TRUPLAYA FEROX (INSECTA: DIPTERA: MYCETOPHILOIDEA), A NEW MALAYSIAN KEROPLATID FROM BAMBOO PHYTOTELMATA WITH LARVAE PREDACEOUS ON ANTS

Damir Kovac and **Loïc Matile**

ABSTRACT. - *Truplaya ferox*, new species, from Peninsular Malaysia is described and illustrated. This is the first description of a larva of the genus *Truplaya.* A peculiar spinose premandibular teeth of the larva might be autapomorphic for the genus or species and the presence of only two anal lobes corroborates the diagnostic value of this feature at the tribe level. The larvae live in water-filled internodes of upright bamboo culms, whose walls have been pierced by various wood-boring organisms. They build slimy webs above the water surface and prey on internode inhabitants or on animals walking on the bamboo surface, which are caught by a method not previously recorded for the Keroplatidae: the larvae stick the forepart of the body far out of the hole, grab the passing prey and pull it into the web. Another remarkable behavioural trait of the larva is the occasional complete closure of the entrance by a membraneous layers, where newly eclosed flying insects are probably seized when trying to leave the internode. Most prey items found in the field were ants (80.7%). Thus, *Truplaya* has a similar prey spectrum as web-building spiders occuring in the same habitat. This and other observations indicate competition between *Truplaya* and the spiders for both food and space. The adults of *T. ferox* are larger than other species of *Truplaya* and are wasp mimics. The eggs are "shot" into the internodes from flight. In bamboo culms with artificial holes *Truplaya* colonized up to 30 % of the available internodes. The evolutionary significance of the life-habit of the new species is discussed.

KEY WORDS. - *Truplaya*, new species, taxonomy, Diptera, Malaysia.

INTRODUCTION

The first record of a predaceous keroplatid from the Oriental region has been that of the larva of *Xenoplatyura beaveri* Matile of the tribe Orfeliini, which preys on small insects entangled in its slime web when entering or leaving the pitcher *Nepenthes ampullaria* Jack

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(Beaver, 1979; Matile, 1979). While the predatory habit of some representatives of this tribe has been known in other zoogeographical regions, the specialization on pitcher plants as habitat had not previously been reported for the Keroplatidae.

We record here another new habitat for a predaceous larva of the Orfeliini, the water-filled internode cavities of bamboos, and a more agressive behaviour, since the larva of *Truplaya ferox*, new species, is able to drag into its web such dangerous insects as ants. Curiously enough, two other species of Orfeliini associated with ants have been discovered in the recent years, one in Sri Lanka (Chandler & Matile, in prep.), the other in Panama (Matile, in prep.). We also present the first morphological description of a larva of the genus *Truplaya*.

MATERIAL AND METHODS

Biology. - All field observations and experimental work were done by the senior author during an ongoing investigation on the animal community of bamboo in Peninsular Malaysia (Kovac, 1994; Kovac & Streit, 1996). Various methods were used to investigate the biology of *Truplaya*:

(a) Thirty bamboo culms (several years old) were felled randomly. The internodes with natural holes (4-5 holes per culm on average) were sawn open and the internode inhabitants collected.

(b) In order to test whether *T. ferox* prefers internodes with holes of a particular size and/or height above the ground, artificial holes were bored into the 16 lowest internodes of 1-2 year old bamboo culms. Four different types of holes were bored in the following sequence, starting with the lowest internode: (1) circular hole, diameter 10 mm; (2) circular hole, diameter 5 mm; (3) circular hole, diameter 1.2 mm; and (4) slit-shaped hole, 20 x 8 mm. A ladder was used to reach the higher internodes (up to 6-7 m high). Altogether 13 culms were provided with holes, thus there were 52 available internodes for each of the four types of holes. After three years the culms were felled and the internode inhabitants collected.

(c) For the observation of the internode inhabitants and for additional studies on the rate of occupation of bamboo internodes by *T. ferox*, 200 holes of 9 mm diameter were bored into easily accessible internodes (up to 1.8 m high) at 10 different sites and during two field research stays. The holes were bored at the lower third of the internodes. Two to three culms were needed per site for the preparation of 10 internodes. Internodes which had already been punctured naturally by animals were not used. Hundred holes were bored on 1 May 1993 ("May-group") and the remaining 100 holes on 19 August 1993 (August-group). Both groups of internodes were inspected weekly with an endoscope between 27 August 1993 and 31 December 1993 ("first study period", 18 weeks) and between 7 June 1994 and 16 August 1994 ("second study period", 10 weeks). This means the "May-group" was checked for the first time c. 4 months after the boring of the holes, the "August-group" already after one week. It was checked, whether the internodes were inhabited by *Truplaya* and if there was any prey in the webs (the prey could not, of course, be taken to the lab for further identification). In one case a larva pupated during the second study period. After the pupation the entrance was covered with a plastic bag so that the adult was easily captured when it left the internode.

Taxonomy. - Seven samples, all collected by the senior author in Peninsular Malaysia, University of Malaya, Ulu Gombak Field Studies Centre, altitude 250 m, were studied by the junior author for the description of the new species (1 male, 1 female, 4 larvae, 1 pupa). Probably due to inappropriate conditions of storage, the larvae were in very poor condition. One had severely deteriorated in alcohol, and only the elements of the cephalic capsule could be saved. The others broke in several pieces when treated with KOH. Microscopic slides of these fragments were prepared after staining with chlorazol black (Carayon, 1969). On the other hand, the imagines were in very good condition and were easily dry-mounted by the method of Sabrosky (1966), modified by the replacement of cellosolve by monoethylene glycol (Matile, 1994). They were then glued to a classical entomological cardboard piece. The apex of the male abdomen was cut and cleared in KOH, the genitalia were then further extracted and stored in glycerine in a microvial, and the pregenital tergites and sternites dried and glued to the cardboard bearing the insect.

All the drawings were executed under the microscope with the help of a camera lucida.

SYSTEMATICS

Truplaya (Truplaya) ferox, new species
(Figs. 1-12)

Material examined. - Holotype - male (SMF D 3699), Peninsular Malaysia, University of Malaya, Ulu Gombak Field Studies Centre (University of Malaya), location 3°19´32´´N, 101°45´16´´ E, altitude c. 250 m, ex pupa in a bamboo internode of *Gigantochloa scortechinii*, coll. D. Kovac, 24 Jun.1994.

Paratype - female, same data as in holotype, collected while hovering in front of an internode entrance of *G. scotrechinii*, coll. D. Kovac, 6 Jul.1994.

The type material has been deposited in the Senckenberg Museum, Frankfurt a. M. (SMF; holotype male) and in Muséum national d'Histoire naturelle, Paris (MNHN; paratype female).

Further material examined: 4 larvae, same data as above, collected from felled bamboo culms of *G. scortechinii*; 1 pupa, same data as above, all collected by D. Kovac, deposited in MNHN.

Male (holotype) - Length of body: 14 mm (without antennae). Length of wing: 9 mm. Occiput brownish behind the ocellar callus, the rest yellowish. Ocellar callus brown, frons yellow. Antennae: scape, pedicel and the first two flagellomeres yellow, rest of flagellum brown. Face and palpi pale yellow, clypeus and mouthparts darker.

Thorax: prothorax yellow with a silvery sheen, prosternum without bristles. Scutum: ground color silvery yellow, the disk bearing three wide brown longitudinal stripes, very narrowly separated, the median one extending to anterior margin, the lateral ones to scutellum. Scutal bristles dense and short on disk, sparse and longer laterally, an elongated tuft of black dense bristles in the prealar area. Scutellum brown, with marginal bristles, the apical one longer. Mediotergite brown, strongly silvery laterally, without bristles. Lateral sclerites of meso- and metathorax light brown, membranous areas yellow. Pleural sclerites and laterotergite without bristles, with a silvery sheen appearing according to light incidence.

Legs yellow, the median coxa with a median longitudinal light brown streak, the hind one with an oval, darker basal spot and a faint postero-apical spot. Tibial spurs brown. Tibial setulae irregular on basal fourth of T I, less than basal fifth on T III, basal half on T III. Fore pretarsus a little shorter than the tibia (6 : 5.8).

Wings clear, yellow-tinged, the apical third slightly clouded. Costa ending widely basad of apex of wing. Sc ending a little distad of base of Rs; Sc2 very close to humeral transverse. R4 short, distant of apex of R1 by about its own length. Frm shorter than stem of anterior fork (1 : 1.8), with setulae. M2 and M3 interrupted before wind margin, anal complete. Halteres whitish yellow.

Abdomen petiolate as in the other species of the genus. Ground colour of first two tergites yellow, indistinctly darker at basis. Tergite III yellow, brown dorsally except apical fourth. Tergite IV brownish, apical and ventral margins yellow. V entirely brownish, the following yellowish-brown. On all tergites the dense brown setae, closely appressed, can give a dark appearance masking the yellow ground color. Sternites I-IV whitish yellow, V brown with a basal ventral yellowish triangle, VI-VII brown.

Postabdomen: Tergite IX and cerci short, yellow. Genitalia (Fig. 1) yellow. Ventral lobe of gonocoxites long, rounded at apex, bearing some short bristles on the distal half dorsally, and a row of strong downwards directed setae, the most basal short, the following long and progressively shorter; two medium-sized apical bristles. External lobe of gonostyles short, bearing only two distal bristles. Internal lobe longer, sickle-shaped, bearing three subdorsal bristles and a row of ventral bristles. Aedeagus long and strongly sclerotisized as in the rest of the genus.

Female. - Length of body: 13 mm (without antennae). Length of wing: 11.5 mm. Similar to male, except darker coloration. Occiput entirely yellowish. Third antennal flagellomere slightly yellowed below. Scutal stripes black. Scutellum black, reddish at margin. Mediotergite black with silvery sheen. Lateral sclerites of thorax black-brown, the laterotergite brown dorsally. Markings of abdominal tergites darker. Ovipositor yellow.

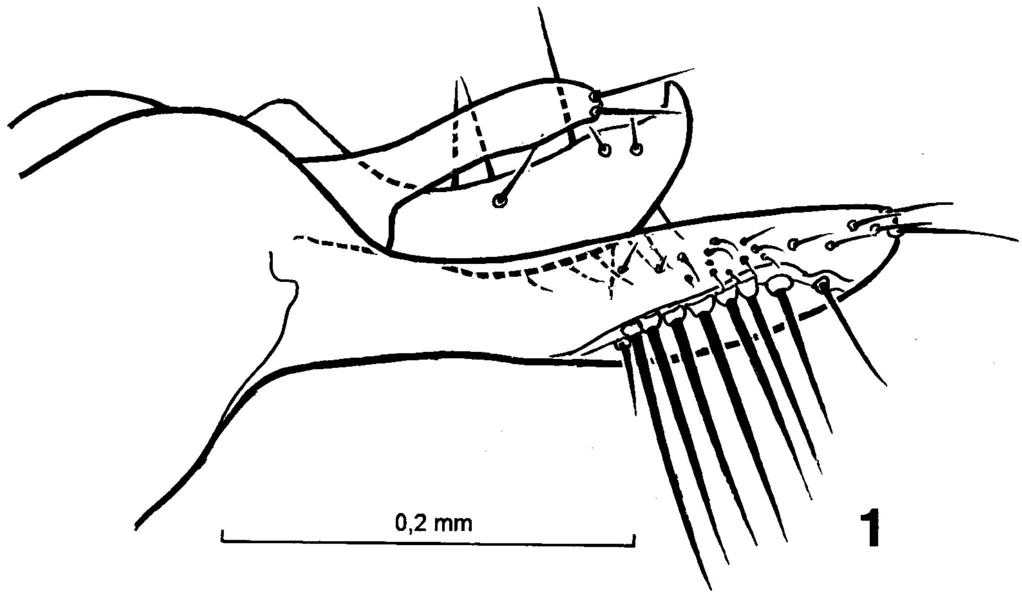

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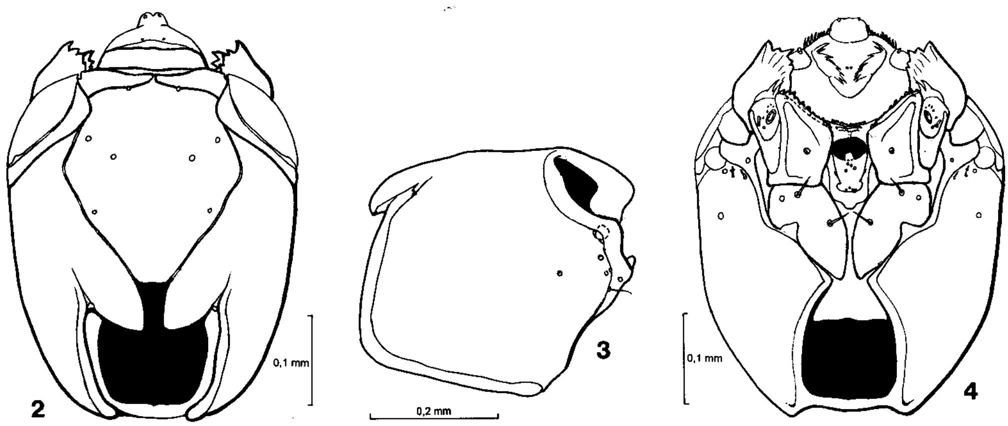
Fig. 1. *Truplaya ferox,* new species, male holotype, apex of synsclerite and gonostyles, lateral.

Larva (apparently mature). - Long (22 mm), cylindric, vermiform, apneustic. Head distinctly longer than wide (11 : 7.5), rectangular with rounded angles, antennae in antero-lateral position. Occipital foramen dihedral at 90°. Clypeofrontal apotome pentagonal, clypeolabral suture entire. Clypeal area narrowly interrupted on median line, without setae or sensillae, frontal area bearing four pairs of sensillae: one pair close to the clypeal area and the median line, one external and one internal at level of antennal angle, and one somewhat posterior to the middle, along the margin (Fig. 2). Postoccipital bridge not sclerified. Genae convex, not closely approximated ventrally at level of maxillary cardo. Posterior incisions small and not very deep. Postoccipital carinae strongly marked, but narrow. Genae with five sensillae and one long fine seta (Fig. 3). Antennae medium-sized, oval, two very slight emarginations for minute sensillae, dorsal and ventral phragma well developed, the former a little more than the latter. Stemmata very small, partly recovered by strengthening of oral margin. Tentorial posterior bridge present, narrow (Fig. 4), anterior tentorial arms not observed (absent?).



Figs. 2-4. Larva of *Truplaya ferox,* new species. 2, head, dorsal; 3, gena, lateral; 4, head, ventral.

Labrum: Labral sclerite very well developed, not weakened or narrow on dorsal median line, without lateral setae. A pair of dorsal sensillae close to the median line, L7 small, subapical. Tormae short and well sclerotinised, one dorsal and one ventral round sensillae. Three premandibular weakly sclerotinised dorsal teeth, simple, followed by nine strongly sclerotinised teeth, each but the first one with strong secondary oral denticulations, thus forming a kind of second premandibular fan (Fig. 5). No lateral labral lobes observed.

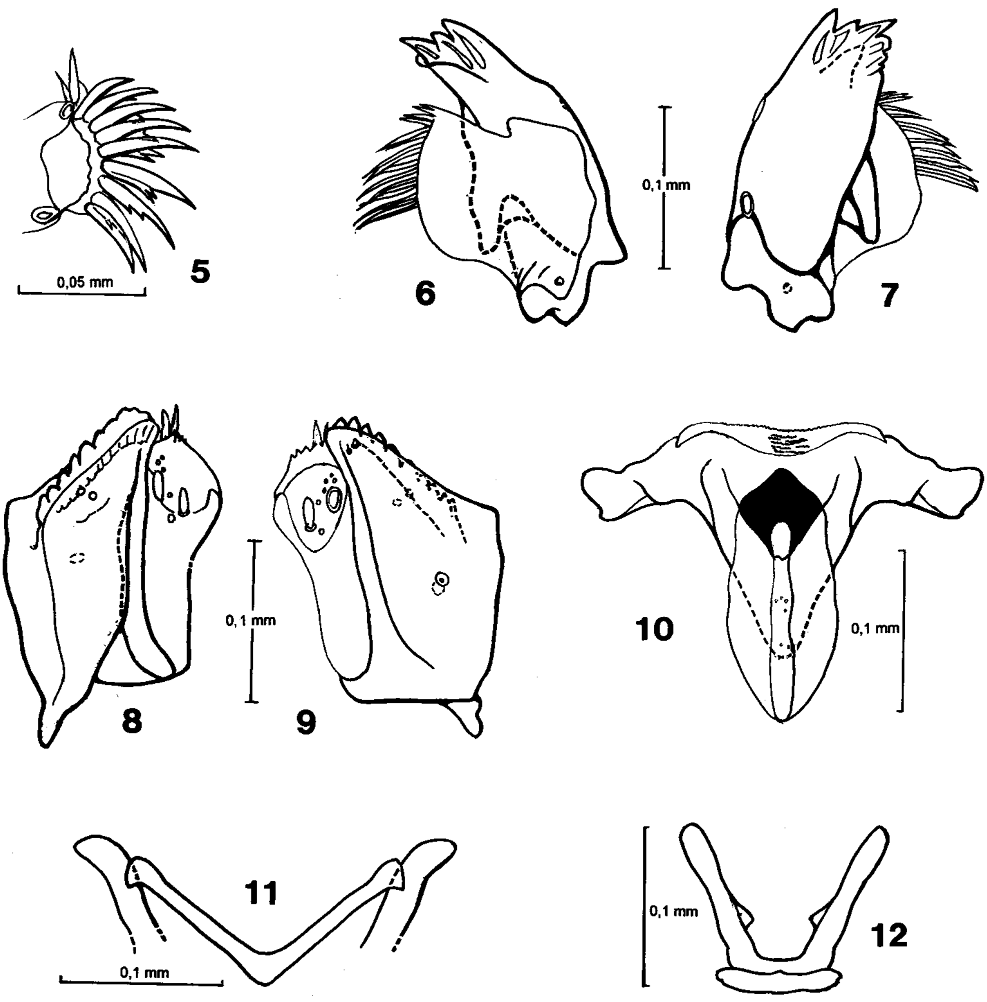
Mandibles (Figs. 6 and 7) forming a three sided pyramid. Ventral face roundly indented, bearing a deep basal pore. Outer face with a single round sensilla. Dorsal face with a strong preapical tooth. Prostheca large, bearing 12-13 transparent, finely barbed setae. Incisor lobe with three strong apical teeth and three smaller inner teeth.

Maxillae (Figs. 8 and 9): Cardo vertical, longer than wide, bearing one outer sensilla and two setae, one close to the anterior margin, one close to the middle of inner margin. Maxillar suture dividing the stipes well marked. Sensorial area of the palpifer bearing 8 sensillae, one large and club-like, one large and ring-like, the other small and circular; apex with two long and three short pointed digitations. Galeolacinia with ten teeth. A big median circular pit, two dorsal and two ventral small sensillae. Maxillary apophysis short.

Labium-hypopharynx (Figs. 10-12): Hypopharyngean lobe with six rows of denticulations, the dorsal one longest. Hypopharyngeal sclerite thick, posterior bridge V-shaped, well sclerotinised. Hypopharyngeal sclerite (cadre) thin and well sclerotinized. Prelabial sclerite U-formed, the basis strong and well separated from the rest of the sclerite, the branches of the V bearing each a small inner triangular expansion. Labial lobe with 8 small circular sensillae.

Thoracic and abdominal segments simple, cylindric, longer than wide. No trace of thoracic spiracles. A few very minute and sparse spinules have been observed in optical microscopy in the ventral face of thorax, but their topography could not be established precisely. Abdominal segments finely wrinkled ventrally, masking the segmentation. Two anal lobes.

Pupa. - We have one pupa, young (integument yellow), female. The thoracic spiracles stand on a small tubercle and have three openings. The abdominal spiracles are simple.



Figs. 5-12. Larva of *Truplaya ferox*, new species. 5, premandibular teeth, lateral; 6, mandible, dorsal; 7, mandible, ventral; 8, maxilla, dorsal; 9, maxilla, ventral; 10, labium-hypopharynx complex, frontal; 11, hypopharyngeal frame, distal; 12, hypopharyngeal and prelabial sclerites, frontal.

Etymology.- The name is derived from the Latin word *ferox* meaning ferocious, alluding to the aggressive attacking behaviour of *T. ferox.*

Discussion. - Three species of *Truplaya* are already known from the Oriental Region, namely *T. flavioralis* (Speiser, 1911), from Taiwan, *T. fumipes* (Brunetti, 1912), from Sri Lanka, and *T. venusta* (Walker, 1856), the genotype, from India and E. Pakistan (Edwards, 1929; Colless & Lipa, 1973); the junior author has examined specimens either belonging to these three or to closely allied species from other geographical regions. The three Oriental species belong to *Truplaya* s. str., as does *T. ferox.* The new species differs from all these by its greater size: *T. ferox:* length of body: 13-14 mm; of wing: 8.5-11.5 mm; *T. flavioralis*: body: 6 mm+, wing: 5.2 mm; *T. fumipes*: body: 9-10 mm; *T. venusta*: body: 6.7 mm (« 3 lines »); wings together: 11.2 mm (« 5 lines »). As mentioned by Edwards (1929), all species of *Truplaya* then known to him had a distinctive type of ornamentation, black with conspicuous white apical bands on abdominal tergites II and IV. Matile (1978) has discussed the monophyly of the genus and its inferred sister-group relationship with *Xenoplatyura* Malloch + *Cloeophoromyia* Matile. He gave a more complete diagnosis of *Truplaya* and noted that several Afrotropical species were differently coloured; *T. ferox* has a very different ornamentation from the other species studied, either Oriental, Afrotropical or Neotropical, and differs also from all of them by its greater size. Pending a revision of *Truplaya,* which contains many yet undescribed species, it is not possible to access what species, or group of species, represents the sister-group of *T. ferox.*

As regards the larval morphology, there are almost 50 genera of Orfeliini, and the larvae of at least one species of the following six genera are known and more or less adequately described: *Neoditomyia* Lane & Sturm, *Orfelia* Costa, *Planarivora* Hickman, *Platyura* Meigen, *Urytalpa* Edwards and *Xenoplatyura* Malloch; the larva of *Platyceridion* Tollet is currently being described by Chandler & Matile (in prep.). None of the specimens investigated by the junior author or other authors seem to possess the peculiar spinose premandibular teeth of *T. ferox,* which might be autapomorphic for the genus or the species, but on the whole we have too few data on the other genera of Orfeliini to recognize the characters of generic significance. On the other hand, the presence of only two anal lobes corroborates the diagnostic value of this feature at the tribe level, as the known Keroplatini possess four anal lobes.

BIOLOGY

Distribution and Habitat. - *Truplaya ferox* has so far been found only in the cavities of bamboo internodes in Peninsular Malaysia. In Ulu Gombak, the larvae inhabited internodes of the bamboo *Gigantochloa scortechinii* Gamble. In Gerik (Perak state), near the Thai border, larvae of probably the same species were found in the internodes of *Gigantochloa latifolia* Ridl.

The culms of *G. scortechinii* reach a height of more than 20 m. The culm segments (internodes) are 20-60 cm long. In the lower part of the culm, the diameter is c. 8-10 cm, the thickness of the wall c. 1 cm. Through the activities of bamboo-boring animals (insects, woodpeckers), holes of various sizes appear in the internode walls, opening access to the hollow interior. During rain such internodes fill with water. In this way phytotelmata (= water bodies in plants) are created which become inhabited by aquatic and terrestrial animals (Kovac, 1994; Kovac & Streit, 1996).

In all cases there was only one *Truplaya* larva per internode. The occurrence of *T. ferox* was limited to living older bamboo culms. The species has not been found in the internodes of shoots or in decaying bamboo culms, despite extensive and thorough searches in these habitats. In one investigation, for example, 100 internode cavities of felled bamboo culms were monitored daily over a 6-months period, but not a single larva of *T. ferox* was encountered (Kovac & Streit, 1996).

In felled bamboo culms with natural holes (see Methods, a), 4 larvae of *T. ferox* were found in 4 out of 129 internodes with holes. The openings of the 4 colonized internodes had been bored by larvae of the chrysomelid beetle *Lasiochila goryi* (n=2; size of holes 10 x 3.5 mm and 6 x 4 mm; height above ground: 1.84 m and 1.13 m), by a pyralid larva (n=1; size of hole 3 x 1.5 mm; height above ground 3.38 m) and by a woodpecker (n=1; size of hole 18 x 4.5 mm; height above ground 6.22 m).

In bamboo culms with artificial holes (see Methods, b) internodes with the smallest (1.2 mm) and the largest hole sizes (20x8 mm) were not inhabited. In the internodes with 5 mm holes, eight larvae were found, in those with 10 mm holes, seven larvae. Obviously, ovipositing females preferred the intermediate hole sizes. If only the two intermediate hole sizes are considered, 16.3 % of the available 104 internodes were inhabited by *Truplaya* larvae or, in two cases, pupae. Within the range of hole heights above the ground investigated (0-6 m), there was no recognizable vertical preference.

Colonization. - In the "August-group" (see Methods, c), the first *Truplaya* larva was detected seven weeks after the holes had been bored. The number of larvae rose to four, but at the end of the first study period the number of inhabited internodes was only two. At the beginning of the second study period, i.e., c. 10 months after the boring of the holes, 22 internodes had been occupied and at the end of that period (10 weeks later) 30 internodes. In the "May-group", 30 internodes were inhabited by the beginning of the initial observation period (i.e., c. 4 months after the holes had been bored), 23 in the end (c. 4 months later). During the second observation period, 14 internodes were inhabited in the beginning, and 16 in the end. A striking difference between the "May-group" and the "August-group" was observed in the rate of colonization of suitable internodes c. 4 months after boring of the artificial holes: 30 internodes of the "May-group" but only 4 internodes of the "August-group" were inhabited. This indicates that season or other factors may play a role.

Developmental cycle. - Only on one occasion an adult *Truplaya* was seen in the field. On a sunny morning at c. 1100 hrs, an insect which at first was thought to be a stenogastrine wasp flew towards a bamboo culm. Its body was held in a horizontal position and the coloration and the type of flight were also very stenogastrine-like. The bamboo culm had artificial holes (diameter 3 mm) in 5 of its lower internodes. The insect started to hover in front of a hole, which was 1.5 m above the ground. It repeatedly made brief flights toward the hole with its abdomen bent forward in the direction of the hole. Then it flew up to the hole in the internode above and repeated its previous behaviour. When it flew up to the third hole the insect was captured with a sweeping net. Only then it was recognized, that the insect belonged to the Diptera. Very likely the captured animal had been ovipositing.

The study periods were too short to determine the duration of the larval stage. Only one larva pupated in the second study period (in the "August-group"). In this case, the larval development must have required less than 6 months. For pupation, the larva constructs a cocoon which is suspended in the web. There are large droplets of a clear liquid on the cocoon. After eclosion, the adult animal remains suspended in the web for several additional days, as many keroplatids do, then leaves the internode. The abandoned web disappears within about 2-3 weeks.

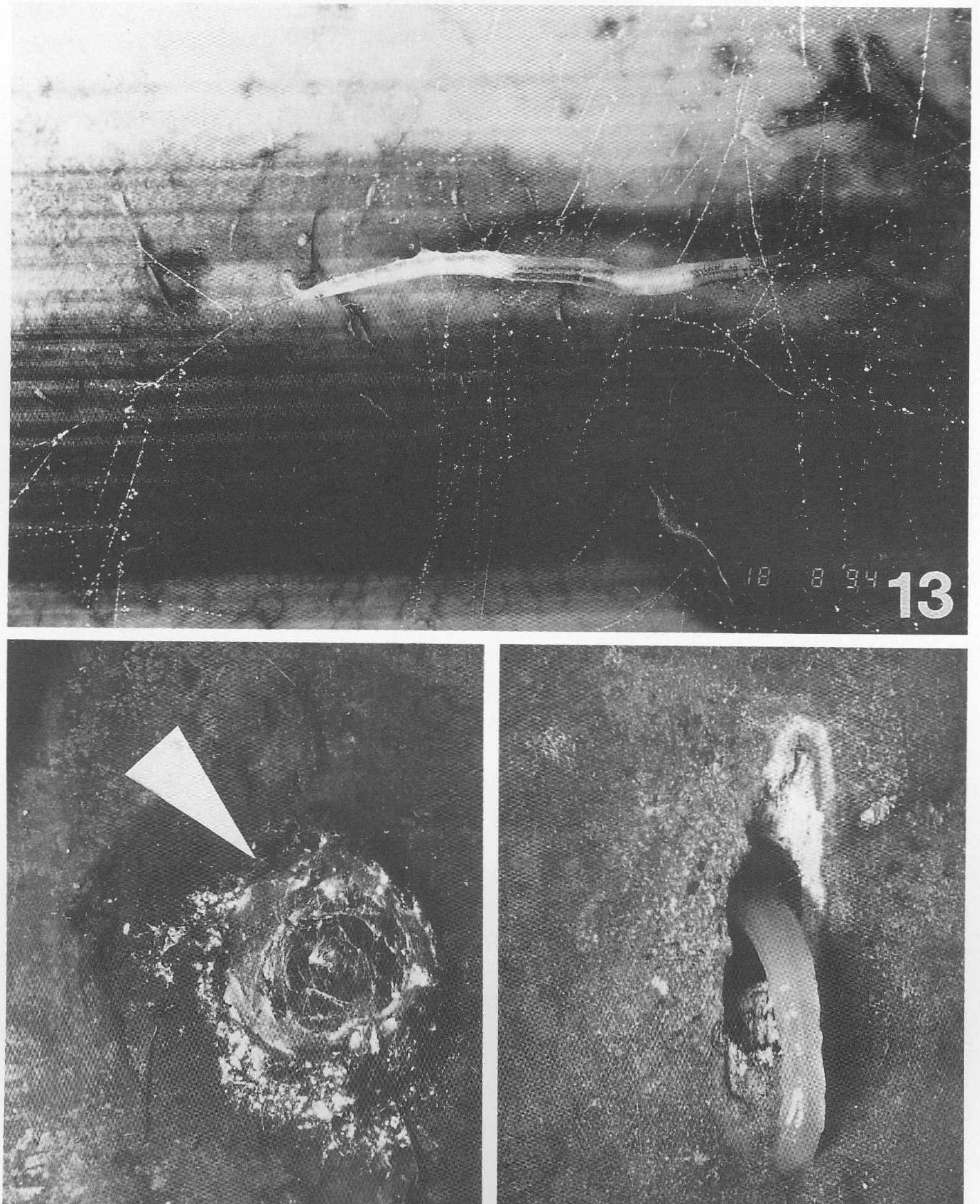
Web, hunting method and prey spectrum of the larva. - The larva of *Truplaya ferox* is predatory. It always stays in its slime web, which has the dual function of both protecting the larva and helping it to catch prey (Fig. 13). The web of the young larva consists of a few horizontal threads leading from the entrance of the internode to the opposite internode wall. The threads are equipped with small droplets of a clear slimy liquid, which is probably secreted by the labial glands as in other Keroplatidae. As the larva grows, the web is enlarged and may eventually fill much of the space of the internode cavity above the water surface. Individual threads hanging from the web reach the water surface.

In two cases it was observed that larvae completely closed up the entrances of their internodes with a transparent membraneous layer (Fig. 14). The membraneous layer was of a brittle consistency. The larvae started to apply the secretion along the edges of the artificial holes, which were 10 mm in diameter. After each round a new layer was applied to the previous one leading to a gradual narrowing of the central opening and eventual complete closure of the hole within a few hours. Two weeks later both holes were still closed. Further observations were made with an endoscope that was inserted through another artificial hole. In both cases the larvae were still young and the webs were small consisting of few threads. The head was usually oriented towards the closed hole. No behavioural or other differences could be detected as compared to the larvae with open internode entrances.

Potential prey sticks at least temporarily to the threads. In the lab, it was observed that the larva, probably alerted by the mechanical cues transmitted by the threads, hurries towards the prey, grabs it and covers it with more slime. Besides, the larva also preys outside of the internode. It frequently lies in wait at the entrance hole and the anterior part of its body sticks out of the hole and hangs down along the bamboo surface (Fig. 15). The larva may rest motionlessly in this position for hours. In one case, the larva was observed sticking out of the internode for three hours. After that, the site was checked in two-hour intervals (4x) and the larva was still hanging out. In response to a mechanical disturbance, the larva quickly withdraws back into the internode, but after a while sticks its head out again. If a potential prey approaches, the larva slowly turnes its head or the whole body part hanging from the hole in the direction of the animal. If the animal is in the immediate vicinity of the larva, the larva abruptly seizes it and pulles it into the internode interior (n=3).

One larva was observed daily both during the day and at night for a week (1-2 hours per day). During this observation period predation on animals walking up and down the bamboo surface was witnessed twice. In one case a small beetle larva was captured, in the other, an ant. In five more instances, the larva unsuccessfully tried to grab passing ants. In the slime web of this larva the remains of up to 15 ants at the same time were detected. These prey items are not included in Table 1, because this bamboo culm did not belong to the experimental set-up.

During the weekly checks of 200 internodes over a total period of 7 months, 88 prey items were detected with the endoscope in the webs of *Truplaya* on 45 occasions (Table 1): Hymenoptera (ants, 30x, a total of 71 individuals), Dermaptera (adult earwigs, 2x), Blattodea (cockroaches, 2x), Lepidoptera (caterpillars, 2x), Coleoptera (adult beetles of *Scirtes,* 2x and the rove beetle *Stilicopsis,* 1x), Diptera (flies, pupa of a Tipulidae, 1x and an adult



Figs. 13-15. Larva of *T. ferox,* new species, web, closing of the entrance hole, hunting posture. 13, larva in its slime web. The head is on the left. The larva was photographed in an internode of a felled bamboo culm, which was sawn open. When the culm was cut down, the larva fell into the water and the web was destroyed. Afterwards, the larva climbed on land and constructed a new web, which is seen on the picture; 14, the entrance hole to the internode has been closed by the larva with a secretion that solidifies when exposed to air (arrow). Diameter of the hole: 9 mm; 15, larva hanging out of the internode entrance and waiting for passing prey. It is kept in this position by a loose tangle of threads. Length of the hole c. 2.5 mm.

mosquito, 1x), Isoptera (termites, 1x, 3 individuals), Arachnida (exuviae of a spider) and two additional unidentified objects. The largest prey object was the aquatic tipulid pupa (length 2-3 cm). The tipulid pupae climb on land before eclosion and stick out their heads out of the hole, thus enabling the adult crane-fly to leave the internode. The tipulid and the beetle *Scirtes*, whose larvae are also aquatic, belong to the permanent internode inhabitants. Other captured animals were guests, like *Stilicopsis*, which prefer decaying bamboo culms, or the caterpillars, which entered the internode for pupation. Most of the prey were ants (80.7%).

Interreactions with spiders.- Besides *Truplaya*, also several web-building spiders are found in bamboo internodes, mainly of the family Theridiidae. The spiders sometimes extend their web from the hole to the opposite bamboo culm and wait in the hole for prey. They are certainly competitors of *Truplaya* as they occupy the same habitat and have a similar prey spectrum, with ants making up almost the half (47.4%) of the prey items (Table 1). The spiders, mostly juveniles but also adults, colonized newly available internodes faster than *Truplaya* and inhabited up to 46% out of hundred internodes (May- or August group, see Material and Methods) at the same time. As already mentioned, the first *Truplaya* larva appeared 7 weeks after the holes had been bored. At that time 35 internodes had already been occupied by web-building spiders. When *Truplaya* larvae appeared in the internodes, in some cases they obviously displaced the resident spiders by gradually enlarging their slimy webs (n=6). On the other hand also *Truplaya*-larvae disappeared from the internodes in which they co-occured with spiders (n=2). Because of the small sample size it is not possible to say with certainty whether *Truplaya* always displaces the web spiders or if spiders with larger webs can also prevent *Truplaya* from colonizing an internode. After the *Truplaya* adults had left and the slimy web had disintegrated the internodes were occassionally recolonized by web spiders. For example, in one case an internode was colonized by a spider, then inhabited by a *Truplaya* larva and two weeks after the eclosion, after the slime-web had disappeared the internode was colonized by a web-building spider again.

Table 1. Prey items captured by larvae of *Truplaya ferox*, new species, and by web-building spiders (mainly Theridiidae) inhabiting the same habitat. All prey items were observed in the field by an endoscope during the weekly checks of 200 internodes over a total period of 7 months. Small preys are probably underrepresented, because they are eaten up faster. See text for further explanations.

prey items	***Truplaya***	***web-spiders***
Blattodea	2	1
Isoptera	3	4
Dermaptera	2	3
Heteroptera	0	3
Coleoptera	3	5
Diptera	2	5
Lepidoptera	2	1
Hymenoptera	71	36
Myriapoda	0	1
Arachnida	1	2
Crustacea	0	1
indet.	2	18
Total	**88**	**76**

DISCUSSION

Like all known species of Orfeliini, the larva of *T. ferox* is predatory. According to the classification proposed by Matile (1981, 1990), the Keroplatidae are divided into three subfamilies, Arachnocampinae, Macrocerinae and Keroplatinae, the latter comprising two tribes, Keroplatini and Orfeliini. The Arachnocampinae, monotypic with the genus *Arachnocampa* (Australian and New Zealand glow-worms), and the known Macrocerinae are predatory. In the Keroplatinae, the Keroplatini are mostly spore-feeders, while all known Orfeliini are predaceous. With the Arachnocampinae being the sister-group of the Macrocerinae + Keroplatinae, one may think that the predatory regime of the Keroplatidae is plesiomorphic for the family.

The predatory behaviour of *T. ferox*, e.g. biting its prey, pulling it into the web and covering it with the labial fluid, has been observed in other genera: *Arachnocampa, Macrocera, Neoditomyia*, and can also be considered as an ancestral attribute of the Keroplatidae. The same can be said of the vertically hanging threads ("fishing lines" of the glow-worms), the formation of which seems to depend on the available space under the main web. Thus *Macrocera* larvae living in rotten wood have very short "fishing lines" or none at all, while the cave-dwelling populations have long ones (cf. Matile, 1990, and references therein). On the other hand, to our knowledge no other predatory keroplatid is able to emerge so far out from its web, as shown in Fig. 15, and grab a prey which is not already at least partly entangled in its snare.

The webs of *Macrocera* larvae and of other four genera of Orfeliini tested on this trait (Beaver, 1979; Plachter, 1979) have an acid pH (2.4-2.7). In *Macrocera* this is due to oxalic acid secreted by the labial glands (Buston, 1933; Plachter, 1979). In *Arachnocampa*, the pH is acid, but no oxalates were found in the labial glands (Matile, 1990). Plachter has noted that the strongly acid pH was a character of the predatory larvae of Keroplatidae, helping to kill the prey, but the presence of oxalic acid has not been experimentally demonstrated elsewhere than in *Macrocera*. It is likely that the droplets of *T. ferox* are also highly acid.

The larvae of *Truplaya ferox* prey on a wide spectrum of insects, with ants constituting the bulk of their prey (Table 1). The likely reason for this is that ants are the most common potential prey in the larvae's habitat. Also the internode inhabiting web-building spiders, which are not specialized either, have a similarly broad food spectrum and also catch mostly ants (Fig. 17). The large number of ants among the prey indicates that a large proportion of the food of both *Truplaya ferox* larvae and web spiders originates from the bamboo surface. Ants may occur there in large numbers visiting trophobiontic Homoptera in the leaf region. The cavity of living bamboo internodes, in contrast (and quite different from the conditions in dead internodes), is a very nutrient-poor habitat. Only at the beginning of the succession, i.e., shortly after a hole has appeared in the wall, the water inside the internode is inhabited by numerous mosquito larvae. These feed on microorganisms breaking down the surface of the bamboo wall. In the later stages of succession, when the nutritious outer layer of the wall has decomposed, the internode inhabitants depend on nutrient input from the outside (e.g., animals taking refuge in the internode). Therefore only few insect species with long larval development, e.g., the beetle *Scirtes* or the predatory mosquito larva *Toxorhynchites,* which easily tolerates extended starving, occur in such internodes.

Another behavioural trait of the new species is remarkable — the young larvae may seal off the entrance of their hole with a membranous sheet. This is the first observation of such a behaviour in the predaceous Keroplatidae. It implies a physical or chemical change in the secretion of the labial fluid at a certain time. A possible explanation for this phenomenon may be that the membrane in the entrance hole prevents newly eclosed insects that developed in the water from leaving the internode. Shortly after an internode hole is made, in the early stage of succession, the water is inhabited by many mosquito larvae. At the same time the *Truplaya* larvae are still young and have only small nets consisting of a few threads. It is possible that the mosquitoes, which fly towards light to leave the internode, bump into the transparent membrane again and again and are then caught by the *Truplaya*-larva, which stays near the internode entrance and is oriented towards the membrane.

Very few facts are known regarding the behaviour of adult Keroplatidae (with the notable exception of *Arachnocampa luminosa*). As far as oviposition is concerned, the "shooting" of eggs in stationary flight is known for the genus *Keroplatus* (Matile, 1990), but it lacks the precision of *Truplaya ferox*. The smallest entrance hole used by *T. ferox* to lay eggs was 3x1.5 mm, while in *Keroplatus* the target is the hymenium of a polyporous fungus, onto which the eggs are haphazardly projected. The mosquito *Toxorhynchites magnificus*, whose predatory larvae also live in the same internodes like the larvae of *Truplaya*, exhibits a very similar behaviour while "shooting" its eggs into the internodes from flight (senior author's observations), as do other *Toxorhynchites* species.

Keroplatus tipuloides Bosc (Keroplatini) is a wasp mimic, and so are, in the Orfeliini, several species of *Isoneuromyia*, among these the Oriental *I. polybioides* (Edwards) and the Neotropical *I. sesiiformis* (Edwards), and two Australasian species, *Nicholsonomyia vespiformis* Tonnoir and *Tamborinea commoni* Matile. In flight, *K. tipuloides* also buzzes like a wasp; the trait has not been observed in the other keroplatid wasp mimics, none having been observed in life except *T. ferox* whose ovipositing flight was silent. The mimicry, in the above taxa, is mainly the result of a modification of the abdomen, combining coloration and petiolation of the basis, either by laterodorsal expansion or by lateral flattening of the middle section (Matile, 1990). As already noted, *T. ferox* resembles a stenogastrine wasp, and this is the first indication of mimicry reported in the genus. All *Truplaya* and allied genera show a petiolate and flattened abdomen and might therefore also contain wasp mimics. One may wonder, for example, whether the very long proctiger tube of the males of some species of *Xenoplatyura*, which has no known function (Matile, 1984), might not play a role here. The Stenogastrinae, a subfamily of Vespidae, live only in the Oriental Region, but the wasp models for the numerous Afrotropical *Truplaya* and *Xenoplatyura* wasp mimics have yet to be identified.

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