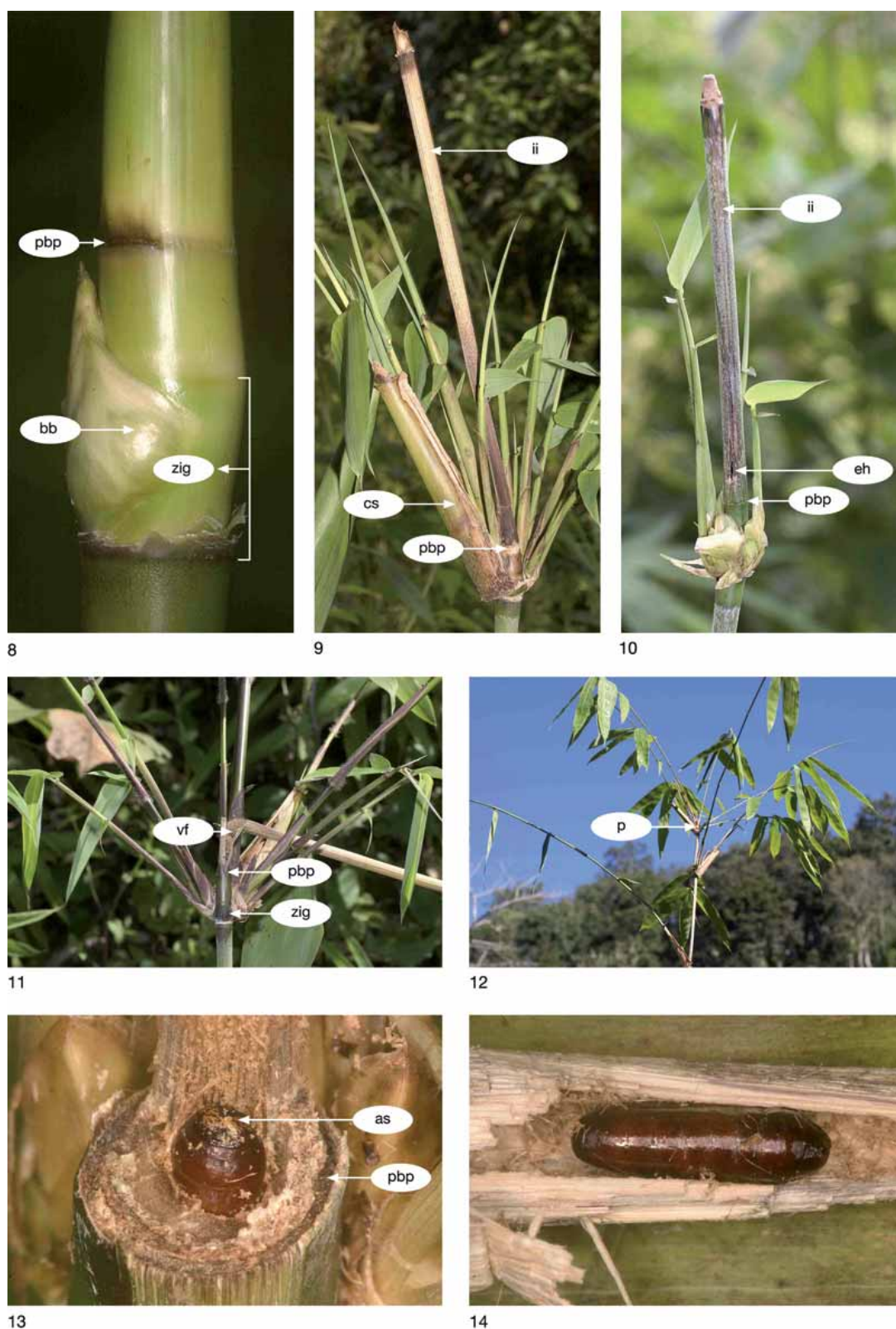
In the last stage of damage caused by *I. burmensis*, the infested bamboo shoots could be recognised by the broken tip of the bamboo shoot encircled by long side branches (Figs. 12, 20). The puparium was located in the short stump of the *I. burmensis* internode, which projected above the base of the side branches (Fig. 21).

Other insects belonging to Coleoptera, Lepidoptera or Diptera also damage the tips of the *Melocalamus compactiflorus* shoots (Kovac, personal observations). However, the damage pattern caused by *I. burmensis* can easily be distinguished from other pest damages by the dimension and position of the infested internode and by the presence of the typical torn off bamboo fibres found inside the internode cavity.

Pupariation. — Larvae of *I. burmensis* pupariated inside the internode cavities, in which they had been feeding. Puparia were either found at the base (Figs. 13, 21) or between the middle and the upper end of the internode (Fig. 14). The majority of larvae pupariated at the base of the internode cavity (frequency of basal versus apical puparia: 31:10).

Fully-grown larvae disposed to pupariate tore off vascular bundles from the bamboo wall in the basal third of the internode cavity (Figs. 6, 7). The length of the torn off bamboo fibres was 5–7 cm. In the same area where the fibres had been torn off, the larvae created a small slit-like hole. The walls surrounding the hole were thin and membranous. The hole was located in the lower third of the internode, above the predetermined breaking point, and was oriented towards the newly emerged side branches (Figs. 10, 18).

For pupation most larvae moved down to the bottom of the internode cavity and compressed the torn off bamboo fibres in the area between them and the exit hole (Fig. 7). When the bamboo fibres were pushed aside by the observer, the larvae moved them back into place. Finally, the larvae enclosed themselves with finer bamboo particles, probably mixed with frass, and then pupariated. The posterior end of the puparium was situated slightly above the upper boundary line of the intercalary zone (Fig. 21). The anterior end of the puparium,

Figs. 8–14. Damage of bamboo shoots caused by *I. burmensis*, and pupariation. 8, Basal part of an *I. burmensis* internode, early stage of infestation. The culm sheath was removed to show the branch bud, the zone of intercalary growth and the predetermined breaking point of the internode. 9, The apical part of the bamboo shoot has fallen down, but the *I. burmensis*-internode is still attached to the bamboo shoot. The emerging side branches have pushed away the culm sheath from the internode wall. 10, *I. burmensis* internode with side branches largely removed in order to show the slit-like exit hole. 11, The *I. burmensis*-internode has cracked at the level of the exit hole (above the predetermined breaking point). The exposed internode cavity is filled with torn off, compressed vascular fibres, which protect the puparium. 12, The cracked upper part of the *I. burmensis*-internode has dropped to the ground. The puparium rests inside the stump of the *I. burmensis* internode at the tip of the bamboo shoot. 13, *I. burmensis* puparium stuck in the basal part of the internode. The internode was broken at the predetermined breaking point in order to show the protruding puparium. 14, *I. burmensis* puparium stuck in the upper part of the internode cavity, anterior end on right hand side. as = anterior spiracle; bb = branch bud; cs = culm sheath; eh = exit hole; ii = *I. burmensis*-internode; p = puparium; pbp = predetermined breaking point; vf = vascular fibres; zig = zone of intercalary growth.
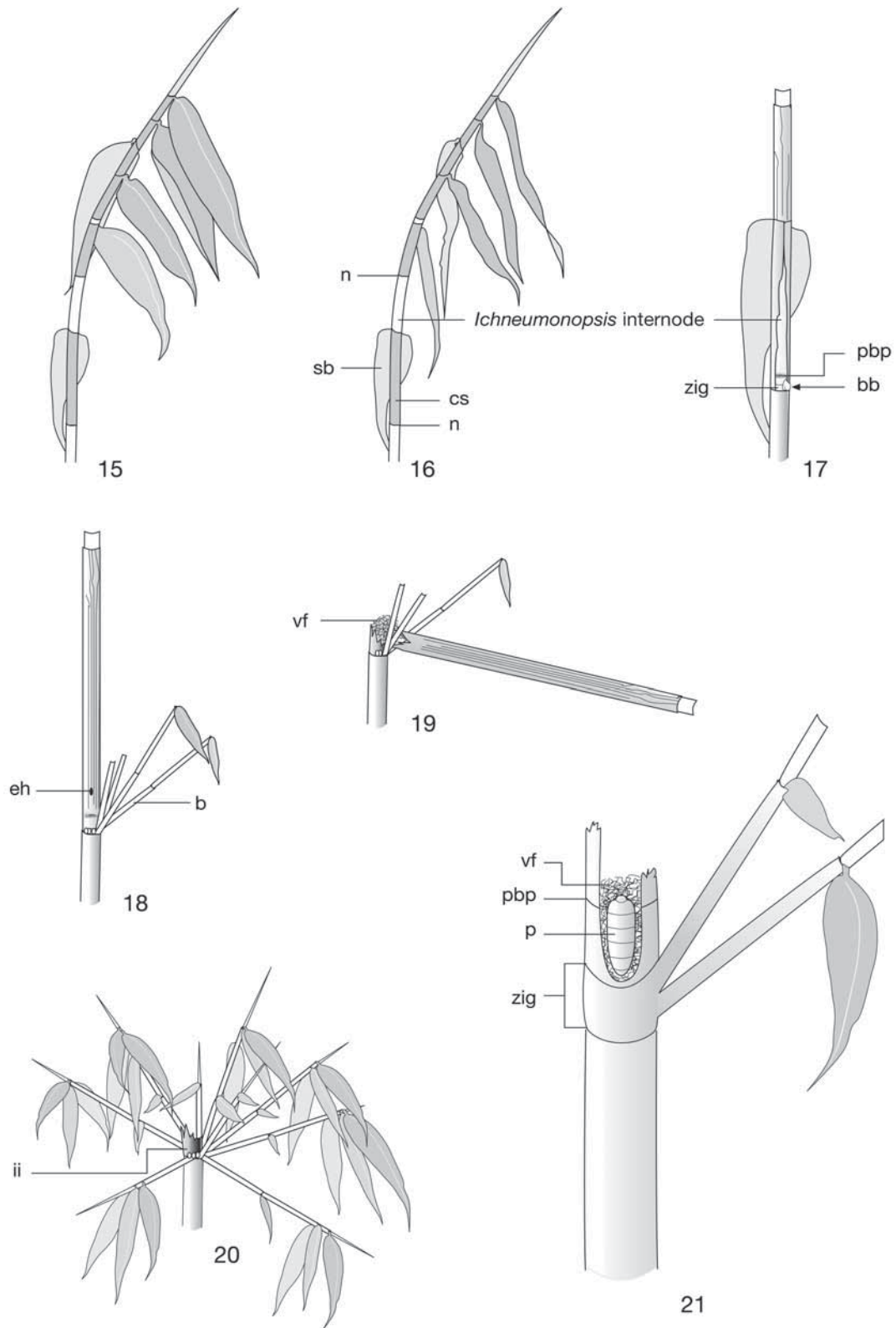
Figs. 15–21. Damage symptoms of bamboo shoots attacked by *I. burmensis*. 15, Tip of an unaffected *Melocalamus compactiflorus* bamboo shoot. 16, Tip of a *Melocalamus compactiflorus* bamboo shoot infested by *I. burmensis*. The leaves of the upper internodes have started to wither. 17, The apical internodes have dropped down to the ground, but the *I. burmensis* internode is still attached to the bamboo shoot. A part of the internode sheath was removed in order to show the location of the bud, the zone of intercalary growth and the predetermined breaking point. 18, The newly emerged branches at the base of the *I. burmensis*-internode have displaced the internode sheath. Most branches are not depicted in order to show the exit hole above the predetermined breaking point. 19, The *I. burmensis* internode has cracked at the level of the exit hole and dangles at the tip of the bamboo shoot. The puparium is still protected by the torn off vascular fibres. 20, The apical part of the *I. burmensis*-internode has dropped to the ground. The basal stump of the internode remains attached at the tip of the bamboo shoot and harbours the puparium. 21, Longitudinal section of the enlarged basal part of an *I. burmensis*-internode showing the location of the puparium. b = branch; bb = branch bud; cs = culm sheath; eh = exit hole; ii = *I. burmensis*-internode; n = node; p = puparium; pbp = predetermined breaking point; sb = sheath blade; vf = vascular fibres; zig = zone of intercalary growth.

bearing the large anterior spiracles, was directed upwards and surpassed the predetermined breaking point (Figs. 13, 21). Sometimes, only the anterior part of the puparium was surrounded by fine particles, whereas the rest of the body was in close contact with the bamboo wall.

Some larvae pupariated in the middle or in the upper end of the internode cavity. They built a bamboo barrier made of bamboo fibres and smaller particles between them and the exit hole. The anterior part of the puparium was oriented downwards, i.e. towards the exit hole, which was formed at the same location as in the basal puparia. If the upper part of the internode containing the puparium broke off and dropped down to the ground, the puparium was still protected by the internode walls and the torn-off bamboo fibres. In the laboratory an adult emerged successfully from a broken off internode infested by *I. burmensis*, which was found laying on the ground.

Seasonal history. — In north Thailand we observed only two adults of *I. burmensis* in the field, both in November. The two females flew very fast between the scattered bamboo stands or walked around on the apical parts of bamboo shoots. Larvae were found from October (first record on 13 October) until the end of November (last record on 28 November). Puparia were present from the beginning of November (first record on 4 November) until the end of April (last record on 26 April). Adults reared from larvae or puparia collected in November or December emerged between the end of March and mid May of the successive year (9 males and 5 females). In NE India, A. Freidberg collected three adults in April.

Predators and parasitoids. — Common predators found on young bamboo shoots were several species of Dermaptera (earwigs). In one case we detected an earwig inside the puparial chamber feeding on the puparium of *I. burmensis*. Three internodes with typical *I. burmensis* feeding markings and torn off bamboo fibres were broken open basally and the puparia were missing. We presume that these internodes were damaged by woodpeckers or other birds.

Two species of gregarious parasitoid wasps were reared from *I. burmensis* puparia. One species belonged to the Chalcidoidea (Family Eulophidae, subfamily Tetrastichinae), the other is not yet identified. Most species of Eulophidae are primary parasitoids of concealed larvae, particularly leaf-mining Lepidoptera, Diptera, Hymenoptera, and Coleoptera (Gibson, 1993).

At the end of the dry season (between the end of March and beginning of April 2010) we collected 23 *I. burmensis*-internodes. In six internodes the puparia were still alive, in five internodes we found remains of puparia probably eaten up by predators, in five internodes the empty puparial exuvia were pierced by parasitoids and in seven internodes we only detected *I. burmensis* feeding marks, but the internode cavities were empty.

DESCRIPTION

Third instar larva. — General. Length: 12–15.6 mm (median: 13.8 mm; n = 7), width: 2.5–3.2 mm (median: 2.8 mm, n = 7). Larva elongate, conical anteriorly, truncated posteriorly, broadest in the area of the first abdominal segment. Mature larva pale yellow, dorsal and lateral parts of meso- and metathorax and at least the first three abdominal segments usually darker yellow. Conspicuous, large ramified anterior spiracles are visible on first thoracic segment.

Pseudocephalon (Figs. 22, 33, 34, p ceph). Facial mask consisting of about 9 non-dentate, short oral ridges (or rdg) on both sides of the preoral cavity merging into the adjacent accessory plate area (Figs. 22, 26). Accessory plates (ac pl) protruding from the body surface (in some figures obscured by debris), covering a larger area than the oral ridges, extending to the antenna (ant) and maxillary sensory organ (max org) and surrounding them (Fig. 22).

Cephalic lobes moderately developed, antenna 2-segmented, consisting of a basal ring and a cone-shaped apical segment (Fig. 23). Maxillary sensory organ on elevated base, consisting of two sensilla groups, each group surrounded by an incomplete cuticular fold, both groups surrounded by another complete cuticular fold, dorsolateral group consisting of one smaller papilla sensillum (pas A) and one larger papilla sensillum (pas B), ventromedial group consisting of three papilla sensilla (pas A) and one peg sensillum (pegs); pit sensilla absent or indiscernible (Fig. 24).

Stomal organ (Figs. 22, 25, sto org) oval, elevated from the head surface, bearing one pit sensillum and two or more peg-like sensilla, surrounded by normal accessory plates. Labial lobe (lal) narrow, slightly widened at apex, covered with large and acute, outwards directed spines (Figs. 22, 26, 27), tip of labial lobe bare, bearing a paired labial organ (Figs. 22, 26, 27, la org). Labial organ elevated from the surface, provided with two large openings leading into cavities containing sensilla (indistinct; Fig. 27). Two pairs of conspicuous pad-like lobes (termed here "pad organ" [pad org], see Material and Methods) containing two tiny sensilla (indistinct), one at the posteroventral corner of the face mask and one posterior to the cephalic lobe (Figs. 22, 26).

Cephalopharyngeal skeleton (slide-mounted, Fig. 32). Large and robust, with most components relatively short and wide (high). Mandible (mh) short and high, apical tooth not sharply pointed, preapical tooth at most vestigial, barely visible; anterodorsal curvature of mandible moderate, not abrupt, slightly dentate, with two indistinct teeth; dorsal and ventral apodemes (da, va) about as high as long, the former not quite posterior in position; dental sclerite absent, depth of mandible (= height of ventral concavity, as per Frías et al. 2006) shallow, about 0.16 times length of mandible; hypopharyngeal sclerite (hs) somewhat elongate, 4 times as long as width of hypopharyngeal bridge (hb); labial sclerite (ls) small, peanut-shaped, close to the hypopharyngeal sclerite, about half way between mandible and hypopharyngeal bridge; parastomal bar (pb) about 0.66 times as long as hypopharyngeal sclerite,
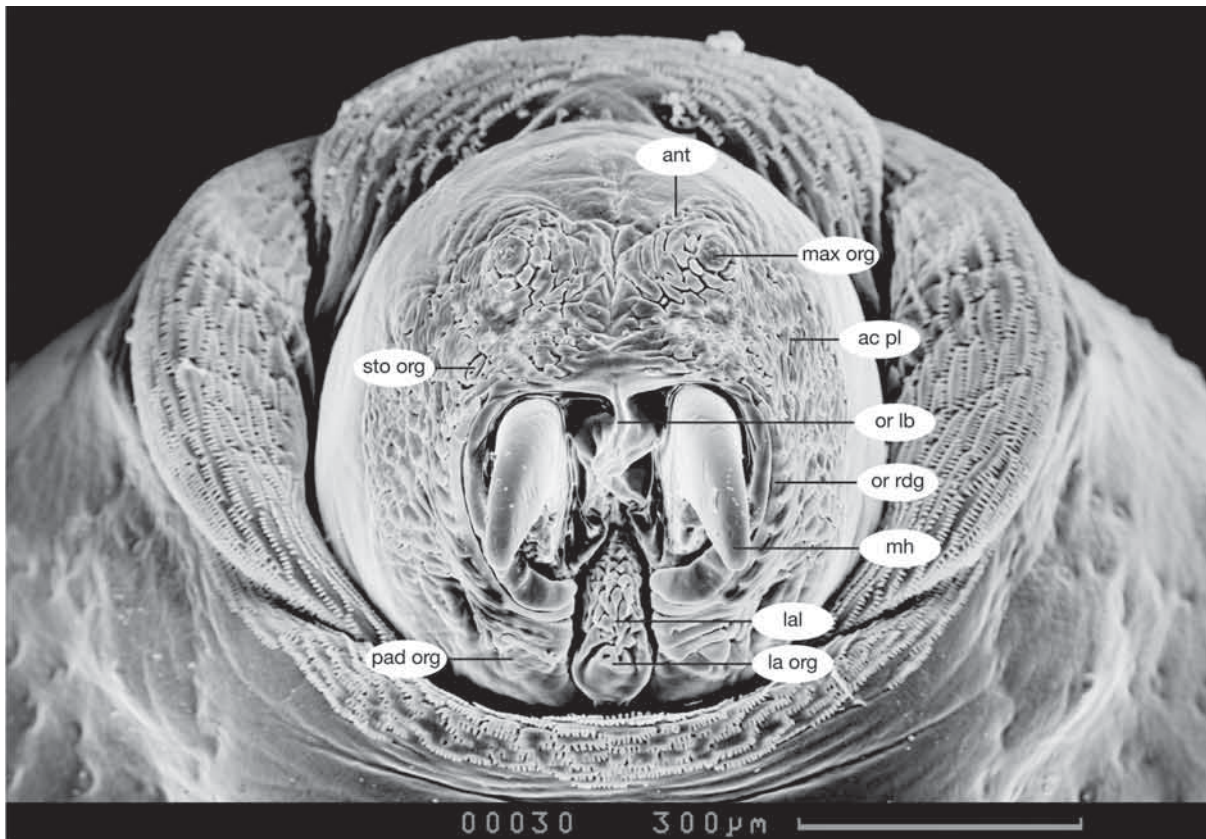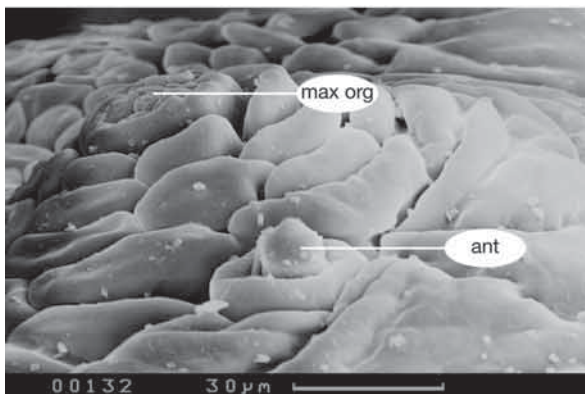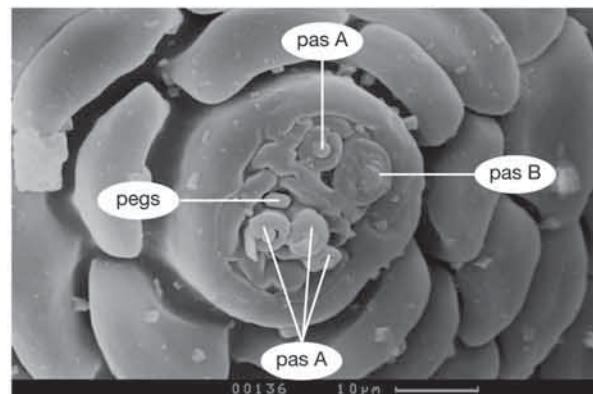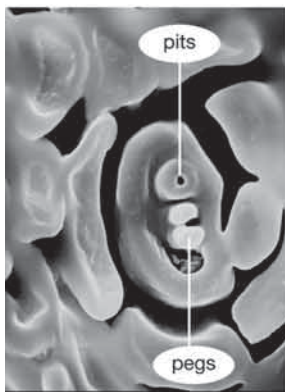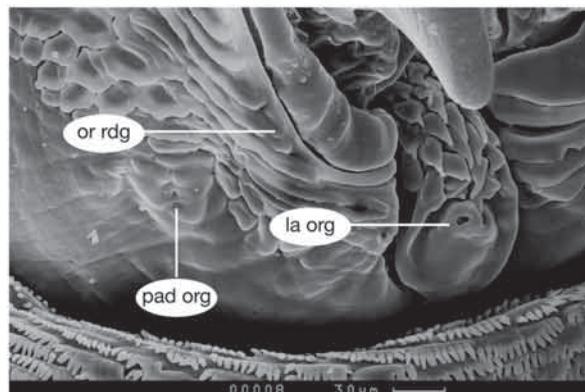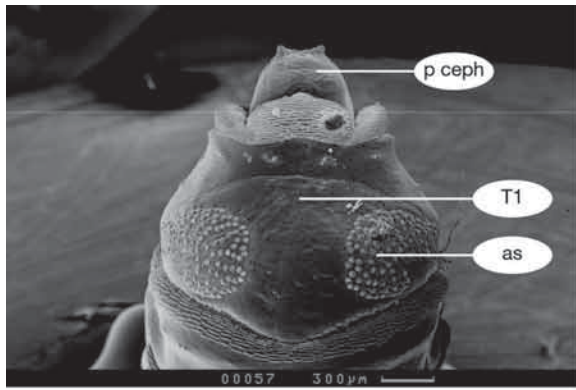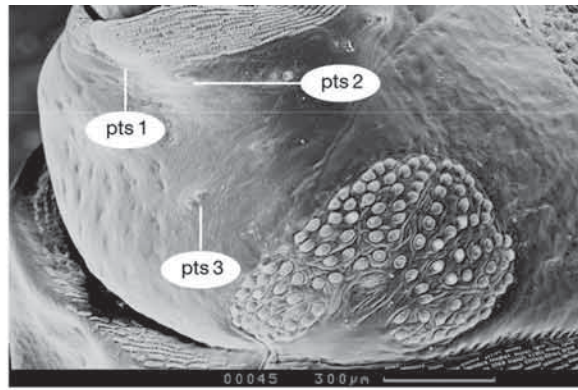
Figs. 22–27. Pseudocephalon of *I. burmensis* larva showing the sense organs (SEM pictures). 22, Pseudocephalon and prothorax. 23, Antenna and maxillary sense organ. 24, Maxillary sense organ. 25, Stomal organ. 26, Detail of pseudocephalon showing the labial lobe, labial organ and pad organ. 27, Apical part of the labial lobe and the labial organ. ac pl = accessory plates; ant = antenna; lal = labial lobe; la org = labial organ; mh = mouth hook; max org = maxillary sense organ; or lb = oral lobe; or rdg = oral ridges; pad org= pad organ; pas A = papilla sensillum A; pas B = papilla sensillum B; pegs = peg sensillum; pits = pit sensillum; sto org = stomal organ.
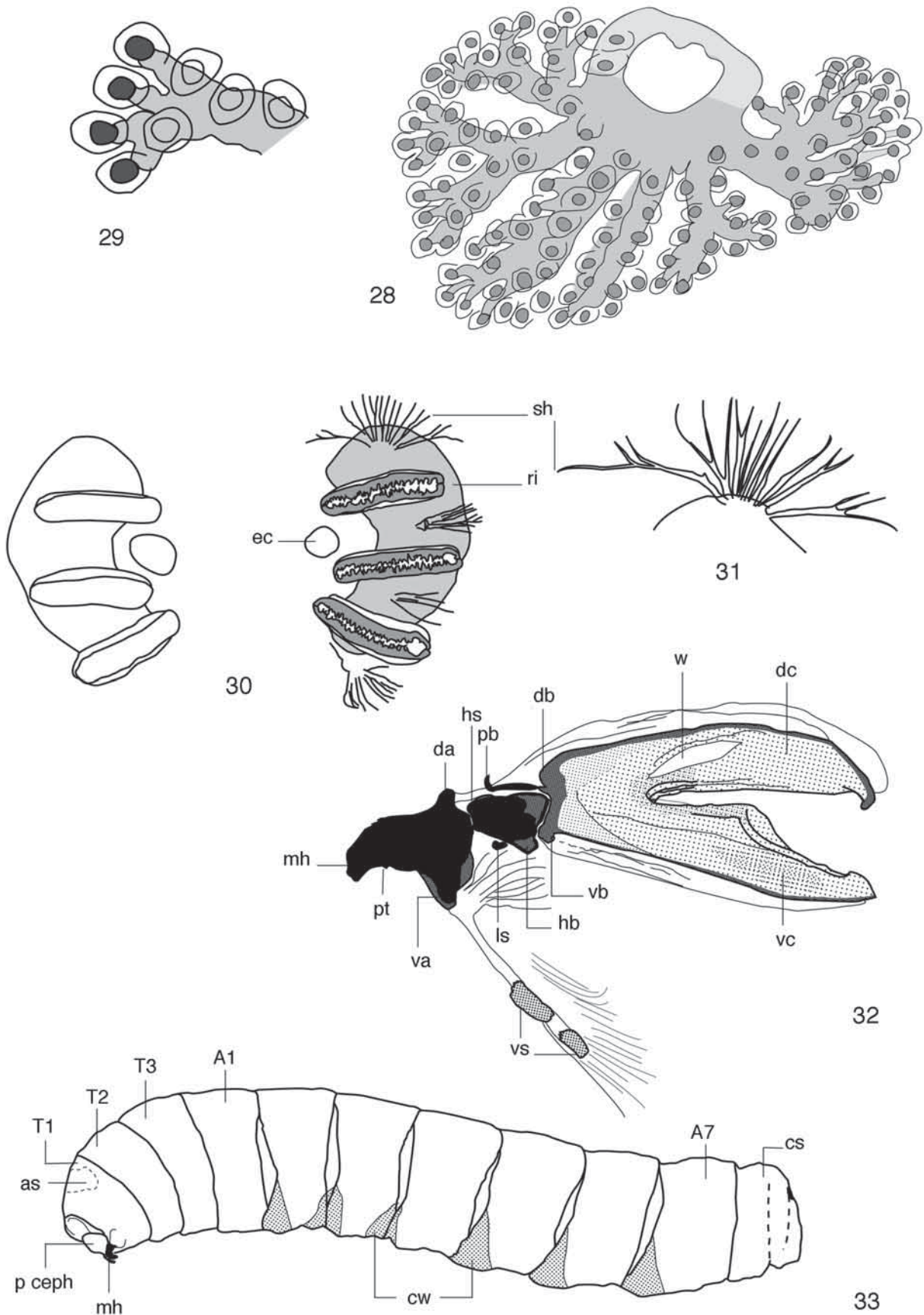
Figs. 28–33. Cephalopharyngeal skeleton, anterior/ posterior spiracles and larval habitus of *I. burmensis* (light microscopy). 28, Anterior spiracle. 29, Detail of anterior spiracle showing the papillae. 30, Posterior spiracle. 31. Spiracular hairs. 32, Cephalopharyngeal skeleton. 33, Larval habitus. A1–A7 = abdominal segments; as = anterior spiracle; cs = caudal segment; cw = creeping welt; da = dorsal apodeme; db = dorsal bridge; dc = dorsal cornu; ec = ecdysial scar; hb = hypopharyngeal bridge; hs = hypopharyngeal sclerite; ls = labial sclerite; mh = mouth hook; p ceph = pseudocephalon; pb = parastomal bar; pt = praeapical tooth; sh = spiracular hairs; T1–T3 = thoracic segments; win = window; va = ventral apodeme; vb = ventral bridge; vc = ventral cornu; vs = ventral sclerite.
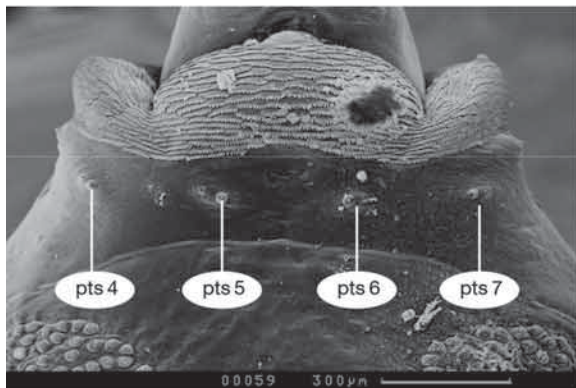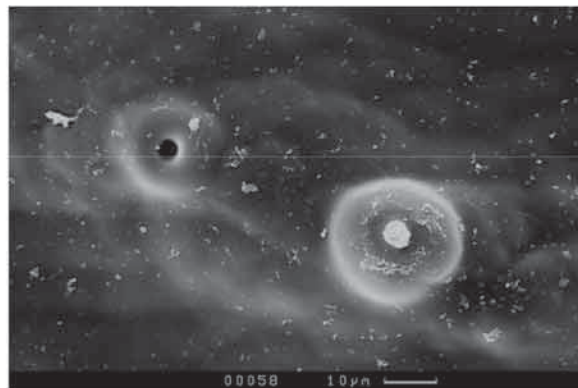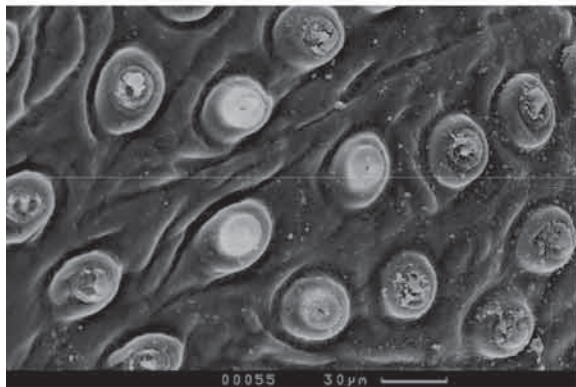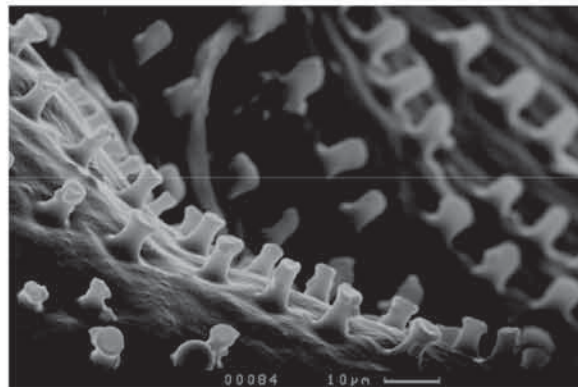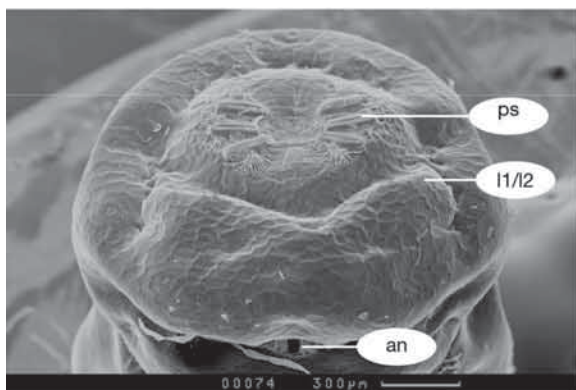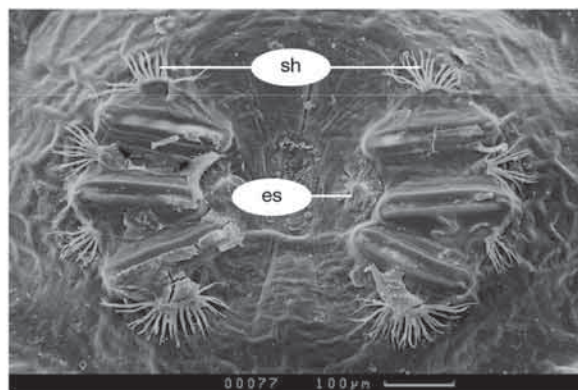
Figs. 34–41. Thoracic and abdominal segments of the *I. burmensis* larva. 34, Pseudocephalon and prothorax, dorsal view. 35, Prothoracic paired sensilla and anterior spiracle (lateral view). 36, Prothoracic paired sensilla (dorsal view). 37, Enlarged paired prothoracic sensilla (pts5). 38, Detail of anterior spiracle showing the papillae. 39, Detail of a creeping welt showing the spinules. 40, Caudal segment showing the posterior spiracle, anus and the locations of some sensilla. 41, Posterior spiracles. T1 = prothorax; an = anus; as = anterior spiracle; es = ecdysial scar; I1, I2 = intermediate sensilla; p ceph = pseudocephalon; pts 1–10 = prothoracic sensilla; ps = posterior spiracle; sh = spiracular hairs.

narrow, anterior end bent dorsally at right angle; pharyngeal sclerite and dorsal and ventral corni (dc, vc) visible, but details not clear; anterior sclerite indistinct; dorsal and ventral bridges (db, vb) normal; an elongate window (win) in middle of dorsal cornu possibly present. Single elongate divided sclerite or two small sclerites (vs) present within the cluster of ventral muscles associated with the cephalopharyngeal skeleton. This structure is possibly equivalent to the "ventral sclerite" found in *Anastrepha* by Frias et al. (2009) and Dutra et al. (2012). Based on a SEM photograph (Fig. 22), the laterally flattened oral lobe (or lb) is visible protruding between the mouth hooks, length about one third of the visible mouth hook length (dorsal view).

Thoracic segments. Segments T1–T3 (Figs. 34–36) with multidentate scales on antero-dorsal margin, less pronounced ventrally. Prothorax with 8 paired sensilla (Fig. 37) and two single sensilla, paired sensilla consisting of one pit sensillum and one papilla-like sensillum (or sensillum with an obscured small peg, Fig. 37), prothoracic sensilla (pts) distributed as follows: two paired sensilla (pts 1 and pts3) and one single pit sensillum (pts2) located laterally on the left side of the prothorax (Fig. 35), 4 paired sensilla (pts 4–7) arranged in a transverse row along the front margin of prothorax (Figs. 34, 36), two paired sensilla and one single pit sensillum (pts 8–10) located laterally on the right side of the prothorax. Two paired sensilla and several single pit sensilla also occurring on dorsum of the mesothorax (paired sensilla found at the locations 4 and 7 as compared to the prothorax). Keilin´s organ (trifid sensillum) present ventrally on both sides of the thoracic segments (shape as in Fig. 44 of Carroll &Wharton, 1989).

Anterior spiracle (Figs. 13, 28, 29, 34, 35, 38, as). Each anterior spiracle usually consists of more than 100 knob-like papillae (96; 100; 106; 110; 115; 124; 128; 3 larvae and 1 puparium examined), number of papillae varies between the right and left side of the body. Papillae arranged on six radiating main branches, some branches ramify once or twice. The spiracle area including papillae occupies about 16% of the visible surface of the prothorax in lateral view. The papilla slit is about 0.16 times as long as the papilla diameter (Figs. 38, 44).

Abdomen. Six creeping welts present on abdominal segments 2–7 (Fig. 33), more obvious ventrally, but extended also dorsally, each creeping welt composed of several rows of spinules with truncate apex and rounded perimeter (Fig. 39), but sometimes slightly pointed.

Caudal segment (Fig. 40). Posterior spiracles (Figs. 30, 40, 41, ps) above midline, with 3 slit-like openings, dorsal and central slits sub-parallel, distance between them about half the length of a rima (Fig. 30, ri), dorsal and ventral slit more medial, ventral slit situated at an angle of about 45° to the central slit, nearly touching it medially. Distance between two spiracles about as wide as the length of a spiracular slit, rima 4–5 times as long as wide. Spiracular hairs (= interspiracular processes, Figs. 30, 31, 41, sh) well developed, longest hairs

about half as long as rimae, arranged in four groups, external spiracular hairs containing more hairs than median ones, about half of the hairs branched once or twice.

Caudal ridge not apparent, dark transverse line in the medial region absent. Anal lobes lacking. Intermediate sensilla (I1 and I2) present, close to each other. Dorsal sensillum (D), lateral sensillum (L) and ventral sensillum (V) seem to be present (not depicted in Fig. 40). Other sensilla to be expected (see White et al. 1999, Fig. 33.7) not visible, maybe due to contaminations.

Puparium. — Length: 7.5–9.3 mm, maximum width: 2.5–2.8 mm (n = 3), width measured between the metathoracic and first abdominal segment. Fresh puparia yellow to pale brown, older puparia dark brown, anterior part (thoracic segments) almost black, caudal end also somewhat darkened (Fig. 14). Puparium with 3 thoracic and 8 abdominal segments, and rounded anterior and posterior ends, surface of all segments except for prothorax and area surrounding the posterior spiracles annulated (Fig. 42).

Prothoracic spinules of the anterior margin partly invaginated, prothoracic sensilla pts 2–9 present, pts 1 and pts 10 probably hidden under invaginated parts of prothorax (Fig. 43). Anterior spiracles (as) prominent and slightly protruding, covering at least one third of the prothoracic surface area. Caudal segment with complex pattern of wrinkles (Figs. 45, 46), posterior spiracle flattened, spiracular hairs and anus as in third instar larva (Figs. 45, 46).

***Comparison of* I. burmensis *larvae with other Gastrozonini and Tephritidae*.** — So far, larvae of four Gastrozonini species have been described (Elson-Harris, 1992): *Chaetellipsis atrata* Hardy, 1973 (= *Chaetellipsis paradoxa*, Bezzi), *Chaetellipsis* sp. (= *C. maculosa* Hancock & Drew; D. Hancock, pers. com.), *Gastrozona fasciventris* (Macquart) and *Taeniostola limbata* Hendel (= *Cyrtostola limbata*, see Hancock & Drew 1999). The main characters of the Gastrozonini larvae described by Elson-Harris (1992) and of *I. burmensis* are compared in Table 1. Elson-Harris explicitly described the stomal organ, facial mask, anterior spiracle, and anal lobes of each species. The data entries in Table 1 for labial lobes, antenna, maxillary organ, pad organ, oral lobe, and paired sensilla are based on our interpretation of her SEM figures.

The facial mask of *I. burmensis* broadly flanks the mouth laterally and extends to the antennal and maxillary sensory organs. It mainly consists of accessory plates. Oral ridges are reduced, non-dentate and cover just a narrow area along the preoral cavity. In Gastrozonini larvae described by Elson-Harris (1992), the facial mask is more or less triangular, confined to the lateral mouth area and consists mainly of dentate oral ridges. In some species a few accessory plates are present at the apices of the oral ridges.

The labial lobe of *I. burmensis* is covered with strong spines and bears a paired labial organ. Both of these features are

Table 1. Comparison of larval characters of Gastrozonini described by Elson-Harris (1992) and of *I. burmensis*.

Species	Facial mask	Labial lobe	Antenna	Maxillary organ	Stomal organ	Pad organ	Oral lobe	Anterior spiracle	Paired sensilla	Anal lobes
Chaetellipsis paradoxa	narrow rounded, oral ridges short, well-developed, dentate; terminal accessory plates lacking	?	?	?	rounded, protuberant, with small sensilla surrounded by 6–7 long and short, unserrated preoral lobes	?	present	fan, 13–16 tubules in 1 row	?	present
Chaetellipsis maculosa	+/– triangular, oral ridges well-developed and dentate; terminal accessory plates lacking	bare	3-segmented	typical	rounded, protuberant, with small sensilla surrounded by 6–7 long and short, unserrated preoral lobes	present	present	fan, 17–20 tubules in 1 row	?	present
Gastrozona fasciventris	triangular, oral ridges well-developed and dentate (accessory plates?)	bare	3-segmented	typical	with 2–3 tapered sensilla surrounded by 8–10 unserrated preoral lobes	?	present	fan, 26–30 tubules in 1–2 parallel row	?	present
Cyrtostola limbata	triangular, oral ridges well-developed and dentate, few terminal accessory plates present	?	3-segmented	typical	small, rounded, with small sensilla surrounded by 5–6 serrated preoral lobes	?	?	fan, 33–36 tubules in 2–3 parallel rows	?	present
Ichneumonopsis burmensis	broad, extending to antenna, oral ridges reduced and non-dentate, accessory plates predominate	covered with spines	2-segmented	typical	small, oval, with small sensilla, surrounded by unserrated accessory plates	present	present	around 100 papillae arranged on 6 radiating main branches	present	absent
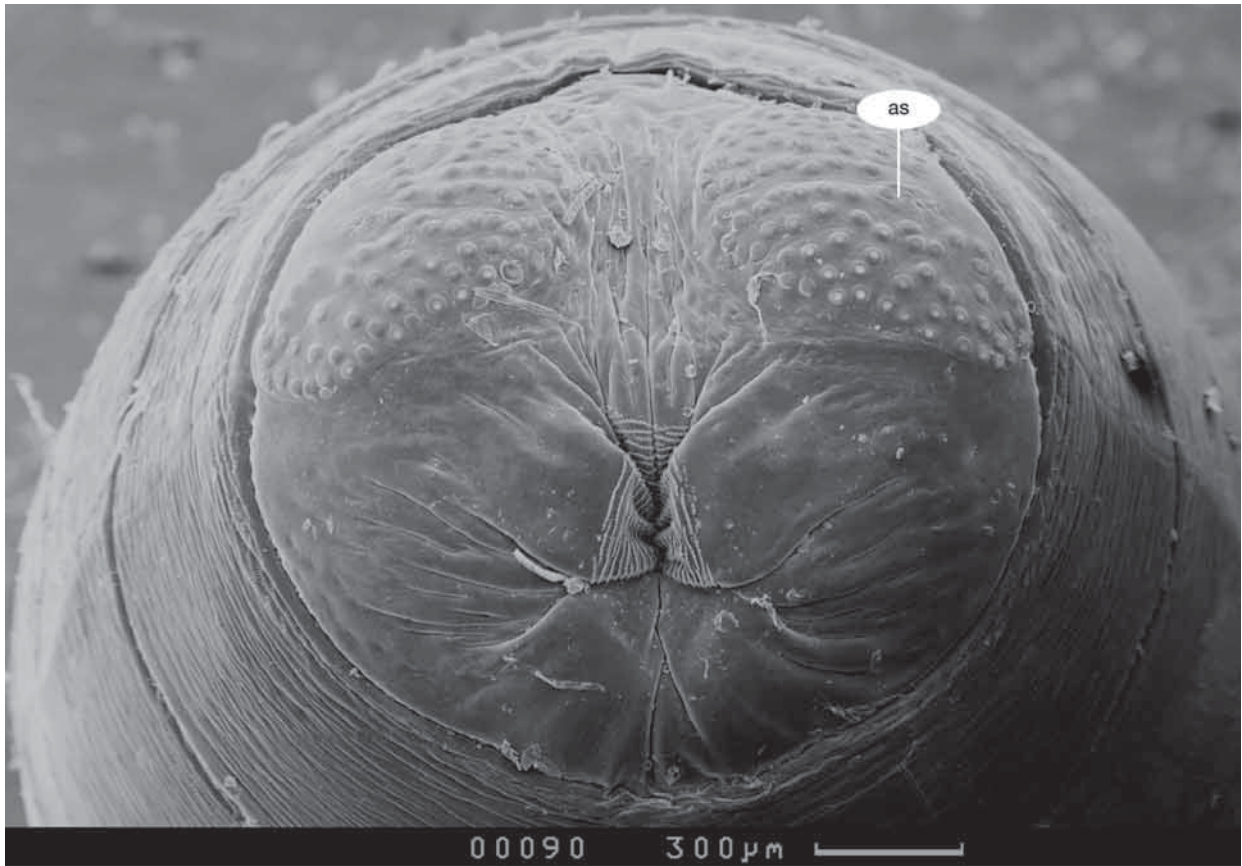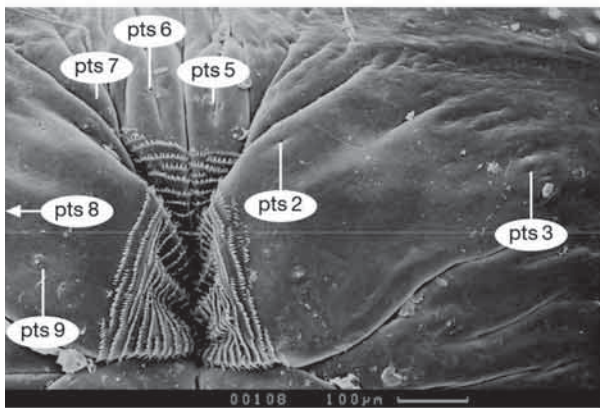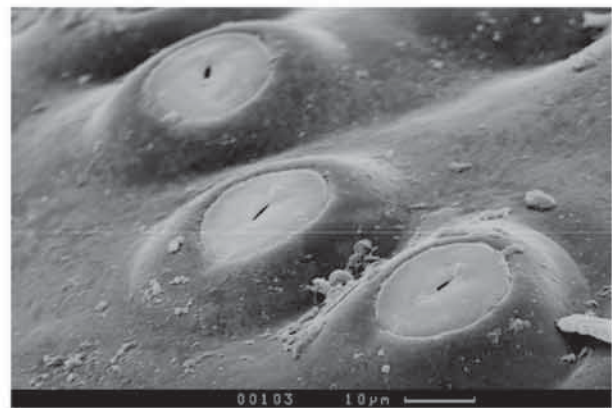
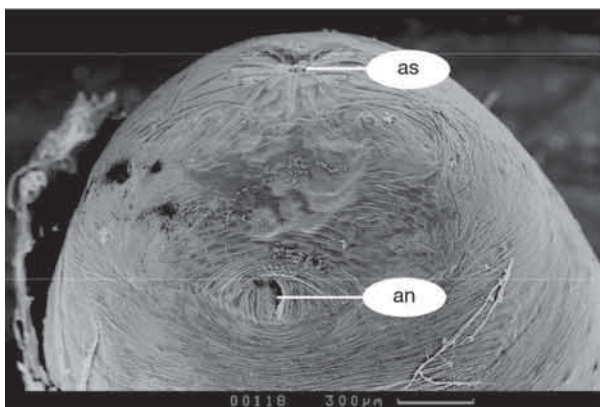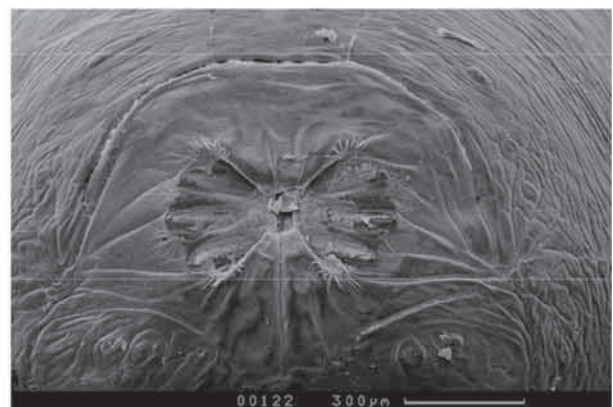Figs. 42–46. Puparium of *I. burmensis* (SEM photographs). 42, Apical end of the puparium showing the anterior spiracles. 43, Detail of invaginated frontal part of prothorax showing the locations of the paired sensilla. 44, Detail of the anterior spiracle showing three papillae. 45, Caudal end of the puparium. 46, Posterior spiracles. an = anus; as = anterior spiracle; pts 2–9 = prothoracic sensillae.

unusual, and perhaps unique, among tephritid larvae described to date. The Gastrozononi studied by Elson-Harris (1992) possess a bare labial lobe.

The antenna of *I. burmensis* is two-segmented, the antennae of Gastrozonini described by Elson-Harris (1992) are 3-segmented. The maxillary sense organ of *I. burmensis* and other Gastrozonini is similar. It consists of two sensilla groups: a group with two papilla sensilla (one of them larger) and a group with three papilla sensilla and a peg or peg-like sensillum. The stomal organ of *I. burmensis* and other Gastrozonini is also similar, containing at least one pit sensillum and several peg-like sensilla.

There are 2 pairs of pad organs in *I. burmensis* (one posterior to the cephalic lobes, one at posteroventral corner of the oral ridge region). Pad organs are also present in other Gastrozonini (not studied in detail) and seem to be widely distributed in Tephritidae. In *Anastrepha ludens* there are 5 pairs of pad organs (Carroll & Wharton, 1989), and in *Ceratitis rosa*, 6 pairs (Carroll, 1998), all arranged in similar positions.

A laterally flattened oral lobe, which is perhaps homologous with the oral lobe of Headrick & Goeden (1990), protrudes between the mouth hooks in *I. burmensis*. In other Gastrozonini an oral lobe or paired oral lobes are also present (Elson-Harris, 1999).

The most striking morphological character of *I. burmensis* larvae is the large and strongly ramified anterior spiracle (Figs. 28, 34, 35), with some 100 comparatively flat papillae. Tephritids (and other Acalyptratae) usually possess tube-like papillae (tubules) arranged in a fan-like row. In Tephritidae the anterior spiracles possess in general 2–20 tubules; in relatively large bodied species there may be more, for example, in some *Rhagoletis*, *Anastrepha* and also in *Strauzia* (Phillips, 1946; Steck et al., 1990). Frías et al. (2006) observed up to 27 tubules in *Toxotrypana*. In the Gastrozonini studied so far (Elson-Harrison, 1992) the anterior spiracles are fan-like and possess 13–36 tubules arranged in 1–3 rows (Table 1).

A conspicuous character of *I. burmensis* larvae is the paired sensilla located on the prothorax (Figs. 34, 36, 37, pts 1–10). They consist of a pit sensillum and a papilla sensillum (or maybe a peg sensillum with an obscured peg). In other Gastrozonini from our collection we have only found single sensilla on the prothorax. Paired sensilla similar to those found in *I. burmensis* also occur on the labial lobe of *Anastrepha ludens* (Carroll & Wharton, 1989, Fig. 42).

Other differences between *I. burmensis* and other Gastrozonini studied by Elson-Harris (1992) include the shape of the spinules of the creeping welt (apex of spinules truncated in *I. burmensis*, pointed in other Gastrozonini), the anal lobes (absent in *I. burmensis*, present in other Gastrozonini). Additionally, we have noted that a caudal ridge is absent in *I. burmensis*, but present in most other Gastrozonini in our possession.

DISCUSSION

Ichneumonopsis burmensis adults are rarely found in collections, maybe due to low population density or because they are difficult to collect, since they are fast fliers and preferably stay in the upper region of the bamboo shoots. In the present study, larvae of *I. burmensis* were easier to find than the adults due to the conspicuous damage patterns caused by the larvae at the tips of the bamboo shoots. To date *I. burmensis* was known from north-eastern India (Meghalaya) and western Myanmar. We have newly recorded this species from northwest Thailand. We expect that *I. burmensis* is also distributed in other locations where the associated bamboo species *Melocalamus compactiflorus* grows, i.e., in Bangladesh, N Thailand, S Yunnan, and Vietnam (Ohrenberger, 1999; Dezhu & Stapleton, 2006).

In north Thailand we have collected *I. burmensis* adults in November. The larvae developed in October and November, they pupariated around November, remained in diapause for several months and emerged in March–May. Adults known from Myanmar and India were collected at about the same time of the year as the Thai specimens, i.e., in April and October (Hardy, 1973; Radhakrishnan, 2000; A. Freidberg, pers. obs.). Since *Melocalamus compactiflorus* has two shooting seasons, one in May–June and one in October–November, and the adults of *I. burmensis* are present at both times of the year, we presume that *I. burmensis* is bivoltine, i.e., has two generations per year.

Judging from the feeding marks found in bamboo shoot internodes collected at different stages of larval development, the freshly hatched larvae penetrated into the basal part of the internode, which is softer than the apical part at that stage of development. The eggs were probably laid under the margin of the culm sheath, as we have observed in most other Gastrozonini (Kovac, personal records). After reaching the internode cavity, the larvae moved upwards in order to feed on the bamboo pith. The bamboo walls were not eaten, but in the basal part of the internode the bamboo wall was damaged, apparently causing the apical part of the bamboo shoot to die off.

Most bamboo species are hollow and lack any filling substrate. Therefore, bamboo pith is a rather uncommon food source for Gastrozonini. Typically, Gastrozonini feed on the soft walls of decaying bamboo shoots. The bamboo walls of decaying shoots are moist, amorphous and pulpy, comparable to fruits, while bamboo pith is relatively dry and fluffy or fibrous. Such differences in texture of the food source have been correlated with the morphological appearance of the facial mask of the larva (White & Elson-Harris, 1992; Courtney et al., 2000).

In saprophagous frugivorous tephritids the facial mask often bears dentate oral ridges flanking the preoral cavity laterally (White & Elson-Harris, 1992). The grooves between the oral ridges are thought to direct food-carrying liquids to the mouth. In truly phytophagous, predatory or parasitoid larvae

the facial mask bears plates or pads (accessory plates) instead of oral ridges or may be strongly reduced (see Courtney et al., 2000).

The structure of the facial masks of Gastrozonini examined in the present study corroborates these observations. The saprophagous Gastrozonini, which feed on decaying bamboo walls, posses a facial mask bearing toothed oral ridges. *I. burmensis* larvae feeding on the fibrous bamboo pith mainly possess accessory plates and the oral ridges are largely reduced. Frias (2008) suggested that the cuticular pads of the facial mask and prothorax of *Rachiptera limbata* Bigot (Tephritinae) may play a role in constructing a cocoon made of salivary secretions.

The different properties of the bamboo microhabitats (persistence, texture of the food substrate) also correspond with the different behaviour of the larvae: Gastrozonini larvae living in decaying bamboo shoots move quickly, skip when disturbed and exit the decaying internode in order to pupariate in the soil. Larvae of *I. burmensis* are sluggish, do not skip and pupate inside the bamboo internode.

We assume that the pupation of *I. burmensis* within the host, correlates with the microhabitat being long-lived (at least several months). In contrast, decaying bamboo shoots utilised by most Gastrozonini decompose after 2–3 weeks, and the larvae abandon the host to pupate in the soil. The lack of the skipping ability in larvae of *I. burmensis* is probably an ecological adaptation to pupation inside the internode, since skipping is supposed to function in reducing the risk of predation when moving to a site for pupation.

I. burmensis larvae are enclosed by internode walls and therefore need to construct an exit opening prior to pupariation. They produce a slit-like hole which is located in the lower third of the internode, above the predetermined breaking point (Figs. 10, 18), and is usually hidden by the newly emerged side branches of the bamboo shoot. The exit hole is narrow, thus restraining larger potential predators such as ants from entering the internode. The freshly emerged fly is probably able to squeeze itself out through the narrow exit hole, because the wall around the slit is thin and also elastic, at least after rain.

In the second shooting season the freshly emerged adults often do not need the prepared exit hole for leaving the internode, because the dry *I. burmensis*-infested internode usually breaks open at the level of the exit hole, and after some time the upper part of the internode falls down to the ground. Thus, two new openings are created on each side of the broken internode. Nevertheless, the puparia remain protected due to the barrier made of bamboo fibres, regardless whether the puparia stay in the basal or upper part of the internode. Even if the prepared exit hole is not used, it is beneficial for the puparium, because it causes the internode to crack at the level of the hole and not at the predetermined breaking point. If the internode were to break at the predetermined breaking point, the apical part of the puparium would be exposed and vulnerable (Fig. 13).

In order to construct the protective barrier, the larvae tear off long strips of vascular fibres from the internode wall and press them together. We have examined the larval pseudocephalon in order to find out if there are any noticeable structures, which may be involved in the barrier-producing activity. We think that the movable labial lobe is involved in this process. The labial lobe is covered by strong, outward oriented spines which may help to tear off the fibres or move them into place. Such strong spines have not been reported in other Gastrozonini. The mechanical strain applied to the labial lobe may be the reason why the labial sensilla are protected in cavities of the labial organ. In other Gastrozonini the labial sensilla are located separately on the surface of the labial lobe and protecting labial organs are lacking.

The most conspicuous morphological structures of *I. burmensis* larvae are the enlarged and ramified anterior spiracles, which are unique within the Tephritidae. The reason for the functional enhancement of the larval anterior spiracles is not known. It may be connected to a reduced air supply in the immediate surroundings of the *I. burmensis* larvae.

Most *I. burmensis* puparia spent the dry season at the tip of exposed bamboo shoots, despite the high temperatures occurring at that time of the year. Even fires, which are frequent in the dry season, did not harm them, because only the undergrowth was burning and not the apical parts of the bamboo stems. The barrier made of torn off fibres, bamboo particles and frass protects the puparia to some extent against predators, parasitoids or desiccation. Nevertheless, the larval mortality was high: only 6 out of 23 puparia collected at the end of the dry season were found alive (mortality of 74%).

Ichneumonopsis is a genus of obscure phylogenetic relationships, which might belong to the tribe Gastrozonini as they are also associated with bamboo shoots. If that is the case, the strong differences between *I. burmensis* and other Gastrozonini larvae suggests that this genus has an isolated position within the Gastrozonini.

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