The remarkable protonymph of *Pseudochthonius* (Chelonethi, Chthoniidae)*

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Summary.- The protonymph of a *Pseudochthonius* species from Cameroon is described. Morphologically, it is highly regressive, representing the first known calyptostasic protonymph of a pseudoscorpion.

Résumé.- La protonymphe d'une espèce de *Pseudochthonius* du Cameroun est décrite. Morphologiquement, elle est fortement régressive et représente la première protonymphe calyptostatique connue des pseudoscorpions.

Introduction

At the ninth European Colloquium of Arachnology in Brussels, André and Jocqué (1986) presented a summary of Grandjean's stase concept and its application to the study of arachnid ontogenies. As they noted, an appreciation of Grandjean's work has been slow to manifest itself in non-acarological circles. This is unfortunate, because it will certainly be important for a unified view of arachnid development.

Pseudoscorpions have a typical arachnid life-cycle of six stases: prelarva (first embryo); larva (second embryo); protonymph; deutonymph, tritonymph; and adult. The prelarva and larva of all species are calyptostasic (Grandjean 1938); an incipient elattostasic protonymph is known in *Chthonius (E.) tetrachelatus* (Preyssler) (André and Jocqué 1986).

During a two month stay in Cameroon in the monsoon season, three females of *Pseudochthonius* aff. *billae* Vachon with attached broods of 'embryos' were collected by hand. Subsequent examination revealed the presence of developing deutonymphs (identified by their trichobothrial complement) within some of the 'embryos'. This indicates that these 'embryos' are in fact highly regressive (calyptostasic) protonymphs, the first such protonymph known in pseudoscorpions.

Materials and methods

The three females with protonymphs were collected from the following localities:

A. Female with 10 protonymphs; Bowanda village (4°11'N, 9°19'E), near Bolifamba, leaf litter on a farm cleared from secondary forest, 6 September 1988.

B. Female with 9 protonymphs (some containing pharate deutonymphs); Movio village (4°05'N, 9°14'E), near Motutu, leaf litter in secondary forest, 1 August 1988.

C. Female with 7 protonymphs; Ekona (4°15'N, 9°29'E), leaf litter in crevice in secondary forest at edge of lava flow, 25 August 1988.

These females appear to have been free-living (i.e. not enclosed in a brood nest) when collected. All three dropped their brood soon afterwards and the protonymphs failed to develop.

Preserved protonymphs were removed from the brood sac, cleared in cold lactic acid, and examined with a Wild M-20 microscope with attached drawing tube.

Description of the protonymph

Colour yellowish-white. Total length (including chelicerae) of largest specimens 0.50mm.

Prosoma with lateral bulges which mark the insertion point of the dilator muscles of the pharynx - the furrows behind these bulges extend ventrally, between the palp coxae and the coxae of leg I. Behind the furrows is the posterior border of the carapace, which is difficult to see, but which is associated with a folding of the cuticle in unexpanded specimens. There is a row of small muscles between the carapace and the anterior margin of the opisthosoma. A pair of eyespots, with reflective tapeta, is present behind the chelicerae. In fully-developed protonymphs (brood B) the eyespots are elongated posteriorly and show signs of dividing into anterior and posterior eyespots.

The posterior part of the opisthosoma is curved downwards and terminates in a closed (non-functional) anal tubercule. Situated on the dorsum of the opisthosoma (i.e. facing posteriorly) are three median tubercules (fig. 1) which decrease in size from anterior to posteriormost. These are thick-walled, without any apparent openings or glandular connections. They are situated above tergites 3, 5 and 6 of developing deutonymphs. The significance of these tubercules is unknown.

A single pair of tracheoles open on small tubercles just behind coxa IV (figs 2 and 3). These presumably represent rudiments of the anterior tracheae, though tracheae could not be seen in enclosed deutonymphs.

Figs 1-2, *Pseudochthonius* cf *billae* protonymph: 1, dorsal view, with detail of first tubercule of opisthosoma; 2, ventral view with right palp and legs removed, left leg I stippled for clarity; detail shows tracheole enlarged. Abbreviations: ap = anchor plate; CH = chelicera; e = eyespot; P = palp; pbc = posterior border of carapace; pr = pore; tr = tracheole; $\mu_i c$ = inferior muscle of chelicera; $\mu_s c$ = superior muscle of chelicera; μld = lateral dilator muscle of pharynx; μoc = opistho-carapacial muscle; ϕ = pharynx; 1-3 = opisthosomal tubercles; I-IV = legs I-IV. Scale bar represents 0.2mm (0.1mm for enlarged details).

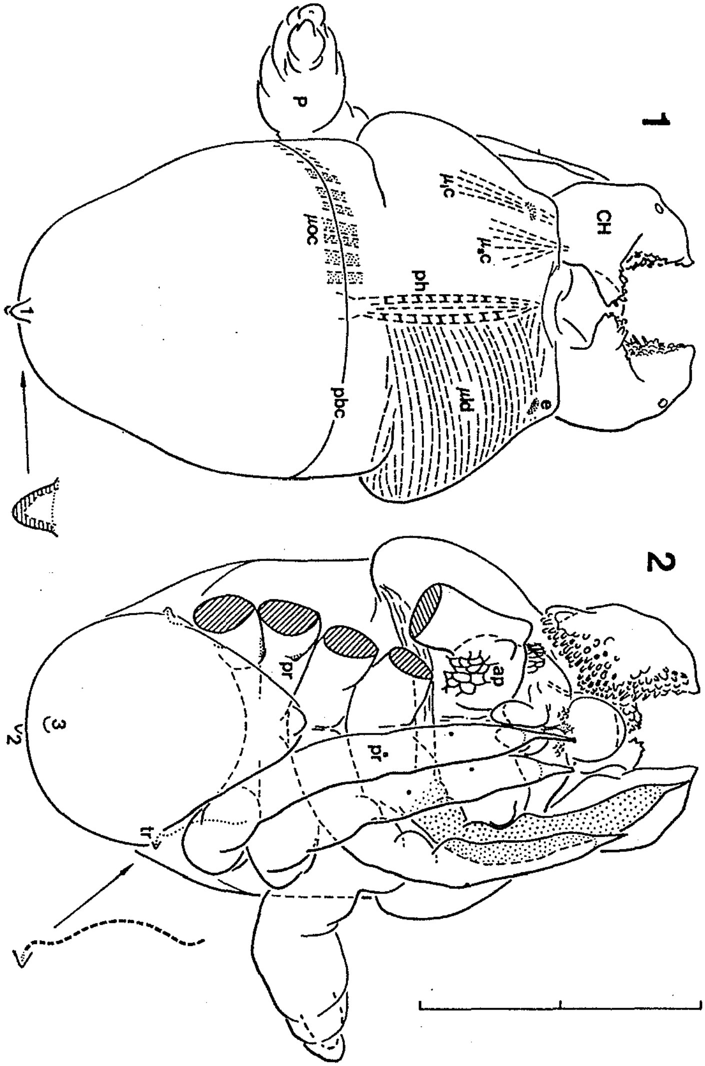
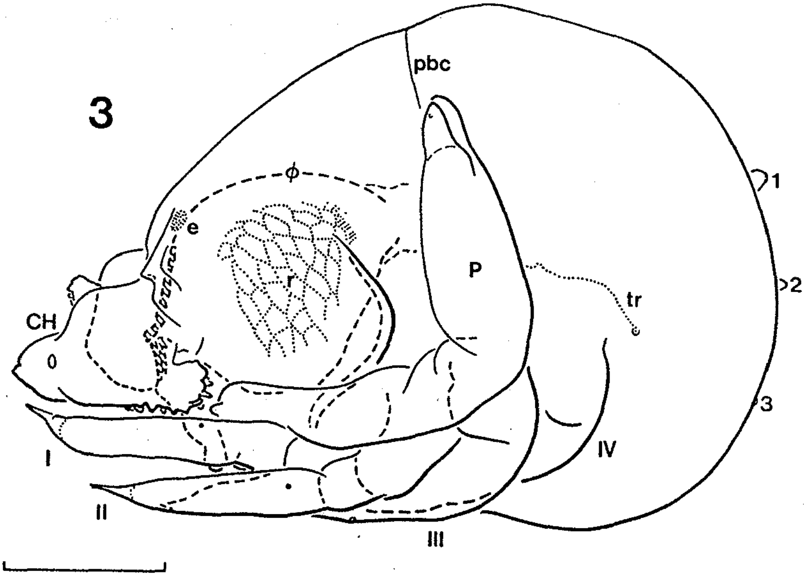


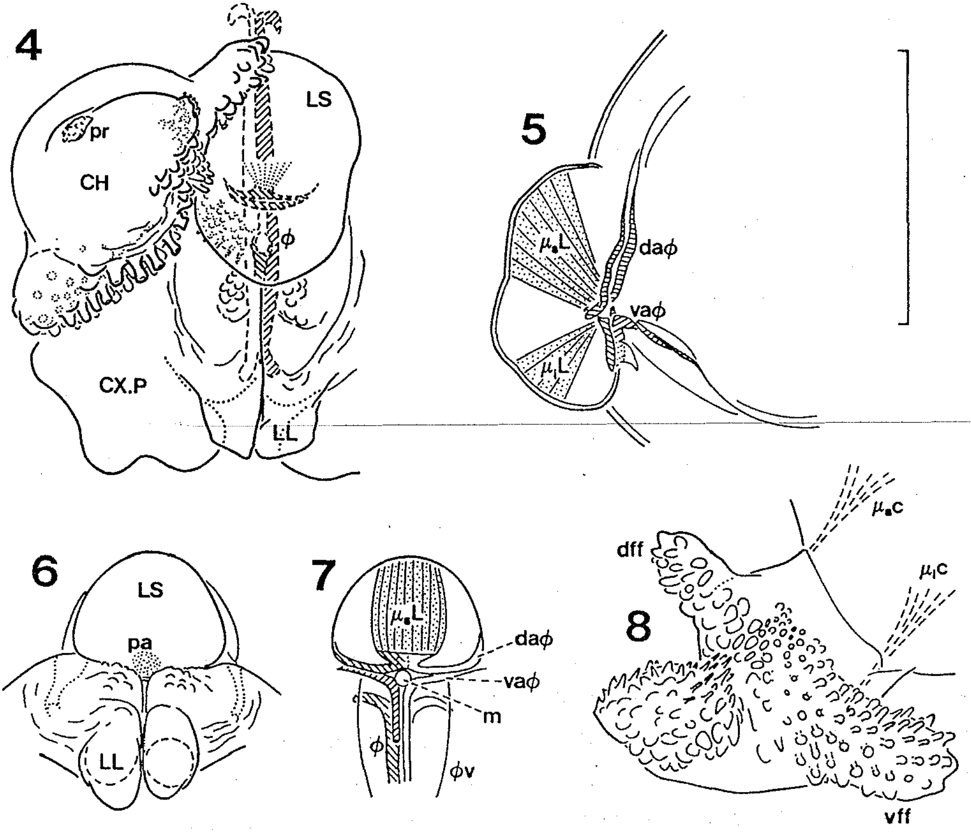
Fig. 3, *Pseudochthonius* cf *billae* protonymph, lateral view. Abbreviations as for figs 1-2, except r = reticulate area of pharynx. Scale bar represents 0.2mm.



The chelicerae (figs 4 & 8) are large and have a bizzare form. Situated on the antiaxiodorsa surface is a large pore (possibly a complex of pores). The homologue of this pore is not clear i the deutonymph. Paraxially, the chelicerae are provided with numerous projections, many o which are elongated, with slightly bulbous tips. The hand of the chelicera bears tw 'false-fingers', one anteriodorsal, lying above the labrum, and the other posterioventral. Th cheliceral fingers of the deutonymph develop in the main part of the protonymphal chelicera. Tw muscles, arising from the carapace are attached to the base of each chelicera - on ventro-paraxially, the other dorso-atiaxially (figs 1 and 8).

The labrum (figs 4-6) has a weak dorsal fold and bears a small, cribrate area of minut pores ventrally just in front of the mouth. Within the labrum are dorsal and ventral muscle whic are attached to the apodemes of the pharynx (fig. 5). The pharynx is composed of a pair of large roughly circular plates, similar to those of the protonymph of *Verrucaditha* (Weygoldt 1968) The plates are slightly flared dorsally and ventrally, and have a reticulate surface which give them a 'ribbed' appearance when viewed dorsally (figs 1 and 3).

Figs 4-8, *Pseudochthonius* cf *billae* protonymph, oral region: 4, anterior view; 5, saggital optical section of pharynx; 6, ventral view; 7, internal mouthparts (semi-diagrammatic; same orientation as fig. 6); 8, paraxial view of right chelicera. Abbreviations: CX.P = coxa of palp; daϕ = dorsal apodeme of pharynx; dff = dorsal false-finger of chelicera; LL = lateral lips; LS = labrum; m = mouth; pa = punctate area; vaϕ = ventral apodeme of pharynx; vff = ventral false-finger of chelicera; ϕv = ventral margin of pharynx; μ_iL = inferior muscle of labrum; μ_sL = superior muscle of labrum; other abbreviations as in figs 1-2. Scale bar represents 0.1mm (all figures to same scale).



Immediately behind the mouth the palpal coxa bears a few, small granules. Posterior to these is a pair of limb-like lobes (fig. 6: LL), equivalent to Weygoldt's 'endites of the palpal coxae' (*copd*). They are similar to the lateral lips of some mite prelarvae (cf. Coineau 1974) and are presumed here to be homologous to the laminae superiores of the subsequent stases. At the sides of the palpal coxae are areas of reticulation, corresponding to the 'anchor plates' described by Weygoldt. It is not clear whether the these areas are internal or external.

At the junction between the coxa and trochanter of the palp is a pair of prominences, one anterior and the other anterioventral. Coxae III and IV each bear a small pore near the junction with the trochanter. No trace of the coxal spines is present.

The palps are held appressed to the sides of the body with the chelae directed upwards. The fingers of the chela are very short; the fingers of developing deutonymphs within extend well into the hand of the protonymph. There is a small, ventral tubercule near the tip of the moveable finger. The segments of the palps and legs are marked by weak constrictions, there being no joints nor membranes. Small muscles are present in all appendages, but it is not clear whether these are functional.

The legs are directed anteriorly, the elongated tips lying around the oral region. The tips of legs II-III are usually weakly bidentate; the tip of leg IV terminates in a pair of dorsally-facing hooks.

Legs I-II bear a single pore on the dorsal surface (appearing lateral due to rotation of the legs) of the telotarsi; two such pores are present on the tarsi of legs III-IV, one on the basitarsus and the other on the telotarsus. These pores are present in subsequent stases, and there presence in deutonymphs within the protonymphs sometimes gives an illusion of their having been doubled. It is possible that these are glandular acini pores.

The brood package covers only the oral region and the ends of the legs. The strong modifications of the chelicerae and the presence of hooks on the last pair of legs probably help to keep the protonymph firmly attached to it.

Discussion

The application of Grandjean's terminology for regressive stases to pseudoscorpions is complicated by the fact that the embryos of this group have specialized mouthparts and feed on a fluid secreted by the female. Both calyptosases and elattostases are defined as being incapable of feeding (calyptostases are additionally incapable of locomotion). In order to avoid this apparen contradiction in the case of pseudoscorpions, I propose here to alter the definitions of elattostase and calyptostase to 'stases incapable of *independent* feeding'.

The protonymph of *Pseudochthonius* represents a logical, if somewhat surprising, result of protelattosis [the trend towards regression of the early stases, Hammen 1978] in the Chthoniidae. Calyptostasic inhibition has resulted in a protonymph which has a rather 'embryonic' appearance.

A regressive protonymph is probably characteristic of the development of all *Pseudochthonius* species: free-living protonymphs of this genus have never been found. The absence of previous records of females carrying protonymphs might be explained by the females' tendency to drop the brood when captured. Females might also construct a brood nest for the initial stages of development and only leave this before the eclosion of the deutonymphs.

Calyptostasis has apparently arisen independently in *Chthonius (Ephippiochthonius)* protonymphs. The protonymph of *Chthonius (E.) tetrachelatus* lacks functional silk glands and is incapable of an independent existence outside the brood nest (Vachon 1941, Weygoldt 1968), whilst free-living protonymphs are known in *Chthonius (Chthonius)* species. Outgroup comparison with the Tridenchthoniidae and Feaelloidea indicates that regression in protonymphs is the derived condition. Free-living protonymphs are unknown in many genera of Chthoniidae and it is likely that other interesting examples of protelattosis remain to be discovered in this family.

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*Results of the Leeds University Expedition to Mount Cameroon, 1988; no. 2.