

HOMOLOGY OF DORSAL OPISTHOSOMAL PLATES, SETAE, AND CUPULES
OF HETEROSTIGMATIC MITES WITH THOSE OF OTHER
ELEUTHERENGONE PROSTIGMATA (ACARI)

BY

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ABSTRACT

Mites representing the Heterostigmata are shown to retain tergal, setal, and cupule elements of the six opisthosomal segments characteristic of larval acariform mites generally. The third opisthosomal dorsal plate is compounded from the tergites of two segments, and should be denoted as such. Further tendencies toward fusion and reduction of opisthosomal tergites in the Heterostigmata are discussed. The notation developed by Grandjean for the dorsal opisthosomal structures of acariform mites is applied so as to reflect these conditions.

RÉSUMÉ

Les Acariens Heterostigmata conservent les mêmes éléments des tergites, poils, et cupules des six segments opisthosomaux qui caractérisent la larve des Acariformes en général. Le troisième bouclier dorsal de l'opisthosoma est constitué de tergites à deux segments, et doit être désigné en conséquence. D'autres tendances de fusion et réduction des tergites de l'opisthosoma chez les Heterostigmata sont discutées. La notation formulée par Grandjean pour les structures dorsales de l'opisthosoma des Acari-formes est appliquée de manière à représenter ces conditions.

Because of the basic arrangement of opisthosomal dorsal plates, each with 1 or 2 pairs of setae, which is common to the larva and adult of all families of Tarsonemina, it is relatively simple to determine the homologies of setae on these plates among mites of any of the families in this group. But what have *not* been effectively established are the homologies of these setae with those of other groups of eleutherengone Prostigmata, of which the Tarsonemina is a part (LINDQUIST, 1976). The key to establishing setal homologies lies in comparing the transverse series of setae, and particularly the associated cupules or lyrifissures, of larval and adult instars of Tarsonemina with those of their sister group, the Tarsocheyleina in the Heterostigmata, and in turn with those of successive out-groups in the Eleutherengona. Such a comparison was briefly made recently for the first time by LINDQUIST (1976), and is further elaborated here.

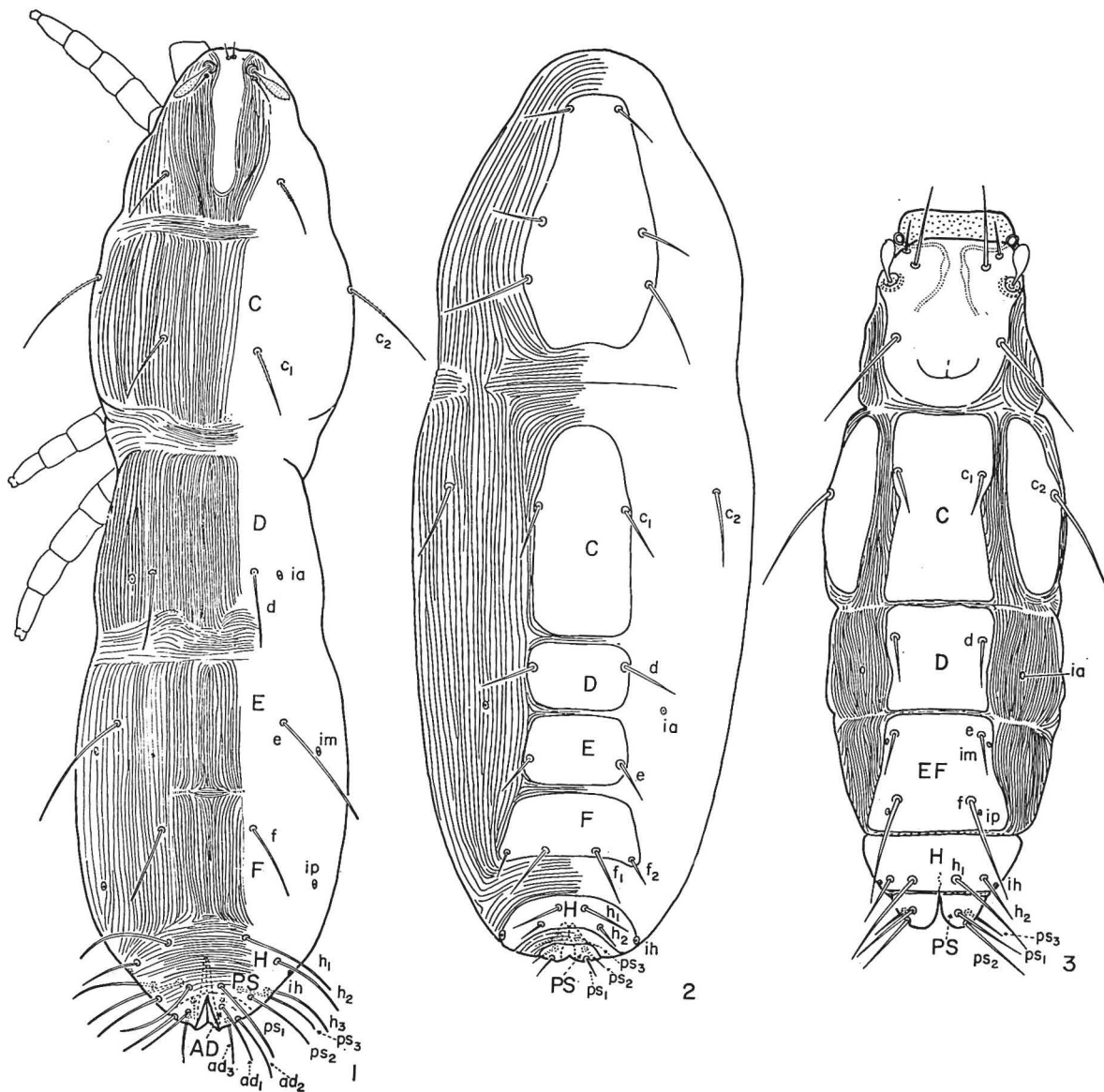
As is the case with the Acariformes generally, the opisthosoma of the larva of all but the most derived families of the sister group of the Heterostigmata (the raphignathoid-cheyletoid-iolinoid-tetranychoid-eriophyoid stock), or of the out-group of these sister groups (the anystoid-caeculoid-parasitengone stock; see the dendrograms and discussion in LINDQUIST, 1976), consists of six segments, as indicated dorsally by their setae and cupules. These segments are denoted as C, D, E, F, H, and PS, according to the standard notation of GRANDJEAN (1939, 1947) for acariform mites. Cupules *ia* are associated with the dorsal setae of segments C and D, *im* with the setae of E, *ip* with F, and *ih* (called *iop* in earlier works of GRANDJEAN, e.g., 1934, 1935) with H. This pattern of segmentation is not altered in postlarval instars of the Heterostigmata or of its sister group; and even in the earlier derived (or "lower") groups of Prostigmata, in which additional, postlarval segments are added, the larval number of cupules is generally retained, unchanged (GRANDJEAN, 1935). The discussion by GRANDJEAN (1935) leaves no doubt that the cupules may be used with confidence as segmental indicators. In some of the more derived groups of Prostigmata, some or all of the cupules may be lost; but whatever ones are retained are part of the basic larval complement, and can be homologized as such.

The spatial relationships of the cupules with the dorsal setae of each segment are particularly well shown when the area of each segment is delimited by a differentiated pattern of striation or by a sclerotized dorsal plate, or tergite. For this reason, illustrations (Figs. 1, 2) are given of the idiosomal dorsum of two anystoid genera, *Stigmocheylus* and *Pomerantzia*, as representatives of the out-group of the Heterostigmata and its sister group. This basic arrangement of cupules and setae for opisthosomal segments is the same throughout the eleutherengone families of Prostigmata, whether dorsal plates are present or not¹.

In *Pomerantzia*, the larval arrangement of the cupules and setae with respect to the tergites does not change on nymphs and adults (PRICE, 1974). Note in particular that: (1) cupules *ia* are associated with the setae and tergite of the second segment, D; (2) each segment has only one, transverse or oblique-transverse row of setae, generally with only 1 or 2 pairs of setae; (3) the sixth segment, PS, occupies a caudal or ventrocaudal position, such that frequently only the preceding five segments are visibly dorsal entities (Fig. 2).

The basic larval arrangement of opisthosomal cupules and setae is maintained on the postlarval instars of the more derived families of Prostigmata constituting the Heterostigmata and its sister group, even though it may be superficially obscured by loss of some cupules and by consolidation of the tergites in various ways to form larger plates which sometimes appear to reflect dorsal "segments". This is well exemplified among the genera of Stigmaeidae. When one investigates the manifestation of this larval pattern of dorsal opisthosomal structures in the Heterostigmata, a very interesting condition, crucially important to homology, is found on specimens of the relatively unspecialized Tarsocheyloidea. Superficially, the series of simple plates and their setae appear to indicate only five opisthosomal segments, of which four are dorsal and one caudal (Fig. 3). However, the third plate is actually compounded of two tergites representing segments E and F. The evidence for this is that (1) two pairs of cupules, *im* and *ip*, are on this plate; and (2) the two pairs of setae are aligned longitudinally on the plate, and actually represent two transverse rows of setae, each associated with one pair of cupules. To

1. Before GRANDJEAN (1947) standardized a scheme of notation for the dorsal setae of opisthosomal segments of acariform mites, he had employed several different notations for these setae (but not the cupules) in his earlier studies on various families of prostigmatic mites, e.g., the Stigmaeidae (see GRANDJEAN, 1944). Although some of these notations are still used, with modification, by specialists of these families, they are a source of confusion when one compares setae of homologous segments on mites of different families. They should be abandoned in favor of Grandjean's standardized notation.



FIGS. 1-3. — Idiosomal dorsum of adult females :
 1) *Stigmocheylus* sp. ; 2) *Pomerantzia* sp. ; 3) *Hoplocheylus* sp.

homologize correctly the setae of this plate, therefore, the anterior pair of setae associated with cupules *im* should be recognized as belonging to segment E, and called setae *e*; and the posterior pair of setae associated with cupules *ip* should be recognized as belonging to segment F, and called setae *f*. The plate should be denoted as EF. One could argue that the pits here interpreted as cupules *ip* are alveolar vestiges of a lost pair of setae. This possibility is unlikely, since there is no visible difference in appearance between this pair of pits and the others situated on plates and interpreted as cupules *im* and *ih*; also, the lateral position of these pits with respect to the neighboring setae *f* is consistent with their being cupules rather than setal alveoli. However, even if these pits were setal alveoli, this would still be evidence for denoting the plate as compound EF, because none of the segments D, E, F, and H are known to carry more than two pairs of setae in the Heterostigmata.

The significance of the condition found in the Tarsocheyloidea, as a relatively unspecialized superfamily of the Tarsocheylina, becomes apparent when one considers the sister group Tarsonemina and attempts to determine correct homologies and notations for the cupules and setae of the opisthosoma of mites of the superfamilies constituting this group. In the more generalized, apparently early-derivative genera of Pyemotoidea, a condition similar to that in the Tarsocheyloidea is retained. In the adult female of *Dolichocybe*, *Dolichomotes*, *Pavania*, and *Cara-boacarus*, the third opisthosomal plate has two transverse rows of setae, each with one pair, which should be called *e* and *f* (Fig. 4); one pair of cupules, *im*, is present but the posterior pair, *ip*, is apparently consistently absent (this needs confirmation by a careful study of as many representatives as possible of species of the above genera and others of Dolichocybidae). In the more derived groups of Pyemotoidea, and in the Pygmephoroida and Tarsonemoida, the third opisthosomal plate becomes shortened and widened in the larva and particularly in the adult female, on which the dorsal plates are modified to overlap and telescope successively into each other. Correlated with the shape of the third plate, the alignment of the two pairs of setae with each other has become oblique to fully transverse (Fig. 5). In the Tarsonemidae, the lateral pair of setae is more closely associated with cupules *im*, and usually is inserted at a level slightly anterior of the medial setae in the larva and adult female. The lateral pair is, therefore, regarded here as setae *e*, and the medial pair as setae *f*.

The recent attempts made by a few other authors to apply the setal notation of GRANDJEAN (1939, 1947) to the mites in various families of Tarsonemina must be reconciled with the new insight into setal homologies for the opisthosomal dorsum presented above. Van der HAMMEN (1970) was the first to apply Grandjean's notation to a representative of the Tarsonemina. But in his study of the adult female of a species of Tarsonemidae, he misinterpreted the limits of the overlapping dorsal plates, such that his notations are totally confused except for the first tergite. Van der Hammen's setal notations for the opisthosomal dorsum are equated below with those proposed herein. His misinterpretations of tergal limits, such that D is without setae, and of cupule and setal homologies, are discussed further by LINDQUIST (1976); the latter erred, however, in equating van der Hammen's pf_1 (rather than pe_2) with *e*, and pf_2 (rather than pf_1) with *f*. Following van der Hammen's example, a few other authors have adopted Grandjean's notation, particularly MAHUNKA (1971, 1972, and a series of other papers since then) for various families of Tarsonemina. The setal notations applied by these authors are similar to one another, and are equated with those proposed herein, as well as with those of van der Hammen, as follows:

Hammen (1970)	pc_1	pc_2	pe_1	pe_2	pf_1	pf_2	ph_1			
Mahunka & Others	c_1	c_2	d	e_2	e_1	f_1	f_2	h_1	h_2	h_3
Newly proposed	c_1	c_2	d	e	f	h_1	h_2	ps_1	ps_2	ps_3

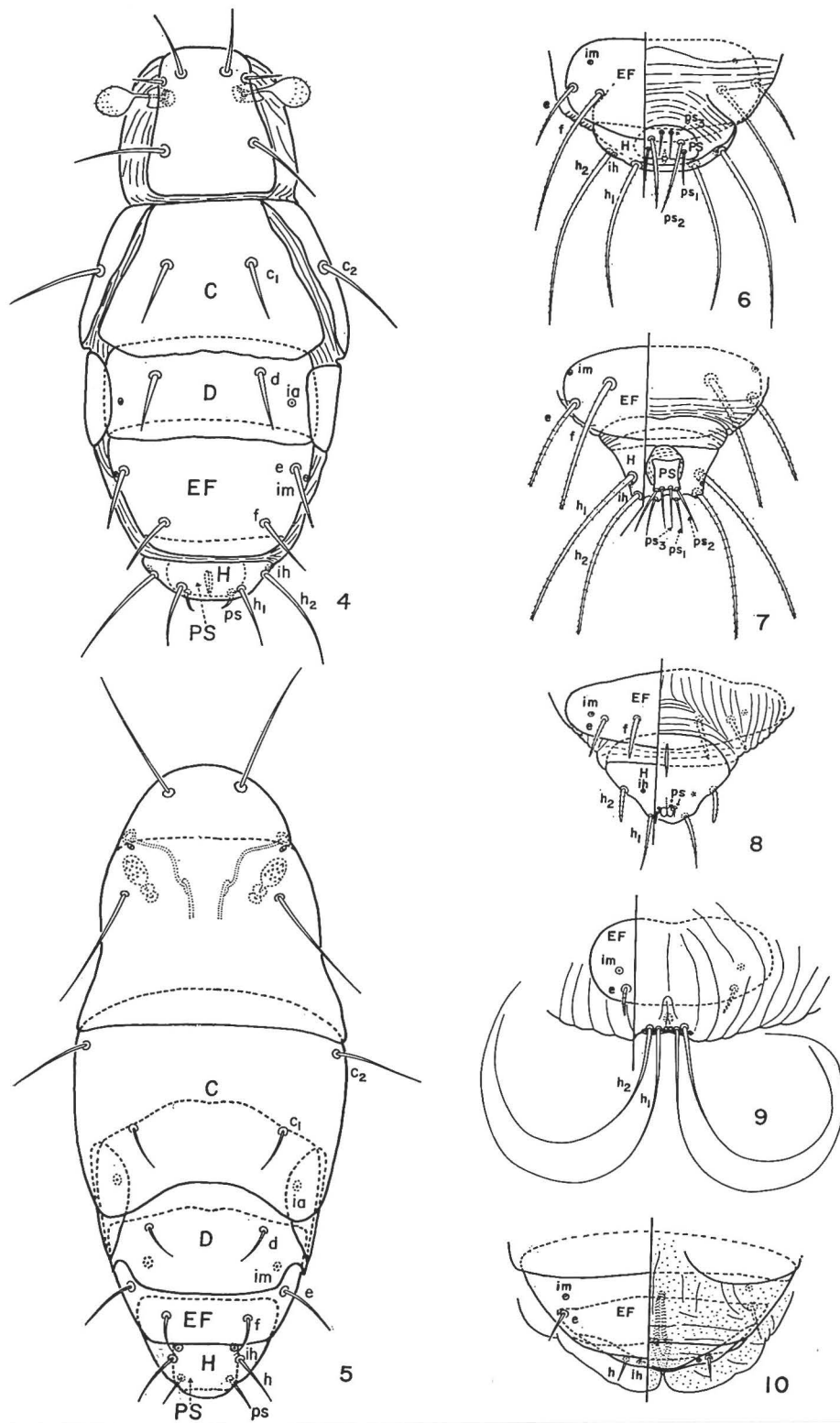
In the larva and adult female of the Podapolipidae, plate EF bears just one pair of setae, *e*, plus a pair of pits (Figs. 9, 10). The latter are interpreted here to represent cupules *im*, because they are morphologically similar to cupules *ia* associated with setae *d* on the preceding tergite of these instars, and because they are positioned relatively close to setae *e*.

The consolidation of tergites E and F into one plate is an apomorphic character state common to the larval and postlarval instars of all members of the Heterostigmata. Further apomorphic tergal consolidations have arisen among superfamilies within the Heterostigmata, but they are not characteristic of this group as a whole. In the Heterocheyleoidea, tergites C and D are partly or completely united into one large plate, bearing setae *c*₁, *c*₂, *d*, and cupules *ia* in the immature and adult instars of both sexes. In the families of Pyemotoidea excepting Dolichocybidae, and in all families of Pygmephoroidae and Tarsonemoidae, tergites C and D are completely united into one large plate in the adult male, but not in the larva or adult female. This compound plate is superficially similar to that of the Heterocheyleoidea in bearing the same setae and cupules; but it is thought to be an independently derived character state since it is linked to adult sexual dimorphism. In the adult male of the Podapolipidae, plate CD is sometimes subdivided medially into two lateral plates, as sometimes are tergites C and D in the larva and adult female (see figs. 6, 8 in EICKWORT, 1975); but the compound nature of the lateral plates is still retained in the male. In the early derivative pyemotoid family Dolichocybidae, tergite C remains completely separate from D on the adult male (see fig. 16 in CROSS, 1965), as it does in the Tarsocheyleoidea.

Segment H has undergone considerable modification in structure and setation, including integration with segment PS on the larva and adult male, in the Tarsonemoidae. This is evident both in comparing tarsonemoids with pyemotoids and pygmephoroids, and in noting changes during the ontogeny of tarsonemoids. The full complement of two pairs of setae *h*, cupules *ih*- and three pairs of setae *ps*, as found in the Tarsocheyleoidea and many other groups of Eleutherozonia (Fig. 3), is retained on the larva and adult female in many species of Pyemotoidea and Pygmephoroidae (Figs. 6, 7), though one or two pairs of *ps* may be rudimentary or absent on the adult male of the same species. In the larva and adult male, segments H and PS become increasingly integrated in the more derived families of Tarsonemina (compare Figs. 6, 7, 8). But in the adult female, PS generally remains recognizable as a discrete caudal or ventrocaudal structure, with its own sclerotization, and with one to three pairs of caudal setae, *ps*; cupules *ips* remain absent.

In the larvae of Tarsonemidae, two pairs of usually prominent, often barbed setae *h*, cupules *ih*, and two pairs of usually minute setae *ps* are present on a caudal, sclerotized cone that embodies segments H and PS (Fig. 8). However, the adult female tarsonemid consistently retains only one pair each of setae *h* and *ps* (Fig. 5). Because of this, SCHAARSCHMIDT (1959) regarded the caudalmost pair of setae *h* on the larva to be homologous with an external pair of ventrocaudal, or *ps*, setae. That this is not the case is indicated by three lines of evidence: (1) the structure of these setae is like that of the other pair of *h* setae and the other dorsal setae, rather than being short and fine like the *ps* setae; (2) these setae are inserted clearly on tergite H, rather than on the reduced PS, on larvae of the related Pyemotoidea and Pygmephoroidae, in which the regions comprising H and PS are still distinguishable from each other (Figs. 6, 7); (3) the full complement of two pairs of *h* setae and three pairs of *ps* setae of the larva is retained on the adult female in many species of Pyemotoidea and Pygmephoroidae, and thus by elimination alone, the caudalmost pair of larval setae must be of the *h* row.

The two pairs of setae *ps* of the larva in the Tarsonemidae (Fig. 8) flank the uropore anterolaterally, as in the Pygmephoroidae (Figs. 6-7). Of these, consistently only one pair persists on the adult female (Fig. 5), and none on the adult male. This pair of *ps*, commonly called the



FIGS. 4-10. — 4-5, Idiosomal dorsum of adult females : 4) *Pavania* sp.; 5) Tarsonemidae, gen. et sp.

6-10, caudal part of opisthosoma, dorsal aspect on left side, ventral aspect on right : 6) *Siteroptes* sp., larva ; 7) *Scutacarus* sp., larva ; 8) *Iponemus* sp., larva ; 9) *Chrysomelobia* sp., larva ; 10) *Chrysomelobia* sp., adult female.

“caudal setae” by various authors, was misinterpreted as part of the ventral opisthosomal chaetotaxy by NUCIFORA (1965), who considered that PS had no dorsal setae.

On the larvae of Podapolipidae, segments H and PS are not distinguished as a sclerotized area. Nevertheless, the two pairs of setae *h* are retained, behind the level of the uropore (Fig. 9); usually *h*₁, and sometimes *h*₂, are markedly elongate; cupules *ih* are not evident. These setae could be misinterpreted as *ps* setae, but their size and position *behind* the uropore indicate that they are *h* setae for which no discernible tergite H remains; even on the adult female, tergite H is vestigial or absent. As in the Tarsonemidae, the adult podapolipid retains only one of these two pairs of setae, again *h*₂ according to its position laterad of cupules *ih* (these are sometimes evident on the remnants of tergite H of the female, as in Fig. 10). These setae, cupules, and tergal remnants of segment H are entirely lost on the adult female of some of the more derived groups of Podapolipidae.

Only in the Podapolipidae among the families of Tarsonemina is segment PS unrecognizable as a region; there is no ventrocaudal sclerotized entity, and the *ps* setae are absent on the adult female; no *ps* setae flank the uropore anterolaterally on the larva. Rarely, however, a pair of apparently true *ps* setae are expressed on the adult male, posteriad of the genital capsule (see setae “c” in fig. 6 of EICKWORT, 1975); their homologues are not found on the adult female (setae “c” in fig. 1 of EICKWORT, 1975 are *h* setae as explained above).

The integration of segments H and PS is most highly developed in the adult male of the Tarsonemina, in which they constitute a specialized housing for the genitalia. This is discussed by the author in another paper, in preparation.

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