

OBSERVATIONS ON THE LARVA AND PROTONYMPH OF TARSOCHEYLID MITES (ACARI : HETEROSTIGMATA)

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TARSOCHEYLIDAE
SHIELDS
LEG CHAETOTAXY
POSTEMBRYONIC
DEVELOPMENT
HETEROSTIGMATA
TARSONEMINA

ABSTRACT : A general description, with illustrations, of the larva of Tarsocheylidæ, based on material of *Tarsocheylus* Berlese and *Hoplocheylus* Atyeo and Baker, is presented for the first time. In light of observations on this instar, the homology of structures and application of standard systems of notation of GRANDJEAN, especially that for the leg tarsi, are determined more precisely than was formerly possible. A previous interpretation, that the third opisthosomal dorsal plate EF in postlarval instars of tarsocheylidæ is compounded from the tergites of two segments, is confirmed by the component plates E and F remaining separate in the larva. Observations on the ontogeny of various structures, particularly on the changes between larva, protonymph, and deutonymph, treat the opisthosomal dorsum and caudal bend, the proral and tectal setae of tarsi I to IV, and the denudation of setae on leg IV of the protonymph. The significance of these ontogenetic phenomena for cladistic analysis and classification of the Tarsocheyloidea and the Heterostigmata is discussed. Diagnoses are provided for the family Tarsocheylidæ and its genera, based on the larva and nymphal instars, in comparison with the subcohort Raphignathæ, the Heterocheylidæ, and the Tarsonemina.

TARSOCHEYLIDAE
BOUCLIERS
CHAETOTAXIE
PÉDIEUSE
DÉVELOPPEMENT
POSTEMBRYONNAIRE
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RÉSUMÉ : On présente pour la première fois une description générale ainsi que des illustrations de la larve des Tarsocheylidæ, basées sur des échantillons de *Tarsocheylus* Berlese et *Hoplocheylus* Atyeo et Baker. On démontre l'homologie des structures et on applique, particulièrement en ce qui a trait aux tarses des pattes, les systèmes fondamentaux de notation formulés par GRANDJEAN, d'une manière plus précise qu'on ne le faisait auparavant. La présence sur l'opisthosoma de boucliers E et F séparés chez la larve des Tarsocheylidæ confirme une interprétation antérieure selon laquelle le troisième bouclier dorsal de l'opisthosoma, EF, est constitué de tergites à deux segments chez les stases postlarvaires. Les observations sur l'ontogenèse des diverses structures, en particulier des changements entre la larve, la protonymph, et la deutonymph, traitent du dorsum opisthosomal, de la courbe caudale, des poils proraux et tectaux des tarses I à IV, et de la dénudation des poils de la patte IV de la protonymph. L'importance de ces phénomènes ontogénétiques pour l'analyse cladistique et la classification des Tarsocheyloidea et des Heterostigmata est discutée. On donne les diagnoses pour la famille des Tarsocheylidæ et ses genres, basées sur la larve et les stases nymphaux, en comparaison avec la sous-cohorte Raphignathæ, les Heterocheylidæ, et le groupe Tarsonemina.

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INTRODUCTION

Among the various families of mites comprising the subcohort Heterostigmata *sensu* LINDQUIST (1976), or the Heterostigmae *sensu* KRANTZ (1978), the Tarsocheylidae Atyeo and Baker, 1964 is of particular theoretical interest in representing apparently the earliest-derivative, or ancient, extant lineage. Because of this position, which will be discussed further below, the family is especially useful for out-group comparisons in cladistic analyses of other families of Heterostigmata (LINDQUIST 1986). Until the present, however, the full potential of this usefulness has been hampered by a lack of data on the larval instar of tarsocheylids, which has precluded understanding the ontogeny of structures expressed in adults. This paper presents for the first time a general description and illustrations of the larva of Tarsocheylidae, based on material representing both of the described genera, *Tarsocheylus* Berlese, 1904 and *Hoplocheylus* Atyeo and Baker, 1964. In turn, this has enabled a more correct and precise determination of homology of structures and application of the standard notation of GRANDJEAN (1939, 1940, 1941a) than previously. These observations are of critical importance both in re-evaluation of the phylogenetic relationships of the Tarsocheylidae within the Heterostigmata, and in future evaluation of the phylogenetic relationships of the Heterostigmata among other major lineages of Eleutherengona.

MATERIAL EXAMINED

Representatives of about 10 species of Tarsocheylidae were at hand for this study. Determinations of specimens to species were uncertain in most cases,

without comparison with type-material, because the published descriptions of species are inadequate and are based on insufficient type-series to account for intraspecific variability. Several species synonymies are anticipated, and reliable distinctions between species with closely similar forms are needed. Material of the following taxa was examined from the Canadian National Collection (C.N.C.), Ottawa, and the Laboratory of Acarology, Ohio State University (O.S.U.), Columbus :

Tarsocheylus paradoxus Berlese, 1904 (= *Hoplocheylus discalis* Atyeo & Baker, 1964) : all instars, ex. moist insect frass and litter in white pine log, Thwartway I., St. Lawrence Islands Natl. Park, Ontario, Canada (C.N.C.).

Hoplocheylus sp. near *similis* Delfinado & Baker, 1974 (possible junior synonym of *H. pickardi* Smiley & Moser, 1968) : all instars, ex. ant nest in trunk of white pine, Kouchibouguac Natl. Park, New Brunswick, Canada (C.N.C.).

Hoplocheylus sp. near *longispinosus* Atyeo & Baker, 1964 : larvae, protonymph, adults, ex. spruce stump and aspen litter in mixed woods, Kouchibouguac Natl. Park, New Brunswick, Canada (C.N.C.).

Hoplocheylus canadensis Marshall, 1966 (possible junior synonym of *H. atomarius* (Berlese, 1913)) : larva, ex. pine litter and rotten wood, Storrs, Connecticut U.S.A. (O.S.U.); adults, ex. moss and litter under mature oaks, Grenadier I., St. Lawrence Islands Natl. Park, Ontario, and hemlock and beech mor, Montreal I., Québec, Canada (C.N.C.).

Hoplocheylus johnstoni Atyeo & Baker, 1964 : protonymph, ex. dirt under rotting deciduous log, Oconee Co., Georgia, U.S.A. (O.S.U.); deutonymph & adult, ex. rotting stump, Point Pelee, Ontario, Canada (O.S.U. & C.N.C., resp.).

In addition, deutonymphs of *Hoplocheylus* sp. near *arnoldii* Livshitz & Mitrofanov, 1973 and of an undetermined species of *Hoplocheylus*, both from eastern Canada, and adults of three undetermined species of *Hoplocheylus* from western United States were examined (C.N.C.).

GENERAL DESCRIPTION OF THE TARSOCHEYLID LARVA

All of the gnathosomal structures, as described by LINDQUIST (1976) for the postlarval instars of tarsocheylids, are present. These include : 2 pairs of dorsal

setae on the stylophore, 2 pairs of subcapitular setae, 1 or 2 pairs of minute adoral setae, 1 pair of palpal supracoxal setae, palpal femorogenu with 2 dorsal

setae (1 femoral and 1 genual), palpal tibiotarsus with 6 setae (1 of which may be modified in shape), 1 solenidion, 1 terminal claw, and 2 subterminal setigenous, flangelike or spinelike processes which may be partly fused together. The differences in form of certain of the palptibial structures, which may be used to distinguish members of *Hoplocheylus* from those of *Tarsocheylus* (compare figs. 3 and 4 in

LINDQUIST 1976), are also manifested in the larvae. The styletlike movable cheliceral digits and the pharyngeal complex, with its paired series of finlike extensions laterally, are fully developed (Fig. 2).

Structures of the prodorsum are as expressed on the nymphal instars, and include : 4 pairs of simple setae with normal alveoli arise from a weakly sclerotized prodorsal shield ; eyes, stigmatic openings and

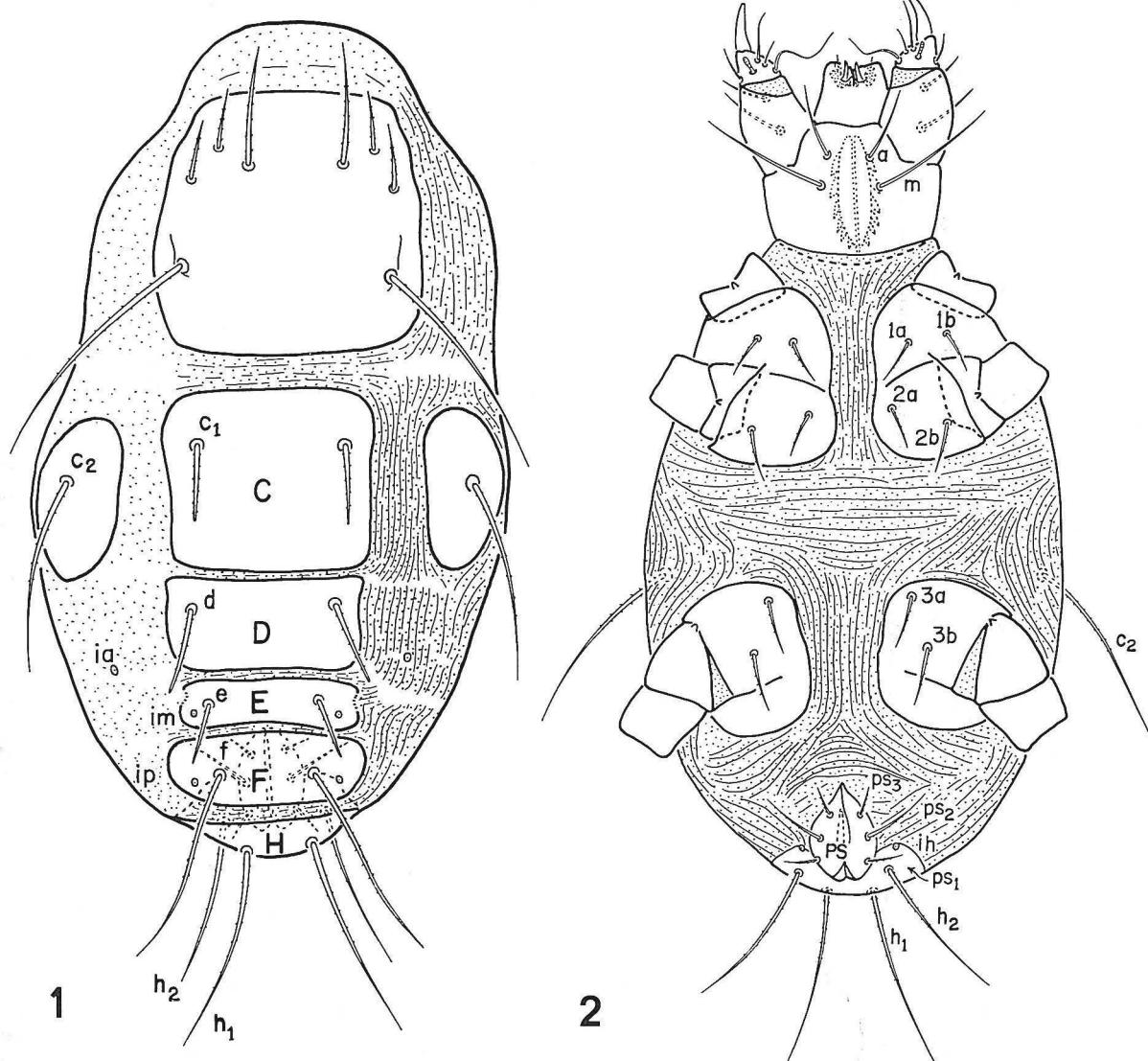


FIG. 1 : Idiosomal dorsum of larva of *Tarsocheylus paradoxus* Berlese. Notation of opisthosomal structures based on GRANDJEAN (1939).

FIG. 2 : Body venter of larva of *Tarsocheylus paradoxus* Berlese (dorsal setae of palpal tibiotarsus omitted). Notation of podosomal structures based on GRANDJEAN (1934) and of opisthosomal structures, GRANDJEAN (1939).

associated tracheae are absent. A podocephalic canal system is evident in the larval, as in the postlarval, instars.

Opisthosomal structures differ from those of the postlarval instars in three significant aspects. First, plate E, bearing setae *e* and cupules *im*, is usually separated by a narrow strip of membranous cuticle from plate F, which bears setae *f* and cupules *ip* (Fig. 1). The separation of plate E from F is clear among ample larval material at hand of *Tarsocheylus paradoxus* Berlese and *Hoplocheylus canadensis* Marshall; however, on one larva of another species of *Hoplocheylus*, determined as *H.* sp. near *similis* Delfinado & Baker, plate E is not clearly delineated from F, though there is an emargination of the lateral edge of plate EF at the level where the separation would otherwise be. Second, plate H and setae *h_{1,2}* are terminal, and the anus (possibly a uropore) and the 3 pairs of pseudanal setae are displaced caudoventrally (Fig. 2). Third, aggenital plating and setae are absent (the statement by LINDQUIST (1976), that the opisthogaster bears a large plate, without setae, in the larva, was based on heterocheylid mites and is erroneous for tarsocheylid larvae, which were not available during that study).

On the podosomal venter, coxisternal plates I and II are united with each other on either side, but they are separated medially by a longitudinal band of membranous cuticle, as in postlarval instars (Fig. 2). However, each of plates I and II has only 2 setae, rather than the 4 and 3 setae, respectively, characteristic of postlarval instars. Apodemes 2, delineating coxisternal plates I from II on either side, are weakly defined. Similarly, coxisternal plates III are separated medially by membranous

cuticle, and each plate has only 2 setae rather than the 3 setae of postlarval instars (Fig. 2). The midventral plate, present in the large area separating coxisternal plates II from plates III in postlarval instars, is absent. The absence of Claparède organs, or urstigmata, between coxisternal plates I and II correlates with the absence of genital papillae in postlarval instars.

As in the postlarval instars, paired claws are present on all legs, tarsus I lacks an empodium, and tarsi II and III each have a smooth, membranous empodium that is stalked at its origin between the claws and is narrowly lanceolate to broadly rounded or truncated apically, depending on the species (Figs. 3, 5, 6; see also figs. 15-17 in LINDQUIST 1976). One solenidion is present on each of tibiae I-II-III and tarsi I-II; solenidia φ_2 of tibia I and ω_2 of tarsus I are not added until the protonymph, or rarely these solenidia are completely suppressed. The patterns of setation (solenidia excluded) of the segments of legs I-II-III are as follows: trochanters, 0-0-0 (setae *l'* of trochanter III not added until protonymph, and *v'* of trochanters I-III until deutonymph); femora, 5-3-2 (as in postlarval instars); genua, 5-4-4 or rarely 4-3-3 (as in postlarval instars); tibiae, 6-5-5 or rarely 6-4-4 (as in postlarval instars); tarsi, 11-8-8, or rarely 11-7-7 or 11-4-4 (setation of tarsi II-III as in postlarval instars; proral eupathidia *p'-p''* and anterolateral seta *l'* of tarsus I not added until protonymph). On tarsus I the tectal setae *tc'-tc''* and fastigial seta *ft'* are eupathidial (as in postlarval instars), but *ft''* usually is setiform. On tibia I the anteroventral seta *v'* may be enlarged or not (as in postlarval instars).

DETERMINATION OF HOMOLOGY, NOTATION AND ONTOGENY OF LEG SETAE ON TARSOCHEYLID MITES

Clarification of setal homologies and application of a standard, or fundamental, system of setal notation are of utmost importance as a prerequisite to recognizing character states and hypothesizing character state polarities and transformations. LINDQUIST (1976) made the first attempt at applying the standard verticil system of setal notation of

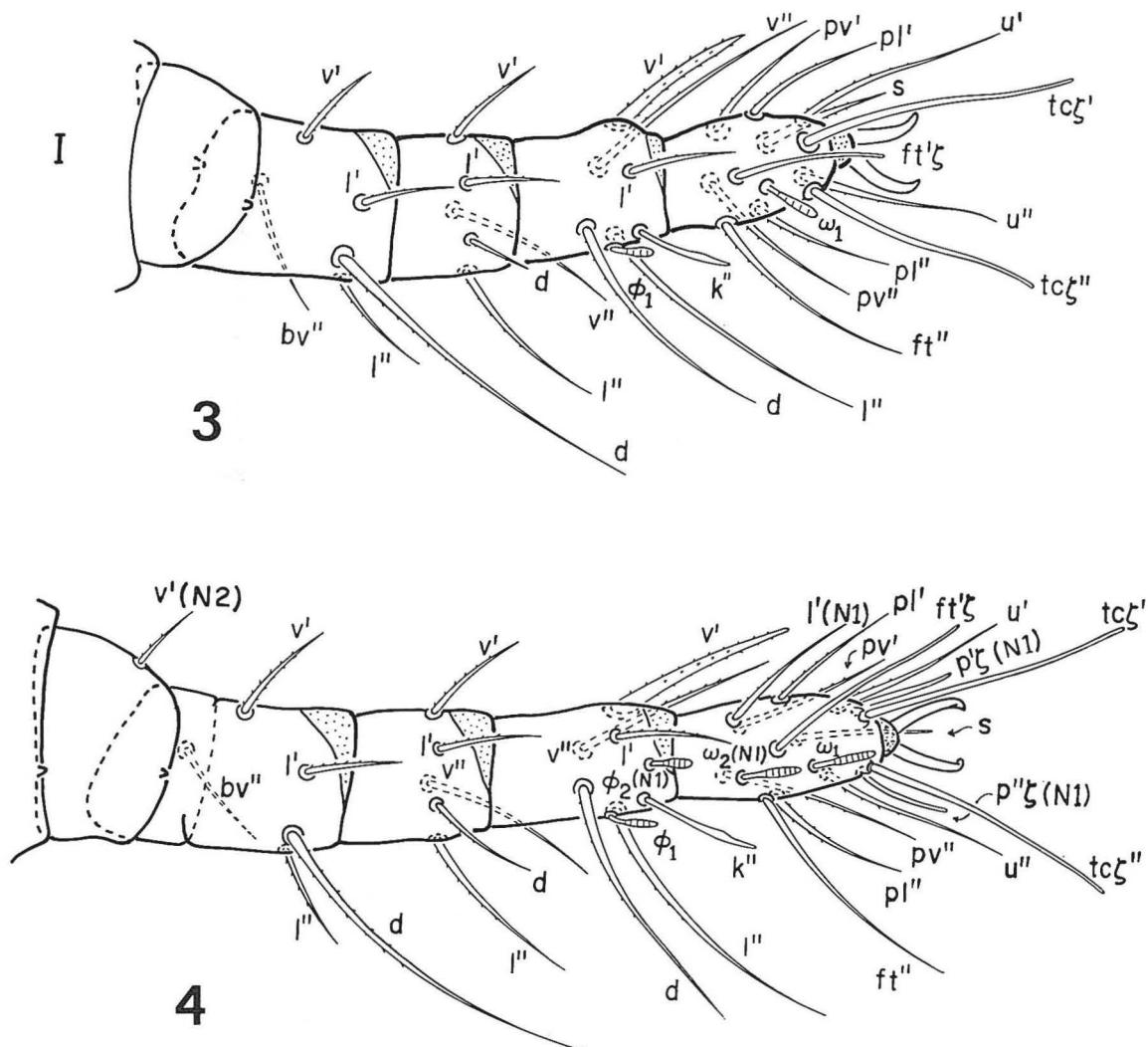
GRANDJEAN (1940) to the legs of tarsocheylid mites, but he did not attempt to apply the special notation developed by GRANDJEAN (1940, 1941a) for the leg tarsi. Based on the present study of tarsocheylid larvae and postlarval instars, and on comprehensive comparative studies of leg setation in other families of the subcohort Heterostigmata

on the one hand (LINDQUIST 1986) and of the sister-subcohort Raphignathae on the other (LINDQUIST 1985a), the homologies, notation, and ontogenetic patterns of addition of leg setae are fully determined here in a comparative manner for Tarsocheylidae (Figs. 3-7).

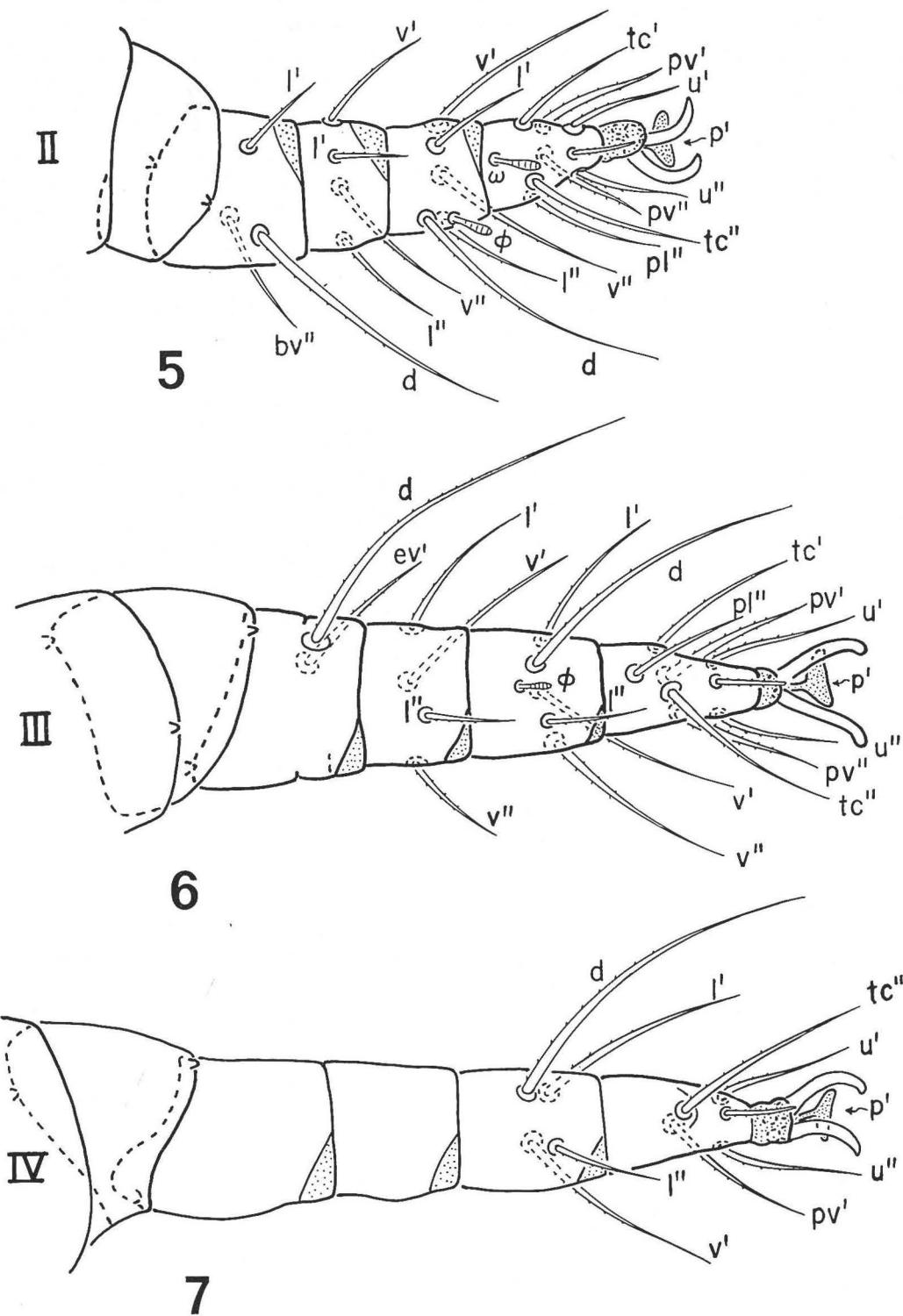
Trochanters. The trochanters retain the basic complement and ontogeny of setae as found widely among members of the subcohort Raphignathae, and this affords ready distinctions among all immature instars of Tarsocheylidae. Trochanters I to III lack setae in the larva. The pattern of 0-0-1-0 in the

protonymph reflects the addition of but one seta, I' , on trochanter III. The pattern of 1-1-2-0 in the deutonymph reflects the appearance of seta v' on each of the trochanters except on leg IV, where this seta does not appear until the adult.

Femora. The pattern of 5-3-2 setae on femora I-II-III in the larva is retained, without additions, to adulthood. The setal homologues were, in general, denoted correctly by LINDQUIST (1976, figs. 11-13); but it is preferable to denote the subproximal femoral seta of legs I and II by the signature bv'' (rather than v''), as introduced by GRANDJEAN



FIGS. 3-4 : Leg I of *Tarsocheylus paradoxus* Berlese, dorsal aspect : 3, larva ; 4, deutonymph. Signatures for chaetotaxy and solenidiotaxy based on systems of notation of GRANDJEAN (1940, 1941a).



FIGS. 5-7 : Legs II to IV of *Tarsocheylus paradoxus* Berlese, dorsal aspect : 5, leg II of larva ; 6, leg III of larva ; 7, leg IV of protonymph.
Signatures for chaetotaxy and solenidiotaxy based on systems of notation of GRANDJEAN (1940, 1941a).

(1942b, 1943, 1947) for oribatid and certain pros-tigmatic mites, to indicate that it is a remnant of a basifemoral verticil, or whorl, of setae that originally belonged to the proximal of the two femoral segments on the legs of early-derivative acariform mites (Figs. 3, 5). The leg femora of larval and postlarval tarsocheylid mites, like those in the Raphignathae, are undivided, yet there is sometimes remnant sutural evidence of the line of fusion between the two former segments (Figs. 4, 6), and their setal complement is a composite of the two primitive, fundamental verticils, representing the basal and distal femoral segments. Theoretically, bv'' is restricted to femora I and II, with another fundamental seta of the basifemoral verticil, ev' , present instead on femora III and IV (GRANDJEAN 1942b, NORTON 1977, LINDQUIST 1985a); this was noted also by GRANDJEAN (1944) for some raphignathoid taxa. This interpretation is provisionally accepted here for the Tarsocheylidae (Fig. 6) but, as noted in my recent studies of the Tetranychoidea (LINDQUIST 1985a, b), there is some doubt whether bv'' is truly replaced by ev' on femora III-IV or is simply displaced to a v' position on legs III and IV in order to maintain a functionally antiaxial position, as on legs I and II. On postlarval instars, femur IV is devoid of setae in the protonymph (Fig. 7) but it has the same complement of setae, d and ev' , as on femur III in the deutonymph and adult (LINDQUIST 1976, figs. 13-14).

Genua. The general pattern of 5-4-4 setae on genua I-II-III in the larva (Figs. 3, 5, 6) is retained, without additions, to adulthood. The setal homologues were denoted correctly by LINDQUIST (1976, figs. 11-13). On postlarval instars, genu IV is devoid of setae in the protonymph (Fig. 7) but it has a verticil of four or five setae in the deutonymph and adult, i.e., sometimes with one more seta, d , present than on genua II and III (LINDQUIST 1976, fig. 14).

The general adult setal pattern of 5-4-4-4 or 5-4-4-5 for genua I-II-III-IV is reduced to 4-3-3-2 in the deutonymph of an apparently undescribed species of *Hoplocheylus*, near *arnoldii* Livshitz & Mitrofanov, at hand. In this case, genu I lacks d , genua II and III lack l'' , and genu IV lacks l' and l'' . Such losses on genua I to III represent suppression of

setae, though larval specimens of this species are not at hand to confirm this.

Tibiae. The general pattern of 6-5-5 setae and 1-1-1 solenidia on tibiae I-II-III in the larva is retained to adulthood, without additions except for solenidion φ_2 being added to tibia I in the protonymph. The tibia of each leg has one complete verticil of setae, and their homologues were denoted correctly by LINDQUIST (1976, figs. 11-13) except that in fig. 11, famulus k'' was misrepresented as an ordinary seta and denoted as d_1 , and seta d was denoted as d_2 , on tibia I (compare with Fig. 4 herein). On postlarval instars, tibia IV of the protonymph (Fig. 7) usually lacks one seta, v'' , of the adult complement, and the verticil of 5 setae is completed in the deutonymph. In a species of *Hoplocheylus* near *similis*, however, seta v'' is not retarded, and the tibial verticil is complete on leg IV in the protonymph. Tibia IV lacks a solenidion in all postlarval instars.

The general adult setal (solenidial) pattern of 6(2 φ)-5(1)-5(1)-5(0) for tibiae I-II-III-IV is reduced to 6(1)-4(1)-4(1)-4(0) in the deutonymph of the same species of *Hoplocheylus* with genual setal deficiencies, noted above. In this case, tibiae II to IV lack seta l'' , tibia I lacks solenidion φ_2 , and the single solenidion present on each of tibiae I to III is so small as to be hardly discernible. The loss of l'' on tibiae II and III again represents suppression of a larval seta, and the loss of φ_2 on tibia I is suppression of a protonymphal solenidion. The loss of l'' on tibia IV is interesting because this seta is generally among the first setae to appear on tibia IV during ontogeny, yet it is the first to be lost, rather than v'' which is added in the deutonymph.

Tarsi. The general larval pattern of tarsal setae is 11-8-8, and of tarsal solenidia, 1-1-0. The special notation developed by GRANDJEAN (1940, 1941a) for the tarsal structures of the legs of acariform mites is applied here for the first time to tarsocheylid mites. Tarsus I generally bears five pseudosymmetrically paired sets of setae, the tectals $tc'-tc''$ which are elongate and eupathidial in form, fastigials $ft'-ft''$ of which sometimes only ft' is eupathidial, unguinals $u'-u''$, primiventrales $pv'-pv''$, and

primilaterals $p''-pl''$, plus one unpaired seta, the subunguinal s (Fig. 3). The larval complement is usually augmented in the protonymph by a pseudosymmetric pair of proral setae, $p'-p''$, which are eupathidial, an anterolateral seta, l' , (denoted simply as l' in Fig. 4), and another solenidion, ω_2 . The protonymphal complement is retained, without additions, to adulthood. Despite their suppression in the larval instar, the prorals are denoted as such on postlarval instars because of their eupathidial nature and their apical position; this is thought to be an instance of retardation in expression of a pseudosymmetric pair of fundamental setae. However, the other postlarval setal addition is given a revised denotation here as an accessory seta, l'_1 , rather than as a delayed fundamental seta such as an antelateral a' (as denoted by LINDQUIST, 1986), because of its being added proximally of the other setae, which is typical of accessory setal additions during ontogeny.

The larval complement of setae on tarsi II and III is retained, without additions, to adulthood and generally includes the pseudosymmetrically paired tectals, unguinals, primiventrals, and the unpaired proral p' and primilaterial pl'' (Figs. 5-6). None of these setae is clearly eupathidial, though p' is sometimes less tapered and slightly truncated apically. Tectal seta tc'' is usually noticeably longer and more dorsal in position than tc' . On postlarval instars, tarsus IV of the protonymph (Fig. 7) lacks two setae, apparently tc' and pv'' , of the adult complement, and these are added in the deutonymph. Seta tc'' has a more anterolateral position, and pv' a more posterolateral position, on tarsus IV in the protonymph than in subsequent instars, due

to what is thought to be a compensatory position effect which minimizes the space left by missing setae (GRANDJEAN 1940, LINDQUIST 1986); the position of these setae on tarsus IV of the protonymph (Fig. 7) may be compared with that for the metamerically homologous setae on tarsus III of the larva and protonymph (Fig. 6) which approximates the position these setae occupy in the presence of tc' and pv'' on tarsus IV in the deutonymph and adult (see fig. 14 in LINDQUIST 1976).

In general, species of Tarsocheylidae have one seta less on tarsus IV than on tarsi II and III. In adults, when tarsi II and III retain their maximum complement of eight setae, including tc' and pl'' as noted above, then tarsus IV has seven setae and lacks pl'' ; when tarsi II and III each have seven setae, including tc' but lacking pl'' , then tarsus IV has six setae and lacks both pl'' and tc' . These characteristics result in the tarsal setal (solenidial) patterns of legs I-II-III-IV of adults being 14(2 ω)-8(1)-8(0)-7(0), or less frequently, 14(2)-7(1)-7(0)-6(0), as noted by LINDQUIST (1976). The loss of pl'' on tarsi II and III in these instances is suppression of a larval seta. Rarely, further reductions in the setation of tarsi II to IV occur, with each tarsus retaining the same complement of four setae, including tc'' , $u'-u''$, pv' , and lacking p' , tc' , pv'' , pl'' . In the deutonymph of the same species of *Hoplocheylus* with genual and tibial deficiencies noted above, these tarsal losses result in a setal (solenidial) pattern of 14(1)-4(1)-4(0)-4(0). In this species, the losses of p' , tc' , pv'' and pl'' on tarsi II and III are all suppressions of larval setae, and the loss of ω_2 on tarsus I is suppression of a protonymphal solenidion.

SIGNIFICANCE AND IMPLICATIONS OF LARVAL TARSOCHEYLID CHARACTERISTICS

1. *Opisthosomal dorsum*. Heterostigmatic mites superficially appear to have only five opisthosomal segments, as indicated by their dorsal and caudal plates, rather than the six opisthosomal segments characteristic of larval acariform mites generally (GRANDJEAN 1939). It is essential, therefore, to

clarify whether the external structures of one segment of the opisthosoma have been repressed, or the structures of two segments have become consolidated, in the evolution of the ancestral stock of Heterostigmata.

Based on evidence of cupules and setae, LIND-

QUIST (1977) hypothesized that the third opisthosomal plate on adult females of tarsocheylid mites, and of heterostigmatic mites in general, is compounded of the tergites of two opisthosomal segments, E and F. The new observations presented herein, that plates E and F are usually separated by a narrow strip of membranous cuticle in the larva, and subsequently in the same species are completely consolidated into one plate EF in all postlarval instars in both genera of Tarsocheylidae, should remove any lingering doubt about the validity of this hypothesis. The importance of this hypothesis in determination of homologies and assignment of correct notations for the opisthosomal setae among mites of the more derivative superfamilies of Tarsonemina is discussed elsewhere (LINDQUIST 1977, 1986).

The significance of this ontogenetic condition in the Tarsocheylidae, of plates E and F remaining separate from each other in the larva, then becoming fully consolidated in postlarval instars, is to be found in hypothesizing a transformation series of states for the character under consideration. Maintenance of separation between plates E and F throughout larval and postlarval instars is regarded to be the plesiomorphic state, as found in Pomerantziidae and several genera of Stigmaeidae and Eupalopsellidae (LINDQUIST 1977, SUMMERS 1966, MEYER and UECKERMANN 1984). Consolidation of plates E and F is hypothesized to have started, as a first step, in the adult instar (much as plates C and D consolidate only in the adult male in most families of Tarsonemina). Subsequent steps in the transformation series would result in the increasing suppression of the separate condition of plates E and F during postembryonic development, until the consolidated state is manifested in all postembryonic instars. The condition in Tarsocheyloidea is seen as an intermediate state, but nevertheless an apomorphy, not because plates E and F are separate in the larva but *because they become consolidated in a postlarval instar*. The consolidation of plates E and F in the larval and postlarval instars in all other known superfamilies of Heterostigmata, including the Heterocheyloidea, is a more advanced state than that found in Tarsocheyloidea. The sharing of this state between Heterocheyloidea

and all superfamilies constituting the Tarsonemina is one of several possible synapomorphies supporting a hypothesis that the Heterocheyloidea may be more closely related, as the sister group, to the Tarsonemina than they are to the Tarsocheyloidea (LINDQUIST, 1986).

2. *Caudal bend.* As shown in Fig. 2, the structures of the pseudanal segment are caudoventral in position in the larva, rather than being terminal as in postlarval instars (see figs. 1, 8-10 in LINDQUIST 1976). Such a posteroventral curvature of the opisthosoma caudally, or "caudal bend", is characteristic of the larva of most early-derivative mites, as figured diagrammatically by GRANDJEAN (1939) and as discussed by SITNIKOVA (1978) and LINDQUIST (1984). The absence of a caudal bend in larval and nymphal Opilioacarida was regarded by LINDQUIST (1984) as retention of a plesiomorphic, orthosomatic condition as found in other orders of the Arachnida. Since the presence of a caudal bend is, along with anamorphosis, characteristic of larval and nymphal instars of various early-derivative substocks of acariform mites, this state, along with anamorphosis, may be hypothesized as apomorphic for the ancestral stock of Acariformes, if not for an even more ancestral stock that embraces Acariformes and Parasitiformes. Amidst the various substocks of mites *within* the Acariformes, then, a larval caudal bend must be regarded as plesiomorphic. An apparent transformation reversal to an orthosomatic state is found among the postlarval instars of some mites of more derivative groups within the Acariformes, in which anamorphosis is suppressed and the pseudanal segment is located terminally, as in the Raphignathoidea and Tarsocheyloidea. However, the larvae of these groups retain the caudal bend.

Within the Heterostigmata other than the Tarsocheyloidea, in those superfamilies which retain an active free-living larva, the larva generally retains some aspect of a caudal bend. The caudoventral aspect is more discernible in larvae of Pygmephoidea in which the PS structures are separate from, and ventrocaudal to, the covering dorsocaudal plate H (see figs. 8-9 in LINDQUIST, 1986); but even when the PS structures are consolidated with

segment H to form a terminal capsule HPS, as in larvae of Tarsonemidae, the *ps* setae are still ventrocaudal in position on the capsule (fig. 10 in LINDQUIST, 1986). Larvae of the heterostigmatic superfamily Heterocheyloidea, however, are truly orthosomatic, like the postlarval instars. A larval orthosomatic condition is hypothesized here to be apomorphic for Heterocheyloidea in distinction to Tarsocheyloidea and to the superfamilies of Tarsonemina in which a free-living larva is retained. This condition probably is one of a suite of adaptations for all active instars of heterocheylid mites to live as parasites in confined spaces under the elytra of passalid beetles.

3. *Proral setae of tarsus I.* In the Tarsocheyloidea, the suppression of the proral eupathidia *p'-p''* on the larva, followed by their appearance on the protonymph, is another finding of phylogenetic significance. This ontogenetic pattern, of delay of expression of the prorals of tarsus I until the next active instar after the larva, characterizes all members of Heterostigmata and appears to be a synapomorphy, in addition to those given by LINDQUIST (1976), for this entire assemblage. In members of the Heterocheyloidea, which retain two active nymphal instars, the prorals of tarsus I first appear on the protonymph, as in the Tarsocheyloidea. In members of all superfamilies of Tarsonemina, they first appear on the adult, which is the only active instar after the larva. The latter character state may be considered as a synapomorphy for the entire assemblage Tarsonemina, though it is directly correlated with the synapomorphic suppression of active nymphal instars in this group. The state shared by Heterocheyloidea and Tarsocheyloidea, however, should *not* be regarded as a synapomorphy; since this state is a basic apomorphy for the subcohort Heterostigmata as a whole, it becomes a plesiomorphy for any taxon *within* this subcohort.

4. *Seta p' of tarsi II to IV.* The presence of proral seta *p'*, in an unpaired and possibly eupathidial state, is confirmed on tarsi II and III of the larva, as it is on tarsi II to IV of postlarval instars, of Tarsocheyloidea. A similar condition is found among a few of the early-derivative members of the

Tarsonemina (e.g., *Trochometridium* and *Carabocarus*), except that an active larva is suppressed in these taxa. In other early-derivative taxa of Tarsonemina in which an active larval instar is retained (e.g., *Siteroptes*), seta *p'* is absent on tarsi II and III in the larva and adult. It is therefore problematic whether the ancestral stock of Tarsonemina retained seta *p'* on tarsi II and III of the larva, though there is no evidence for retardation of its expression until adulthood.

An unpaired eupathidial *p'* is also found on tarsi II, and sometimes III, in the larval and postlarval instars of representatives of Raphignathidae, Stigmeidae, Cheyletidae, and some Caligonellidae. It is problematical whether this may be evidence for a basic synapomorphy between the Raphignathoidea + Cheyletoidea and the Heterostigmata as sister groups, subsequent to the splitting off of the Tetranychoidea which was characterized by LINDQUIST (1985b) as having both proral eupathidia *p'-p''* present on tarsus II, and both absent on tarsus III, in larval and postlarval instars.

5. *Setae tc'-tc'' of tarsi I to IV.* The presence of tectal setae *tc'-tc''*, as eupathidia on tarsus I and as simple setae on tarsi II and III, is confirmed in the larva, as it is in postlarval instars, of Tarsocheyloidea. A similar condition is found in general among members of the superfamilies of Tarsonemina, including the larva whenever it is retained as a free-living instar (LINDQUIST, 1986).

On tarsi II and III of the larva, and on tarsus IV of active postlarval instars, tectal seta *tc''* is distinguished from *tc'* by its dorsal position and usually by its greater length and attenuation in the Tarsocheyloidea, Heterocheyloidea, and the superfamilies of Tarsonemina. Among the families of Raphignathoidea a similar asymmetry in position and size of the tectals is found commonly on tarsi II to IV, but in the Cheyletoidea and Tetranychoidea, setae *tc'-tc''* generally appear as a pseudosymmetric pair on each leg.

6. *Denudation of setae on leg IV of the protonymph.* On leg IV of the protonymph in Tarsocheyloidea (Fig. 7), the trochanter, femur, and genu are each devoid of setae, the tibia has usually 4 or

rarely 5, and the tarsus, 5. The result is a basic leg IV setal formula of 0-0-0-4 or 5-5 in the protonymph, in contrast to 1-2-5-5-7 in the adult. The single trochanteral seta, v' , is delayed until adulthood. The two femoral setae, d and ev' , and the complete verticil of five genual setae are delayed until the deutonymph. However, usually only one seta, v'' , of the complete tibial verticil, and only two, tc' and pv'' , of the tarsal complement are delayed until the deutonymph. Not surprisingly then, pv'' is the seta most commonly absent, and tc' the next most commonly absent, among adults of species of Tarsocheylidae with a reduced setation on tarsus IV, or on tarsi II to IV. Perhaps surprisingly in contrast, v'' , which is the only seta of the tibial verticil that is delayed until the deutonymph, is not the seta lost among adults of tarsocheylid species with a reduced setation on tibia IV; rather, it is l'' . Since seta l'' is also lost on tibiae II and III in these species, it appears that a selective pressure effecting the loss of a serially homologous structure of legs II to IV is stronger than the pressure of ontogenetic retardation, due to nymphal denudation, which affects just leg IV. A listing of the setae of tibia IV of adult Tarsocheylidae in order of their prevalence or stability ("priority" or "force" in the sense of GRANDJEAN 1941b, 1942a) would have been anticipated to be (d , v' , l' , l''), v'' based on the ontogenetic sequence of setae evident in several species; however, it is (d , v' , v'' , l'), l'' based on the suppression of a metamerically homologous seta evident in both the deutonymph at hand of a species closely related to *H. arnoldii* and the adult of *H. arnoldii* itself, as figured by LIVSHITZ and MITROFANOV (1973). The relative strength of these two sources of setal suppression may be expressed together in one hypothetical listing of prevalence as (d , v' , l'), v'' , l'' .

The first comprehensive and comparative discussion of protonymphal denudation of legs IV among acariform mites was presented by GRANDJEAN (1946). The extent of leg IV denudation in protonymphs of Tarsocheyloidea most closely approximates the examples given by GRANDJEAN for the Raphignathoidea and Cheyletoidea (e.g., 0-1-0-5-6 for *Stigmaeus* and *Eustigmaeus*, 0-0-1-3-8 for *Raphignathus*, 0-1-1-4-8 for *Caligonella*, and 0-1-0-4-5 for

Cheyletia). A lesser extent of denudation has been noted for the Tetranychidae (e.g., 0-2-2-5-6 for several bryobiine and tetranychine genera studied by GRANDJEAN, 1946 and LINDQUIST, 1985a), but the extent among representatives of other families of Tetranychoidea studied by LINDQUIST (1985a, b) is similar to that in Tarsocheyloidea (e.g., 0-1-0-3-4 in *Linotetranus* and *Tuckerella*, and 0-1-0-3-3 in *Aegyptobia*). The significance of these similarities is problematical from a phylogenetic standpoint because of the difficulty in determining the direction of character state transformations. GRANDJEAN (1946) concluded that these changes in setation are directed toward increased denudation. He termed this phenomenon "progressive denudation", and regarded it as an example of regressive orthogenesis that has evolved within the assemblage Acariformes. However, the greatest extent of denudation, and the most frequent formulas encountered are 0-0-0-0-7 and 0-0-0-1-7, which occur among a great diversity of acariform mites, including some members of such early-derivative groups as Endeostigmata, Bdelloidea, Eupodoidea, and the oribatid groups Palaeosomata and Enarthronota. Trends toward a *lessening* of denudation of protonymphal leg IV, therefore, may possibly be apomorphic; however, they are difficult to assess both because of uncertainties about the homologies of setae added (setal counts are not sufficient), and of evidence of considerable homoplasy. Trends toward lessened, or regressive, denudation are evident among the setal formulas given by GRANDJEAN (1946) for certain genera of such early-derivative groups as Endeostigmata, Bdellidae, Labidostommatidae, and Anystoidea.

In view of the above uncertainties, the following notes on shared character states of protonymphal leg IV are made without assessing them as synapomorphies, symplesiomorphies, or homoplasies. Total denudation of the femur in Tarsocheylidae is shared with Raphignathidae, and contrasts with the basic presence of seta d in Cheyletidae, ev' in Stigmaeidae, Caligonellidae, and Tetranychoidea other than Tetranychidae, and of d and ev' in Tetranychidae. Total denudation of the genu is shared with Stigmaeidae, Cheyletidae, and Tetranychidae, and contrasts with the basic presence of seta

v' in Raphignathidae and Caligonellidae, and of v' and l'' in Tetranychidae. The basic tibial complement of setae $v'-v''$, l'' , d in Tarsocheylidae is shared with Caligonellidae and Cheyletidae, and contrasts with the basic presence of either $v'-v''$ and l'' in Linotetranidae and Tuckerellidae or $v'-v''$ and d in Raphignathidae and Tenuipalpidae, and with the full verticil of $v'-v''$, $l'-l''$, d in Stigmaeidae and

Tetranychidae. The basic tarsal complement of setae p' , $u'-u''$, pv' , tc'' is apparently unique to Tarsocheylidae, and is most similar to the complement of p' , $u'-u''$, $tc'-tc''$ in Cheyletidae; as in adults, the protonymphs of none of the other families considered here retain a proral seta on tarsus IV. These comparisons are summarized in Table I.

TABLE I.

Comparative denudation of segments of protonymphal leg IV among families of subcohorts Heterostigmata (excluding Tarsonemina which lack active nymphs) and Raphignathae (excluding Tetrapodili which lack legs IV). Notation based on that of Grandjean (1940, 1941). Observations supplemented in minor part by Grandjean (1946).

	Troch.	Femur	Genu	Tibia	Tarsus
Tarsocheylidae	—	—	—	$v'-v'' l'' d (l')$	$p' u'-u'' pv' tc''$
Heterocheylidae	—	—	—	—	$u'-u'' pv'-pv'' tc''$
Cheyletidae	—	d	—	$v'-v'' l'' d$	$p' u'-u'' tc'-tc''$
Stigmaeidae	—	$ev' (d)$	—	(φ) $v'-v'' l'-l'' (d)$	(ω) $u'-u'' pv'-pv'' tc'-tc''$
Eupalopsellidae	—	(ev')	—	$\varphi v'-v'' l'' d$	$u'-u'' pv'-pv'' tc'-tc''$
Raphignathidae	—	—	v'	$\varphi v'-v'' d^*$	$u'-u'' pv'-pv'' tc'-tc'' v'' s$
Caligonellidae	—	ev'	v'	$v'-v'' l'' d^{**}$	$u'-u'' pv'-pv'' tc'-tc'' v' s$
Cryptognathidae	—	—	—	v'	$u'-u'' pv'-pv'' rc'-tc'' v'$
Linotetranidae	—	ev'	—	$v'-v'' l''$	$u'-u'' ft'-ft''$
Tuckerellidae	—	ev'	(l')	$v'-v'' d$	$u'-u'' ft'$
Tenuipalpidae	—	$ev' d$	$v' (l')$	$v'-v'' l'-l'' d$	$u'-u'' pv'-pv'' ft'-ft''$
Tetranychidae	—	—	—	—	—

Notes: * d denoted as l'' by Grandjean (1946); ** d denoted as l' by Grandjean (1946). Setae in parentheses suppressed on protonymph in some genera of family. Observations based on material of representative genera of families as follows — Tarsocheylidae : *Hoplocheylus*, *Tarsocheylus*; Heterocheylidae : *Heterocheylus*; Cheyletidae : *Cheyletus*, *Euchyletia*, *Cheletogenes*, *Neoeuchelyla*, *Paracheletia*; Stigmaeidae : *Apostigmaeus*, *Eustigmaeus*, *Stigmaeus*, *Zetzellia*; Eupalopsellidae : *Eupalopsellus*, *Exothoris*; Raphignathidae : *Raphignathus*; Caligonellidae : *Caligonella*, *Molothrognathus*; Cryptognathidae : *Cryptognathus*; Linotetranidae : *Linotetranus*; Tuckerellidae : *Tuckerella*; Tenuipalpidae : *Aegyptobia*, *Brevipalpus*; Tetranychidae : *Bryobia*, *Lindquistiella*, *Petrobia*, *Eurytetranychus*, *Tetranychus*, *Schizotetranychus*.

DIAGNOSES OF FAMILY TARSOCHEYLIDAE AND ITS GENERA, BASED ON LARVAL AND NYMPHAL INSTARS

The larva and nymphal instars of Tarsocheylidae differ from those of families of the subcohort Raphignathae as follows. The bladelike or styletlike movable cheliceral digits are somewhat retractable into a stylophore, but they are not nearly as elongate and deeply retractile as in the Raphignathae. The palpi are 3-segmented, with a short inconspicuous trochanter, a moderately long femorogenu, and a short tibiotarsus which retains the tibial "claw", but lacks the tarsal "thumb" that is generally present in the Raphignathae. The body bears a longitudinal series of 4 or 5 dorsal opistho-

somal plates — C, D, E, F (or EF combined), and H; this configuration of plates is not found in immature Raphignathae. Tarsus I has paired sessile claws and lacks an empodium, and each of tarsi II to IV has an unsclerotized pretarsus bearing paired claws and a smooth, membranous empodium; generally in the Raphignathae, the tarsi of all legs have unsclerotized pretarsi which bear paired claws and a rodlike empodium equipped with tenent hairs. An ontogenetic characteristic of Tarsocheylidae is the suppression of the proral pair of eupathidia on tarsus I until the protonymph; in the

Raphignathae, one or both proral eupathidia are present on tarsus I in the larva.

Within the Heterostigmata, the larva and nymphal instars of Tarsocheylidae differ from those of Heterocheylidae as follows. On the opisthosomal dorsum, central plate C is separate from plate D, plate E is usually separate from F, and plate H is caudal, with the pseudanal structures located posteroventrally; in Heterocheylidae, C is at least partly connected to D, E is fully consolidated with F, H is subterminal, and the pseudanal structures are caudal. On the body venter, each of coxisternal plates I to III has 2 setae in tarsocheylids, but only 1 in heterocheylids. All legs have paired claws, each of genua II and III has 3 or 4 setae, and tarsi II to IV have unmodified, setiform unguinal setae; in Heterocheylidae, all legs lack claws, each of genua II and III lacks setae, and each of tarsi II to IV has one of the unguinal setae (apparently *u'*, which was mistakenly denoted as subunguinal *s* by LINDQUIST and KETHLEY 1975) greatly enlarged as a spinelike or clawlike structure.

The larva of Tarsocheylidae differs from the larva, when present as an active instar, of families of the Tarsonemina as follows. The palpi are clearly segmented and strongly developed, extending well beyond the apex of the gnathosoma, and the palptibial "claw" is prominent; in Tarsonemina, the palpi are indistinctly segmented and reduced in size, extending little if any beyond the apex of the gnathosoma, and the palptibial "claw" is small or rudimentary. On the opisthosoma, plates E and F are usually separate, and the pseudanal valves are well developed; in Tarsonemina, plates E and F are fully consolidated, and the pseudanal valves are rudimentary.

Within the family Tarsocheylidae, the two currently recognized genera can be diagnosed on the basis of the same characteristics in immature instars as in adults. In *Tarsocheylus*, one seta of the palpal tibiotarsus is stout and abruptly angled or bent, such that its shape resembles the Greek letter *gamma*; the two subterminal spinelike setae beside the "claw" on the palpal tibiotarsus are dissimilar, with the more distal one retaining a spinelike form but the more proximal one modified to a flattened, disc- or flange-like structure (see fig. 4 in LIND-

QUIST 1976); on leg I, tibial seta *v'* is conspicuously thick and pilose (Fig. 3). In *Hoplocheylus*, none of the setiform setae of the palpal tibiotarsus is modified in shape; the two subterminal spinelike setae of the palpal tibiotarsus are similarly spinelike and sometimes partly united so as to appear like a single bifid structure (see figs. 4, 6 in LINDQUIST 1976); on leg I, tibial seta *v'* may be slightly thickened or not, and slightly pilose or smooth.

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