CHAPTER 2 LITERATURE REVIEW

Proturans are very small, with a length ranging in size from 0.5 to 2 millimeters. Proturans have three distinct body regions (head, thorax, and abdomen). The head displays entognathous mouthparts, but without eyes, or antennae. The thorax is divided into three segments with locomotory appendages and without wings. The forelegs assume sensory function, and are furnished with sensory hairs (sensilla), the shape, number, and arrangement of sensilla are of great systematic importance. The abdomen is divided into twelve segments with abdominal appendages on the first three segments. Proturans are the only insects with anamorphosis, they add body segments during development (Copeland and Imadaté, 1990; Nosek, 1973; Nosek *et al.*, 1978; Szeptycki, 2002; Tuxen, 1964).

2.1 Reproductive characteristics and postembryonic development

Proturans are the only insects with anamorphosis development, meaning during their post-embryonic development the abdomen increases in the number of segments from nine to twelve. They sequentially divide to 6 stages; egg, prelarva, larva I, larva II, maturus junior, and adult (Yin, 1999). Bernard (1976, 1979) show the prelarva as the first stage after eclosion from the egg.

Prelarva (Fig. 1A and B). The mouthparts, foretarsi, and abdominal appendages are not well developed. Foretarsal claws and empodia are absent in suborder Eosentomoidea but present in suborder Acerentomoidea. The abdomen consists of 9 segments.

Larva I (Fig. 1C and D). The mouthparts, abdominal appendages, and claws are developed as in the adult, but the abdomen has only 9 segments. The shape and position of the foretarsal sensilla are only slightly different from adult. During development from larva I to adult, the chaetotaxy evolves progressively. Body setae number usually increases with each molt by adding new setae to those existing in the previous stage. This occurs in every developmental stage.

Larva II (Fig. 1E and F). A new segment emerges between the eighth and terminal segments, giving ten segmented abdomen.

Maturus Junior (Fig. 1G). Two additional segments appear, therefore, the abdomen now possesses twelve segments as in the adult stage. Genitalia in both sexes are still absent.

Adult (Fig. 1H and I). The adult is the final stage of development with twelve segments and well developed outer genitalia.

2.2 Ecology

Proturans occur in all regions of the world where sufficient moisture supports plant growth except in the true arctic and Antarctic. They are among the most abundant soil arthropods. Proturans are to be found in forest litter and humus, in tree cavities, under bark on dead tree, under stones, in peat bogs, in pasture, cultivated field, and grassland soils, on moss and lichens, in underground, small mammal nests, and in caves (Imadaté and Copeland, 1990; Eisenbeis and Wichard, 1985). In Thailand proturan can be found in forest soil and high mountain (Likhitrakarn, 2004).

Likhitrakarn and Chaichana (in press) reported a total proturan population density of 1,031 individuals per square meter (depth 5 centimeters) in Queen Sirikit Botanic Garden, Mae Rim District, Chiang Mai province in Northern Thailand. Proturans were fourth in density behind acari (mites), formicids (ants) and collembolans.

Studies in Europe and Japan have shown that some species are ecologically tolerant and consequently have a wide distributional range, whereas others are intolerant and have more restricted ranges. These studies also indicate that some species with wide ranges are generally abundant, while others with equally broad ranges are less frequently encountered. The limited information available on North American forms makes generalizations hazardous. However, from what we known, a few species occur in both Europe and America or in both Asia and America (Copeland and Imadaté, 1990). Most other species have limited distributions.

They feed on decomposing organic matter, fungal spores and mycorrhizal fungi (Sturm, 1959; Machida and Takahashi, 2004; Triplehorn and Johnson, 2005). Tuxen (1977) suggested to look for proturans at the roots of mycorrhiza-bearing trees.

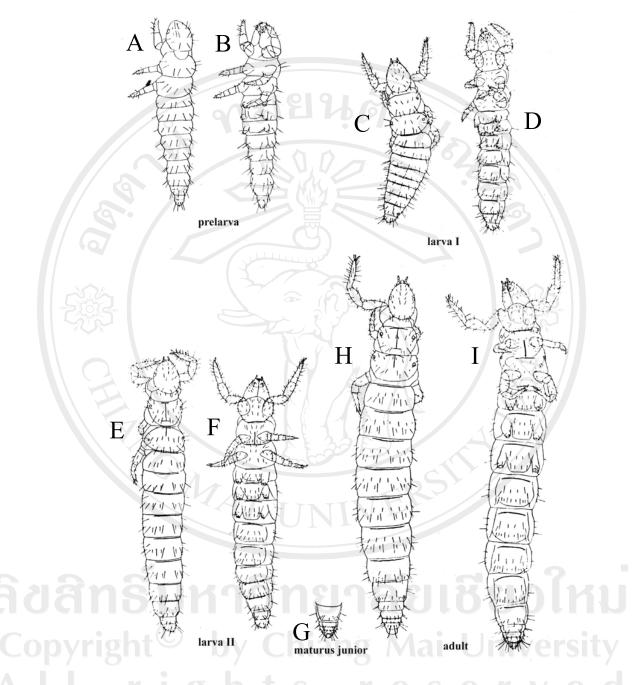


Figure 1 Postembryonic development of proturan, family Eosentomidae, Eosentomon transitorium Berlese.

A-B, prelarva dorsal and ventral; C-D, larva I dorsal and ventral; E-F, larva II dorsal and ventral; G, maturus junior abdomen VIII-XII, ventral view; H-I, adult dorsal and ventral (Nosek, 1973).

2.3 Morphology and diagnostic characters

Proturans are very small, typically with a length of 0.5 to 2 millimeters. Proturans have three distinct body regions (head, thorax, and abdomen). The head has entognathous mouthparts, but without eyes, and antennae. The thorax is divided into three segments with walking legs and without wings. The forelegs have sensory hairs (sensilla). The abdomen is divided into 12 segments with abdominal appendages on the first three segments (Fig. 2).

On the head, the following characters are diagnostically important:

Additional setae (Fig. 3). On dorsal of head, behind rostral setae (RS1) is clypeal setae (CS). In the medium line of the head, there are medium setae 1 (m1), medium setae 2 (m2), medium setae 3 (m3), medium setae 4 (m4), medium setae 5 (m5) and posterior setae (p). There have 5 additional setae: anterior sensilla (as), anterior additional setae (aa), posterior additional setae (pa), sub-posterior setae (sp), and posterior sensilla (ps). The additional setae present are differentiated in each species and can used for species determination.

Labrum and the LR ratio (Figs. 4 and 5). The labrum may be short or long and it can expressed as a LR ratio, head length (base of cranium to rostral setae 1) divided by labrum length.

Pseudoculi and the PR ratio (Figs. 2 and 3). Pseudoculi are round or oval paired sensory structures on the dorso-lateral surfaces of the head. The PR ratio is derived by dividing head length by pseudoculus length.

Rostral setae (Figs. 3 and 4). A row of setae found across the anterior margin of the head. The central pair is the rostral setae 1.

Mandibles (Figs. 4 and 5). In family Acerentomidae, the mandibles (M) are more or less stylet-shaped, at least in family Protentomidae. In family Eosentomidae, they may be very long and extremely narrow, very long and more broad, intermediate, or broad and short.

Maxilly palp (Figs. 2, 4, and 5). Family Eosentomidae have the maxillary palp (MP) with three-segments ending in a tuft of setae, a few setae situated more proximally. On the second segment lateral sensillum *s* is present. In family Protentomidae and family Acerentomidae on the second segment with two sensilla.

Labial palps (Figs. 5 and 6). They usually display one segment, ending in a tuft of setae like the maxillary palp (Fig. 6A) or reduced (Figs. 6B and C), with three or four setae and often sausage-like sensillum.

Canal of maxillary gland (Figs. 2 and 5). There is a single tube in suborder Eosentomoidea but is varied and systematically very important in suborder Acerentomoidea. The canal of maxillary gland (CMG) usually has a heart-shaped widening (calyx) with or without peculiar appendices. Sometimes they are obscured or damaged during the mounting process.

On the thorax, the most important characteristics are:

Thoracic legs (Fig. 2). All three legs normally consist of six segments; coxa, trochanter, femur, tibia, tarsus and pre-tarsus. The middle and hind legs were walking legs but the forelegs use as sensory functions, replacing the missing antennae and the tarsus is very useful systematically.

Abdominal appendages (Figs. 2 and 7). In family Eosentomidae (Fig. 7A-C) all three pairs are similar, each appendage bearing five setae and a terminal vesicle. In family Acerentomidae, the abdominal appendages show differentiation and provide very useful taxonomic characters, especially between the genera. For example, genus *Australentulus* (Fig. 7D-F) has abdominal appendage I with four setae and a terminal vesicle but abdominal appendages II-III with 3 setae without terminal vesicles. Family Protentomidae (Fig. 7G-I) are characterized by the reduction of the third pair which has no terminal vesicle. Three setae are found on the abdominal appendage III in genus *Condeellum*.

Foretarsus (Figs. 2, 8-10).

This character is importance taxonomically and essential for species determination. The foretarsus can be visualized as a four-sided structure with an anterior view (dorsal) surface containing the alpha (α) setae, the posterior view (ventral) with the beta (β) setae, the exterior view with the gamma (γ) setae, and the interior view with the delta (δ) setae. The setae surround the sensilla and serve to locate them. The size, shape, and position of the sensilla in relation to the setae are constant within the species but vary inter-specifically.

In family Acerentomidae (Fig. 8), there are three anterior foretarsal sensilla, t-1, t-2, t-3; seven exterior sensilla, a-g; and three interior sensilla, a', b', c'; seven anterior setae, α 1-7; seven posterior setae, β 1-7; five exterior setae, γ 1-5; and six interior setae; δ 1-6.

In family Eosentomidae (Fig. 9), there finds eight α , nine β , eight δ , and five γ setae. On the anterior surface, the claviform t-1 is easily identified. It is located near the center of the tarsus on the level of seta $\alpha 3'$ or between it and $\alpha 3$. The t-1, t-2, and t-3 form a straight line along the tarsus. The pre-tarsal sensillum s is just beyond the t-3.

In family Protentomidae (Fig. 10), the reduction of sensilla and setae is not rare. An extreme reduction is found in the genus *Condeellum*, which has only seven foretarsal sensilla.

The BS ratio. The distance of sensillum t-1 to the base of tarsus divided by the distance of sensillum t-1 to apex of tarsus.

The TR ratio. The tarsal length divided by claw length.

Empodium (Figs. 8-10). It may be short or long. In family Eosentomidae (Fig. 9) it is long, in family Acerentomidae (Fig. 8) and the Protentomidae (Fig. 10), it is relatively short.

The EU ratio. The empodium length divided by claw length.

Spiracles (Fig. 11). It is situated at mesonotum and metanotum. They are present in suborder Eosentomoidea. These lead to the tracheal system, with longitudinal tracheae to the head, prothorax and mesothorax from mesothoracic spiracle, and to metathorax and abdomen from the metathoracic spiracle (Berlese, 1909). The tracheae from the different spiracles are not connected with each other, neither in the longitudinal nor the transverse direction (Prell, 1911). The spiracles are situated dorsolaterally and protected by a group of bristles. In suborder Acerentomoidea, the spiracles, as well as tracheal system, are wholly absent (Nosek, 1973).

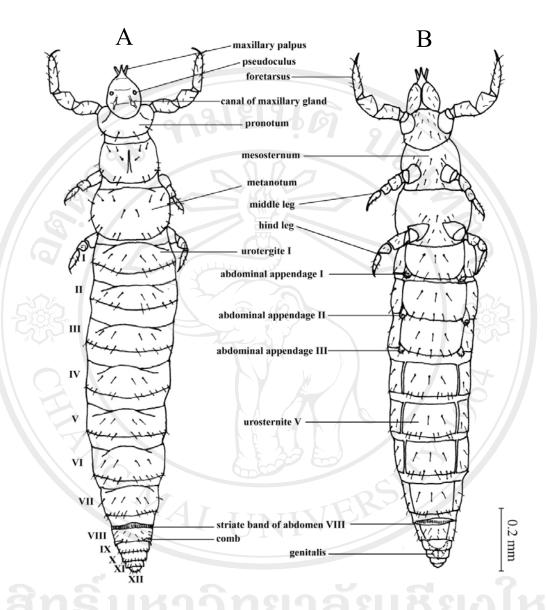
Chaetotaxy (Fig. 12). The system for naming the setae was devised by Tuxen (1949) and slightly modified in 1964. The thoracic and abdominal setae generally occur in two rows, are numbered tergals. Setae in the anterior row are prefixed with the capitals letter A (A1, A2, A3, A4, A5) and those in the posterior row with P plus the numeral. In the posterior rows, there are the accessory setae, and these are

identified with a letter (P1a, P2a, P3a, P4a, P5a). It start count in the center of each row.

Comb (Figs. 2 and 13). The eighth abdominal segment carries posteriorly on either side the opening of the large abdominal glands. This opening is always covered by a "lid", which in family Eosentomidae is undifferentiated but in family Acerentomidae is diverse, with or without teeth differing in number and length; it is often called comb VIII.

Striate band (Figs. 2 and 13). In family Acerentomidae, they have a characteristic, so-called striate band, on the proximal part of the eighth abdominal segment. It consists of two lines, with or without striate in between. In the Protentomidae the band is represented by a single line. In family Eosentomidae it is missing. The striate may have the character of a regular grate, called "striate band well developed", if no striate are visible, it is termed "reduced".

Genitalia (Fig. 14). The external genitalia differ from those of all other insects. In both sexes they open ventrally between the eleventh segments and telsons (the gonotreme). In both sexes there are a pair of basal arms and two styli. The male arms, or periphallus, carry setae but the female arms, perigynium, never do. The gonopore is not the styli, and thus double, in the male but between the styli, and thus single, in the female. The male genitalia are generally alike in all species, though differing between suborder Eosentomoidea and suborder Acerentomoidea, where the genitalia show distinct specific differences in the female. In suborder Eosentomoidea the styli most often carries a curious structure, called the processus sternalis (plural: processus sternales), which is of a characteristic shape between species and thus of great taxonomic importance. In suborder Acerentomoidea there is no such structure; each of the styli ends in an acrostylus, the shape of which may also be of taxonomic value (Tuxen, 1985).



Morphological features of proturan, family Acerentomidae, genus Australentulus. A, dorsal view; B, ventral view.

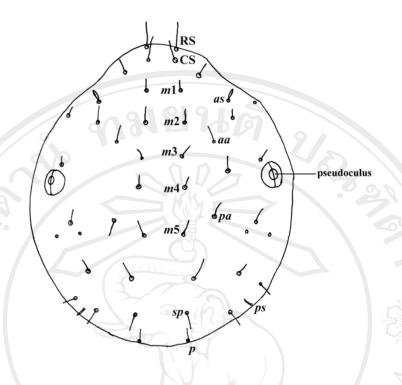


Figure 3 Additional setae on dorsal of head.

RS1, rostral setae; CS, clypeal setae; m1, medium setae 1; m2, medium setae 2; m3, medium setae 3; m4, medium setae 4; m5, medium setae 5; sp, subposterior setae; p, posterior setae; ps, posterior sensilla; pa, posterior additional setae; aa, anterior additional setae; as, anterior sensilla.

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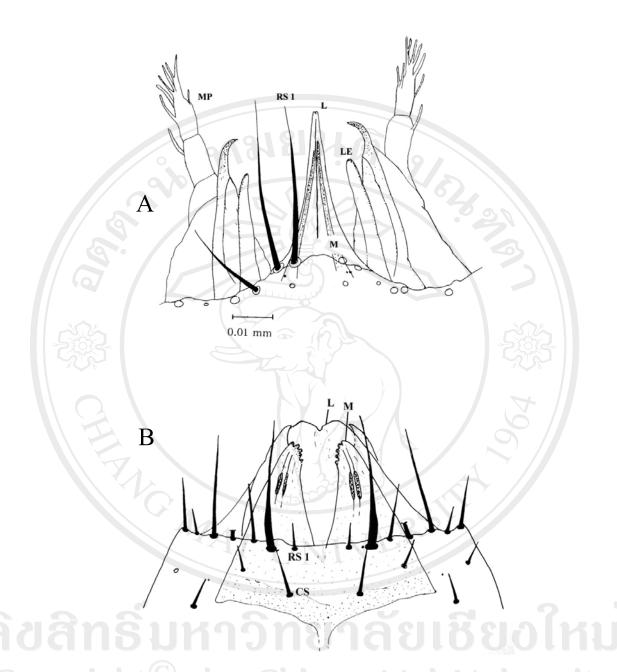


Figure 4 Morphology of the mouthparts, family Acerentomidae, genus *Styletoentomon* and family Eosentomidae, genus *Eosentomon*.

A, genus *Styletoentomon*, anterior of head; B, genus *Eosentomon*, anterior of head; MP, maxillary palp; RS1, rostral setae 1; L, labrum; LE, lobi externi of maxilla; M, mandible; CS, clypeal setae (Nosek, 1973).

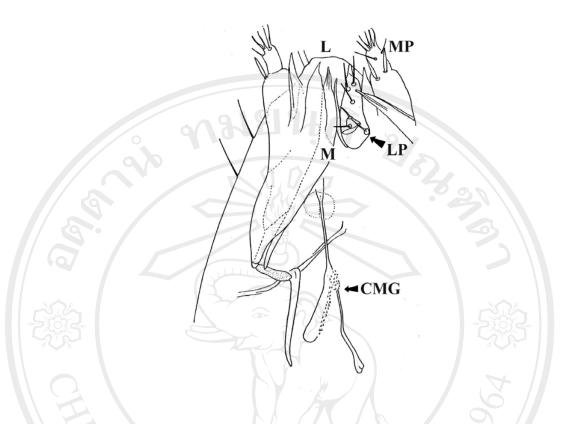


Figure 5 Morphology of the mouthpart, family Acerentomidae, *Acerella muscorum* (Ionescu).

L, labrum; MP, maxillary palp; LP, labial palp; M, mandible; CMG, Canal of maxillary gland.

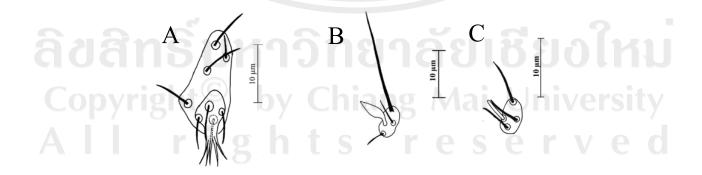


Figure 6 Labial palps of proturans.

A, genus Condeellum; B, genus Australentulus; C, genus Baculentulus.

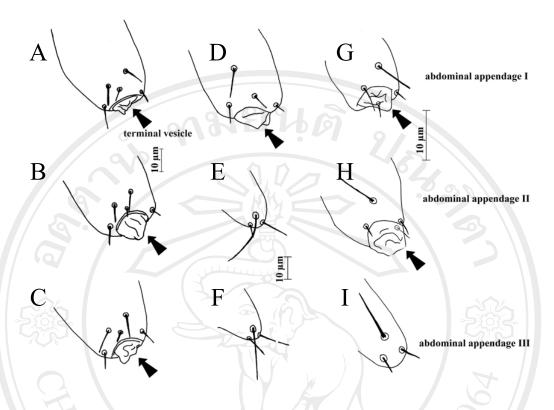


Figure 7 Abdominal appendages of proturans.

A-C, family Eosentomidae, genus *Eosentomon*; D-F, family Acerentomidae, genus *Australentulus*; G-I, family Protentomidae, genus *Condeellum*.

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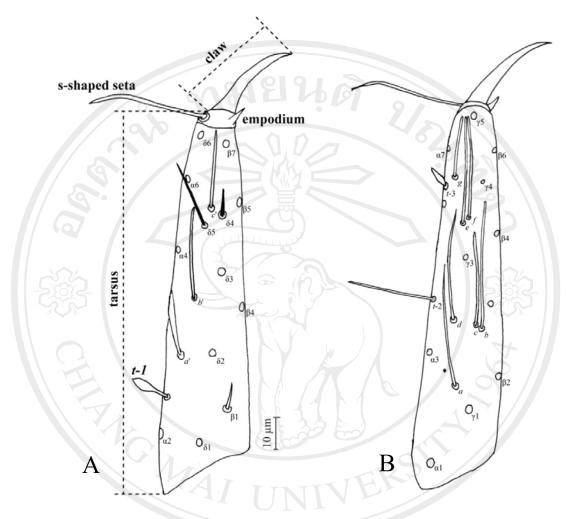


Figure 8 Foretarsus of family Acerentomidae, genus Australentulus.

A, interior view; B, exterior view.

A, interior view; B, exterior view.

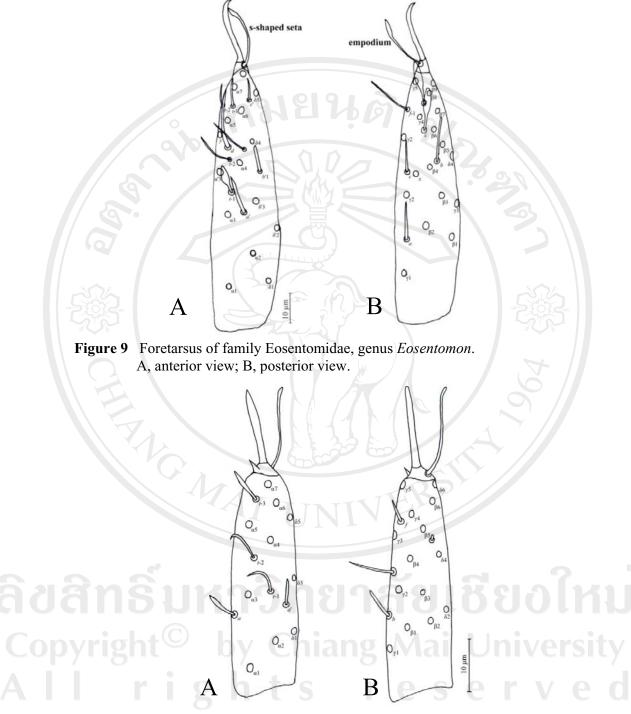


Figure 10 Foretarsus of family Protentomidae, genus *Condeellum*. A, anterior view; B, posterior view.

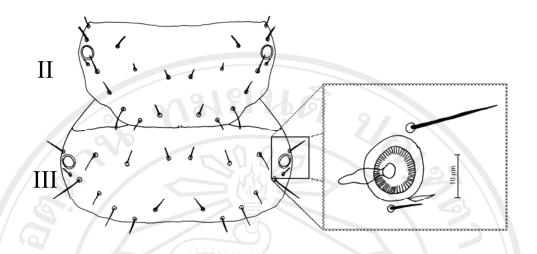


Figure 11 Spiracles on mesonotum and metanotum of suborder Eosentomoidea.

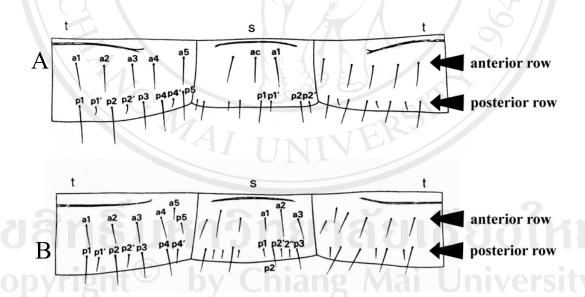


Figure 12 Chaetotaxy of abdominal segment IV.

A, family Eosentomidae; B, family Acerentomidae; s, sternum; t, tergum (Tuxen, 1985).

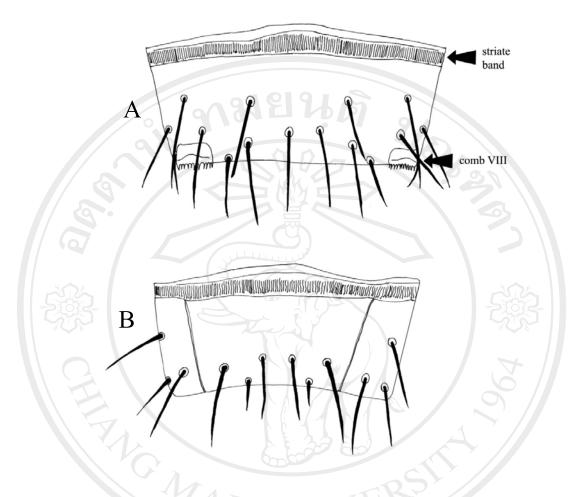


Figure 13 Abdominal segment VIII, family Acerentomidae, genus *Australentulus*. A, dorsal view; B, ventral view.

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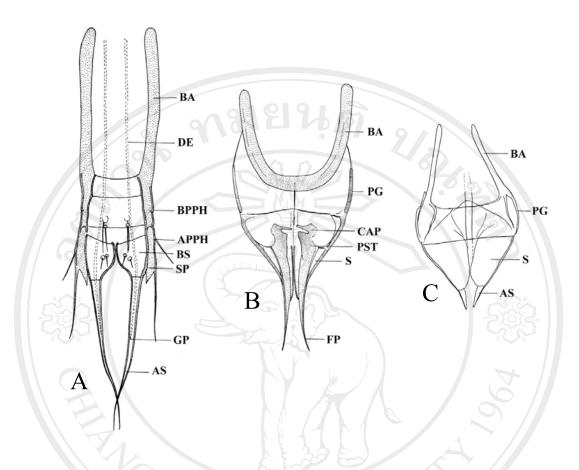


Figure 14 Genitalia of proturans.

A, male squama genitalia, family Eosentomidae, *Eosentomon transitorium* Berlese; BA, basal apodeme; DE, ductus ejaculatorius; BPPH, basiperiphallus; APPH, acroperiphallus; BS, basistylus; SP, side plates; GP, gonopore; AS, acrostylus; B, female squama genitalia, family Eosentomidae, *Eosentomon transitorium* Berlese; C, female squama genitalia, family Acerentomidae, *Acerentomon imadatei* Nosek; BA, basal apodeme; PG, perigynium; CAP, caput processus; PST, processus sternalis; S, stylus (basistylus); FP, filum processus; AS, acrostylus.

2.4 Classification

Copeland and Imadaté (1990) reported that Slivestri described the first proturan species in 1907. His description, followed soon thereafter by Berlese's monograph (1909), treated all aspects of their anatomy and biology as known at the time. Ten species were described in two families and three genera. Condé (1945, 1947) first recognized the systematic value of the foretarsal sensilla and gave them names. Tuxen (1955, 1956) refined the scheme by naming the setae and adapting the entire system to the Eosentomoidea. These advances, along with the recognition of the importance of the female genitalia, made possible, for the first time, the definitive description of species.

Tuxen (1931) monograph addressed proturan morphology with notes on systematics and ecology which was preliminary to his comprehensive book "The Protura", published in 1964 which began the modern era of proturan study. In this encyclopedia study Tuxen re-described, using proven taxonomic characters, all the know species and thoroughly summarized the knowledge concerning their morphology, development, phylogeny, distribution, and ecology. Nosek (1973) followed with his monograph on "The European fauna". Most of our knowledge of Asiatic and Pacific Island proturan has been derived from the many publications and the book by Imadaté and from the papers of Yin (Copeland and Imadaté, 1990). Finally Yin (1999) published the book of proturan in China "Fauna Sinica. Arthropoda Protura". The first survey in Thailand was done by Imadaté (1989). He described 25 species which were only found in Thailand. Later, Likhitrakarn (2004) surveyed the Doi Suthep-Pui National Park, Chiang Mai province, in Northern Thailand. There he found 11 species of which 6 species had been described and another 5 species were new to science. There is little known about proturan in Thailand. Proturan taxonomy is the base from which to develop future studies in biology, distribution, ecology, behavior, and molecular genetics of this curious and fascinating group of insects.

The order Protura contains 4 families: Protentomidae, Acerentomidae, Eosentomidae, and Sinentomidae. In Thailand, 3 families have been found: Protentomidae, Acerentomidae, and Eosentomidae. The taxonomic status follows Tuxen (1985):

2.4.1 Family Protentomidae

The abdominal appendages I-II with terminal vesicle and 4 setae. The abdominal appendage III without vesicle and 3 setae. Eighth abdominal segment with a serrated line. Sternum XII with 8 setae. Female squama genitalis broad, with budlike, occasionally pointed acrostyli and short basal apodemes.

Genus found in Thailand is Condeellum.

2.4.2 Family Acerentomidae

The abdominal appendage I with a terminal vesicle and 4 setae, the the abdominal appendages II-III without a vesicle and each with 3, 2, or 1 seta. Abdominal tergum VIII with a striate band consisting of 2 lines, with or without striate in between. Female squama genitalis more or less pointed, bipartite or, together with distal part of stylus, forming a tripartite structure. Sternum XII with 6 setae.

Genera found in Thailand are Australentulus, Kenyentulus, Gracilentulus, Baculentulus, and Silvestridia.

2.4.3 Family Eosentomidae

Mesonotum and metanotum with spiracles. The abdominal appendages I-III each with a terminal vesicle and 5 setae. Mandible rather broad and stout ending mostly in three small teeth. Abdominal tergum VIII without a striate band or serrate line. Female squama genitalis mostly with processus sternalis but without acrostyli. Sternum XII with 12 setae.

Genus found in Thailand is Eosentomon.

2.5 Proturans in Thailand

The first survey in Thailand was done by Imadaté (1989). He described 25 indigenous species to Thailand. Later Likhitrakarn (2004) surveyed Doi Suthep-Pui National Park, Chiang Mai province, Northern Thailand. There he found 11 species of which 6 species had been previously described and five were *novo* species. This was the species checklist prior to this thesis research.

2.6 Checklist of proturans in Thailand

Suborder Acerentomoidea Condé, 1951

Family Protentomidae, Ewing, 1936

Genus Condeellum Tuxen, 1963

Condeellum regale (Condé, 1958)

Condeellum ishiianum ishiianum Imadaté, 1965

Family Acerentomidae Silvestri, 1907

Genus Australentulus Tuxen, 1967

Australentulus prachedee (Imadaté, 1965)

Genus Silvestridia Bonet, 1942

Silvestridia keijiana (Imadaté, 1965)

Genus Baculentulus Tuxen, 1977

Baculentulus morikawai (Imadaté & Yosii, 1956)

Baculentulus duongkeoi (Imadaté, 1965)

Baculentulus bervinguis (Condé, 1961)

Baculentulus umesaoi (Imadaté, 1965)

Baculentulus matsuokai (Imadaté, 1965)

Baculentulus lanna (Imadaté, 1965)

Baculentulus ogawai (Imadaté, 1965)

Baculentulus oginoi (Imadaté, 1965)

Genus Gracilentulus Tuxen, 1963

Gracilentulus sachikoae Imadaté, 1965

Genus Kenyentulus Tuxen, 1981

Kenyentulus ohyamai (Imadaté, 1965)

Suborder Eosentomoidea condé, 1951

Family Eosentomidae Berlese, 1909

Genus Eosentomon Berlese, 1909

Eosentomon kloomi Imadaté, 1965

Eosentomon paktai Imadaté, 1965

Eosentomon thamnooni Imadaté, 1965

Eosentomon imbutum Imadaté, 1965

Eosentomon yanaka Imadaté, 1965

Eosentomon sawasdi Imadaté, 1965

Eosentomon sayani Imadaté, 1965

Eosentomon pairathi Imadaté, 1965

Eosentomon hyatti Condé, 1958

Eosentomon torbongsi Imadaté, 1965

Eosentomon udorni Imadaté, 1965

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