A NEW ARBOREAL SCHELORIBATIDAE, WITH ECOLOGICAL NOTES ON EPIPHYTIC ORIBATID MITES OF POPOCATÉPETL, MEXICO

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CRYPTOZETES
ORIBATIDA
EPIPHYTIC
MITES

ABSTRACT : This paper describes a new species of the resurrected genus *Cryptozetes* based on all instars, and discusses its systematic relationships. Ecological notes are given for this species, as well as *Belba clavasensilla, Camasia* cf. *horrida, Mycobates* sp., *Scapheremaeus* sp., and *Trichoribates ocotlicus*, all associated with epiphytic mosses and lichens of Popocatépetl, Mexico.

CRYPTOZETES
ORIBATIDA
ACARIENS
EPIPHYTES

RÉSUMÉ : Dans ce travail on décrit une nouvelle espèce de *Cryptozetes* ainsi que son développement ontogénétique. On présente également des données écologiques de cette nouvelle espèce ainsi que celles de *Belba clavasensilla, Camisia* cf. *horrida, Mycobates* sp., *Scapheremaeus* sp., et *Trichoribates ocotlicus*, tous associés aux mousses et lichens épiphytes du Popocatépetl, Mexique.

Since the early 1950's, faunistic studies of epiphytic lichens and mosses have increased in number substantially. Species in these habitats are interesting, not only from systematic, morphological and ethological points of view (AOKI, 1973 ; TRAVÉ, 1969), but also because of their possible use as bioindicators of pollution (ANDRÉ, 1976 a, 1976 b ; AOKI, 1976 ; LEBRUN, 1976). Based on studies of their ethology and feeding habits, principally by GRANDJEAN (1951, 1956) and TRAVÉ (1958, 1961, 1963, 1969), the association of mites with lichens appears to vary from obligatory to accidental. Eighteen species or subspecies are known to be mostly restricted to lichens (SEYD & SEAWARD, 1984) ; nine have been consi-dered to be exclusive lichen inhabitants (group A of SEYD & SEAWARD, *op. cit.*) and belong to the genera *Scapheremaeus* (Cymbaeremaeidae), *Phauloppia* (Oribatulidae), *Pirnodus* (Oripodidae), and *Dometorina* (Scheloribatidae). The latter two families include species known to be among the most highly specialized for dwelling in lichens. Those oribatid mite species represented in mosses generally appear not to be so specialized.

In Mexico, general research on the microarthropods of epiphytic environments (PALACIOS-VARGAS, 1981, 1982 a) has been followed by descriptions of new springtails (PALACIOS-VARGAS, 1982 b) and oribatid mites (NORTON & PALACIOS-VARGAS, 1982 ; PALACIOS-VARGAS & NORTON,

1985), but very little has been said about their ecology ·or habitat specificity. In this paper, we describe a new species of Scheloribatidae from these microhabitats and present ecological notes on this and other oribatid mite species. This is part of a continuing study of the epiphytic microarthropods of the Mexican volcano, Popocatépetl.

Popocatépetl is a Pleistocene volcano in south-central Mexico (19°01′ N, 98°38′ W) which represents the southern extent of the Neovolcanic Axis ; it is vegetated to an elevation of 3,900 m by a succession of natural forest types, each with a rich, but different epiphytic flora. Among all microarthropods inhabiting the epiphytic microhabitats of Popocatépetl, the oribatid mites exhibit the greatest abundance and regularity of occurrence, both spatial and temporal. Sometimes as many as several thousand individuals occur in a small sample of lichens, although their total diversity can be very low.

Specimens for this research were obtained from samples (about 5 × 5 × 5 cm) of epiphytic mosses and/or lichens collected in triplicate, monthly, from February of 1982 to March of 1983 (except for September). They were taken (along with similar samples from soil and litter) at the following altitudes : 3,000, 3,600 and 3,900 m, designated station I, II, and III, respectively. The climate at station I — C (w2) big, after GARCÍA (1973) — exhibits maximum precipitation in June and minimum in February ; minimum temperature (11°C) occurs in December and maximum (close to 15°C) in May. At stations II and III — E(T) HC (w″2) (w) g — the maximum precipitation occurs in July and the minimum in January ; the coldest month is January, when the mean temperature is close to 0°C, and the warmest is March. The year 1982 was unusually dry, with total precipitation being two standard deviations lower than the 22-year mean.

At station I, where epiphytic lichens were not abundant, the substrate was composed entirely of mosses, mainly *Leucodon cryptotheca* collected from branches of *Cupressus benthami* var. *lindleyi*, about 2 m above the ground. At stations II and III the substrate sampled was mainly pendu-lous fruiticose lichens of the species *Pseudovernia intensa* and *Usnea subfloridana*, which were taken from the branches of *Pinus hartwegii*, 2 to 4 m above the ground. All samples were processed in Berlese funnels without heat ; this procedure may not be highly efficient, especially for species which burrow in lichens, for mites but it does provide comparative data.

Cryptozetes usnea n. sp.

ADULT.

Dimensions. The mean total length of ten specimens was 488 μm (range 457-502) ; the mean maximum nostogastral width was 273 μm (range 237-295). Means for females (n = 6) were 490 × 285 μm ; means for males (n = 4) were 485 × 255 μm.

Integument. The cuticle is faintly micropunctate in transmitted light and much of the surface also has minute, irregular, vermiform rugosity, which is best developed ventrally and most easily seen with scanning electron microscopy (SEM) (Fig. 3 D). Large rugae are conspicuous on the adaxial surface of femora III and IV. The integument is clearly microtuberculate in the lateral regions of the podosoma ; the microtubercules are mostly granular in the depressions which accommodate the legs, when the latter are retracted and appressed to the body during disturbance, but they become vermiform or truly striate on pedotecta I and II. Cerotegument is restricted to the lateral podosoma ; it sharply ends at carina *kf* anteriorly, and the sublamella dorsally (Fig. 3 F). It is composed of two sizes of granules, in a rather uniform arrangement.

Prodorsum and lateral podosoma. In both sexes, the rostrum is deeply and roundly emarginate on each side, producing a broad, triangular medial lobe, best seen in frontal aspect (Fig. 3 A). In dorsal aspect, the prodorsum appears somewhat truncated laterally, anteriad of the rostral setae (Figs. 1 A, 3 B). The rostrum is thus quite different from that of *Siculobata sicula* (Berl.), where a relatively small, projecting medial
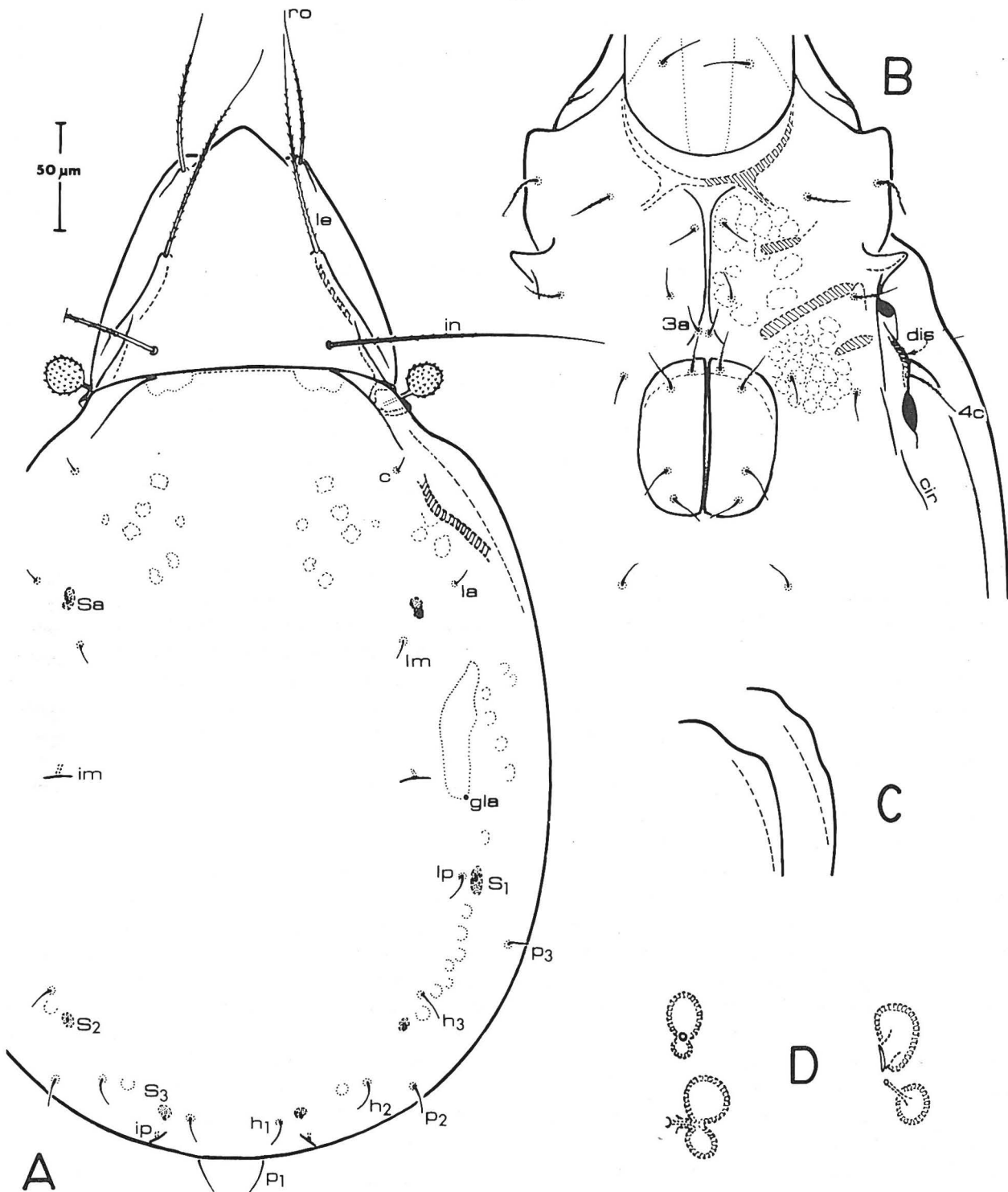
FIG. 1 : *Cryptozetes usnea* n. sp. (adult).

A. — Dorsal aspect. B. — Partial ventral aspect. C. — Variations of humeral tectum. D. — Variations of notogastral saccule Sa ; on the left are a dorsal (top) and lateral (bottom) aspect of a bilobed saccule, and on the right is an oblique aspect of a completely subdivided saccule. A & B to same scale.

tooth exists without distinct, paired emarginations (GRANDJEAN, 1953 : Fig. 5 B). The lamella (Fig. 3 F, *LAM*) is relatively narrow, the sublamella (*SBL*) is well developed, and the prolamella (*PRL*) reaches anteroventrad to the insertion of seta *ro*. In lateral aspect the rostral emargination may result in the illusion of the prolamella continuing beyond *ro* (cf. Figs. 3 A, 3 F).

The sensillus (Fig. 3 C, *ss*) is capitate, with a denticulate head (35-38 μm long) and a smooth, narrow stalk. The bothridium is hidded by the notogaster in dorsal aspect (as is the sensillar stalk), except sometimes for the posterolateral margin (depending on angle of view and perhaps the degree of body distension). The bothridium (*bo*) is surrounded anteriorly and ventrally by distinct rugae, and on its posterior wall is a sharp carina (Fig. 3 C). Setae *in*, *le* and *ro* are finely attenuate and about 140, 105, and 70 μm respectively, in a typical adult (Fig. 1 A) ; the latter two are more strongly barbed than *in*. Setae *in* and *le* are erect, relative to the prodorsal surface, with *ro* being proclinate (Fig. 3 F). Setae *ex* is thin (*ca.* 20 μm) and finely attenuate, with one or two minute barbs.

Porose area *Al* is small and poorly developed, with sparse pores, and is easily mistaken for one of the lateral muscle sigillae. Areas *Ah* and *Aj* are large, well developed (although with imprecise borders), and conspicuous in transmitted light, even in dorsal aspect. Carina *kf* (Fig. 3 F) is well developed ; it delimits a rounded plateau, posteriad and dorsad of which is the depressed region for accommodation of retracted legs I and II. Similar depressions for legs III and IV are separated by conspicuous carinae dorsad of the respective acetabula. Pedotecta I and II are developed, as is typical for the family.

Notogaster (Fig. 1 A). The notogaster is truncate anteriorly, with an almost straight border, capable of little, if any, movement with respect to the prodorsum. The true border is inconspicuous and easily confused with the thicker underlying posterior border of the prodorsum. There is no noticeable pteromorph ; instead, a narrow humeral tectum projects only slightly beyond the general curvature of the notogaster in dorsal aspect, effacing posteriorly at a variable level, somewhat posteriad of seta *lm*. The shape of this humeral tectum is also somewhat variable (Fig. 1 C). Posteriad of the bothridial level, the notogastral border is thickened and reflexed (rebordered) (Fig. 3 C), similar to that described by GRANDJEAN (1953) for *Hemileius initialis* (Berl.). Just behind the anterior notogastral border there is a pair of surface undulations (often marked by contours in dorsal aspect) directed toward setae *c*. The octotaxic series comprises four pairs of saccules, which are clearly porose and have short canals. Saccules *Sa* and *S1* are usually somewhat laterally compressed, sometimes centrally constricted, and often rather bilobed when viewed from the side, with the lobes of *S1* well separated and of different sizes (Fig. 1 D). Saccules *S2* and *S3* are usually simple sacs. The five pairs of lyrifissures are normal, with *ia* located beneath the humeral tectum, *ih* and *ips* near the lateral margin of the notogaster and parallel to it ; *im* and *ip* are larger than the others. The opisthosomal gland is rather small, with an inconspicuous opening (*gla*) ; pigment was never observed, either in its walls or its contents. The ten pairs of notogastral setae are all short (15-20 μm), finely attenuate, and without discernible barbs. They are easily homologized with those of related species, as indicated in Fig. 1 A ; seta *lm* is closer to saccule *Sa* than to lyrifissure *im*.

Ventral region (Figs. 1 B, 3 D). The ventral region is mostly normal for the family. There are four pairs of genital, one pair of aggenital, two pairs of anal, and three pairs of adanal setae in all specimens examined ; seta *ad3* is inserted slightly more mediad than lyrifissure *iad*. The coxisternal setation is 3-1-2-3 ; seta *3c* was never observed. The coxisternal setae (especially *1b*, *1c*, *3b*,) and anterior genital setae are generally larger and more conspicuously barbed than other ventral setae, which are finely attenuate and have at most several minute barbs. Seta *4c* inserts at the edge of the dorsal surface of the discidial carina (*dis*). The latter originates at, and is a continuation of, the ventral wall of acetabulum IV ; it then runs anteriad a short distance, effacing

ventrad of pedotectum II [1]. The circumpedal carina (*cir*) is poorly developed, as in most Scheloribatidae ; it begins at the base of pedotectum II, extends posteriad a short distance beyond acetabulum IV (although often discontinuously), and does not clearly merge with the discidial carina. There is no custodium. A shallow sternal groove is present, best seen with reflected light or SEM (Fig. 3 D *SG*), and setal pair *3a* is inserted in it, separated only by one or two alveolar diameters, where the groove widens just anteriad of the genital aperture.

Gnathosoma. The subcapitulum, chelicerae and palps are normal for the family. The palpal setation (0-2-1-3-9) includes both ventral setae of the tarsus. Tarsal solenidion ω (not included in the above formula), is coupled and fused with eupathidium *acm*, and along with the three other eupathidia (*ul'*, *ul"*, *su*) is positioned distally, near the plane of symmetry. The general setal arrangement is similar to that of *Siculobata sicula* (GRANDJEAN, 1953 : Fig. 5 C), but the tarsus is distally more elongated, and *su* inserts on a terminal 'nipple'. Solenidion ω is also slightly expanded distally, unlike that of *S. sicula*. The palp femur is almost completely encircled by low parallel rugae.

Legs (Fig. 2 A-C). All tarsi are heterotridactyl, with the lateral claws much thinner than the empodial claw. The latter is inconspicuously denticulate along its outside curvature ; the former are smooth, except for a subterminal tooth, formed by a small distal notch in the inner curvature of each claw. Femora I and II lack any trace of proximal retrotecta ('crispins'), but trochanters III, and especially IV, have well developed, ventrodistal protecta, covering the articulation with the respective femora. Femora II-IV have distinct, complete, ventral keels, or blades, which are distally rounded ; femur I has a short, narrow keel in its distal quarter. Each tibia has in its proximoventral midline a small, broad, scale-like spur (Fig. 3 E, *SP*), usually largest on tibia II. The porose areas of trochanter I, II, and all

femora, are similar to those of *Hemileius initialis* (GRANDJEAN, 1953 : Figs. 2, 3), except that those of the femora usually do not reach the dorsal midline. The tibiae do not have porose areas. The tarsal porose areas are restricted to a small proximoventral region which does not extend distad of the level of the guide for the inferior claw tendon ; they are transversely elliptical and reach the abaxial surface only on tarsi I and II. In optical section, the porosity clearly penetrates the ventral cuticle to the tendon canal, but not beyond it to the interior of the segment. The dorsoproximal lyrifissure of tarsi I-IV is totally on the abaxial surface and easily overlooked because of interference from the articulating membrane of the tibia (in transmitted light) ; none is illustrated in Fig. 2.

Setal formulas for the legs are as follows (I-IV, famulus included) : trochanters (1-1-2-1) ; femora (5-5-3-2) ; genua (3-2-1-2) ; tibiae (4-4-3-3) ; tarsi (19-15-12-12). All tarsi have both primiventral setae. Only the proral setae (*p*) of tarsus I are eupathidial. As seta *s* is not eupathidial, it has not moved anteriad of the antelateral (*a*) setae. The famulus is small and rounded or very slightly expanded distally. The solenidial formulas are : genua (1-1-1-0) ; tibiae (2-1-1-1) ; tarsi (2-2-0-0). Solenidion σI is very long, flagellate, more than three times the length of the genu ; φ2 of tibia I is positioned anteriad of φ1, on a distinct dorsodistal projection (Fig. 2 A). Leg setation is discussed further in the next section.

IMMATURES (Fig. 4 A-C).

The total length of the single larva studied was 260 μm. Total lengths (mean and range) of nymphs were as follows : protonymph (n = 3) 297 μm (282-305) ; deutonymph (n = 5) 360 μm (336-400) ; tritonymph (n = 7) 452 μm (424-480).

The aspis is well developed in all instars, forming a complete rostral tectum anteriorly ; it is finely porose throughout. The sensillus is capitate, denticulate, similar to that of adult in all ins-

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1. GRANDJEAN (1953) considered this carina to be part of the circumpedal (= peripodal) carina in the Scheloribatidae, but later considered a clearly homologous structure in the Mochlozetidae to be a discidial carina (GRANDJEAN, 1959 : Fig. 1 B, C ; see also NORTON, 1983 : Fig. 5 B). We feel the latter interpretation is accurate.
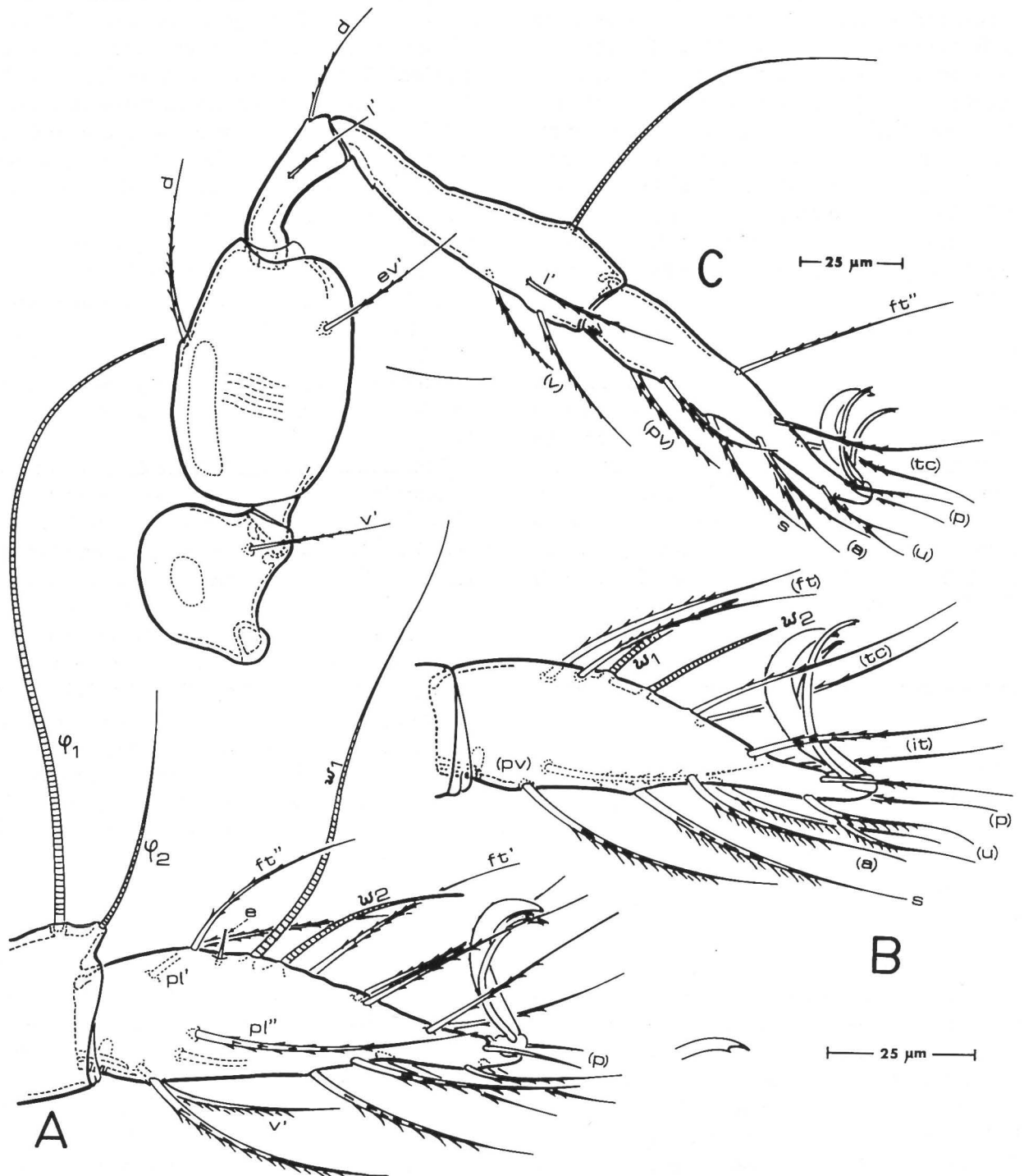
Fig. 2 : *Cryptozetes usnea* n. sp. (adult).

A. — Tarsus I (with part of tibia) and enlarged tip of lateral claw. B. — Tarsus II. C. — Leg IV. All abaxial aspect ; A & B to same scale.
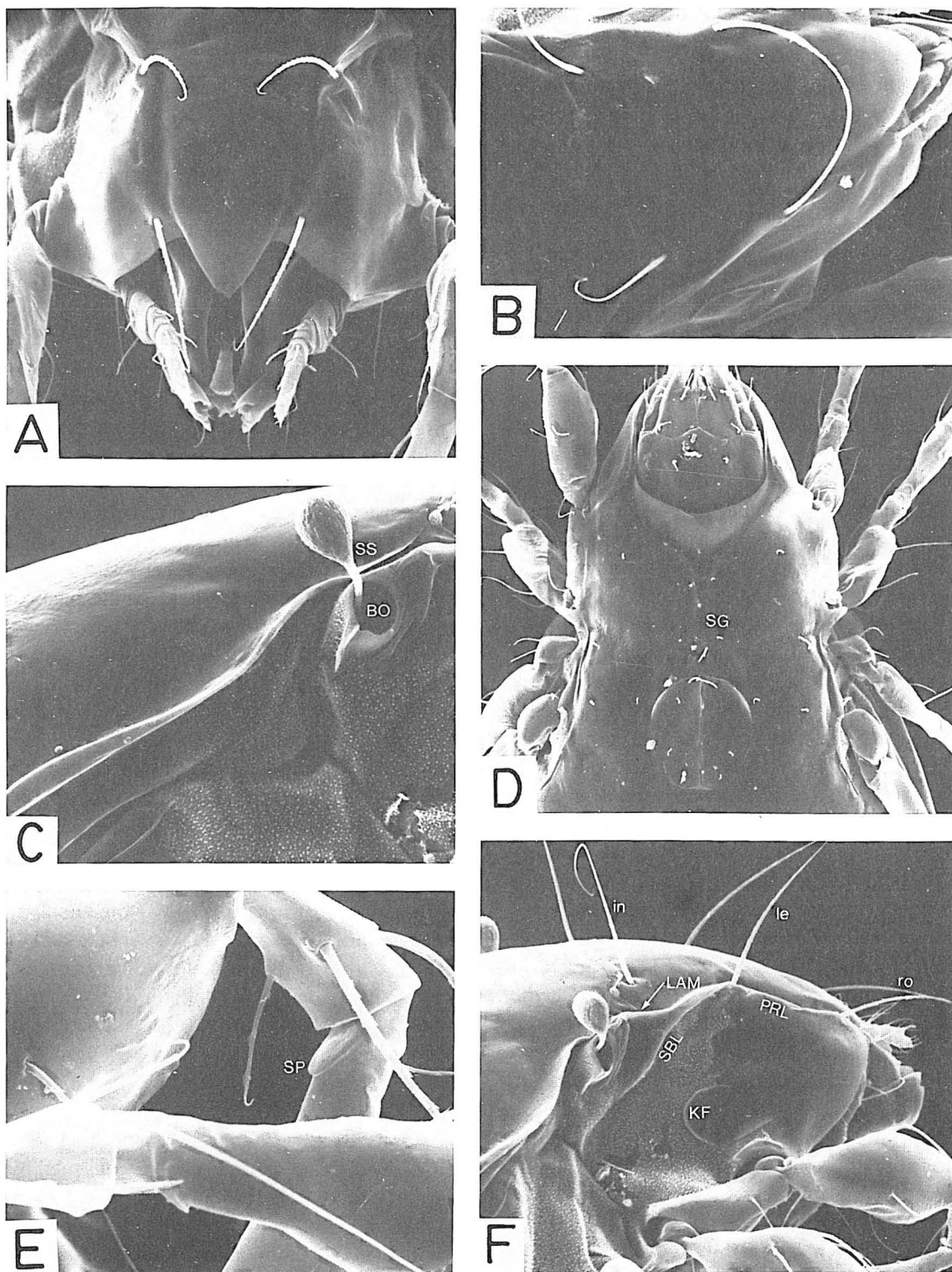
FIG. 3 : *Cryptozetes usnea* n. sp. (adult).

A. — Frontal aspect. B. — Dorsal aspect of prodorsum. C. — Bothridial region and humeral tectum, lateral aspect. D. — Partial ventral aspect. E. — Tibiae III and IV, abaxial view. F. — Lateral view of prodorsum and podosomal region. All scanning electron micrographs.

tars. Setae *in, le,* and *ro* are respectively erect, proclinate, and in same plane as the aspis. They are all attenuate, with small barbs. Their respective lengths in tritonymphs are *ca.* 100, 70 and 45 μm ; *ro* is slightly longer than *le* in the larva, and subequal the to it in the proto- and deutonymph, about half the length of *in*. Seta *ex* is short (*ca.* 10 μm in tritonymph), smooth, acicular in all immatures.

The opisthosoma is rather cylindrical, with irregular, fine, generally transversely directed cuticular striations in all immature instars. The wall of the opisthosomal gland is not sclerotized or pigmented, although its contents are brown or yellow in some specimens. No integumental sclerite is present in the region of the gland opening (gla). Immatures have the normal complement and ontogeny of cupules. The ontogenetic setal formula for the gastronotic region (larva, nymphs, adult) is 11-15-10, normal for the Scheloribatidae ; seta *h3* is absent from the larva, without vestige (Fig. 4 B). Gastronotic setae of the larva are mostly rather stiff, erect, straight or slightly curved, with small barbs ; seta *c3* is the largest, directed straight laterad, *c2* is short, curved laterad ; both are more distinctly barbed than other setae. In nymphs, *c2* and *c3* are similar to those of the larva (*ca.* 25, 80 μm, respectively, in tritonymph), but other gastronotic setae are thinner, more finely attenuate, flexible, and smooth, or have several minute, very inconspicuous barbs (not illustrated). Porose eccentric microsclerites are present at the bases of setae *c2, la,* and *lp* in all immature instars ; the larva also has one at the base of *h1*, but this microsclerite is lost in the protonymph. Setae *h2*, and *h3* have microsclerites in the nymphs, but not the larva ; seta *p1* has a distinct microsclerite in the tritonymph, a very small, inconspicuous one in the deutonymph, but none in protonymph. Microsclerites were never observed at the base of setae *c1, c3, da, dm, dp, lm, p2,* or *p3.*

Setae of the ventral region (*ca.* 20 μm in tritonymph) are similar to most gastronotic setae. The genital setal formula (larva to adult) is 0-1-2-3-4 ; aggenital formula 0-0-1-1-1. The coxisternal setation is : larva 2-1-2 (Claparèdes

organ " scale " not included) ; protonymph 3-1-2-1 ; deutonymph 3-1-2-2 (*4b* present) ; tritonymph 3-1-2-2 ; adult 3-1-2-3. Paraproctal atrichosy affects the larva, protonymph and deutonymph.

The setation of the palp is 0-2-1-3-9 (solenidion not included) in all instars ; both ventral setae are present on the tarsus. Setae *acm, ul'* and *ul"* are always eupathidial ; *su*, which always has a distal position, is setiform in the larva but eupathidial in later instars. Solenidion ω is fully coupled and fused to *acm* in all instars.

Legs have porose areas only on trochanters III and IV and femora I-IV. In all instars, the ventral midline of the tarsal cuticle has a conspicuous guide for the inferior tendon (*ti*) of the claw (Fig. 4 C) ; the tendon is completely enclosed distally for most of its length (in contrast to adult), becoming free proximally in the region of the primiventral setae (therefore gradually further from the tibia in later instars, as the proximal region of the tarsus elongates). In the larva, the guide projects internally as a short tube (Fig. 4 C). Setal ontogeny of the legs is expressed in Table 1. Seta *d* is absent from all genua and tibiae in all instars (except from genu IV, which has no solenidion). Setae *v'* of genu I and *l'* of femur and tibia III are delayed until the adult ; they are absent from all tritonymphs examined. Seta *v'* never develops on genu II. The famulus decreases in relative size during ontogeny (cf. Figs. 2 A, 4 C). The proral setae (*p*) are eupathidial on tarsus I in all instars, but *s* does not become eupathidial. Solenidial ontogeny is normal ; $\omega2$ is protonymphal on tarsus I, deutonymphal on II ; $\varphi2$ of tibia I and φ of tibia IV are deutonymphal ; all other solenidia are larval.

DIAGNOSIS.

Adults of *Cryptozetes usnea* n. sp. can be distinguished from its only known congener by : the large head of the sensillus, not partially covered by the humeral tectum of the notogaster ; the rostrum with a pair of deep, rounded emarginations, forming a triangular medial projection ; the position of seta *lm* closer to saccule *Sa* than to lyrifissure *im* ; seta *ad3* not positioned more laterad than lyrifissure *iad* ; its smaller size (457-502 μm).
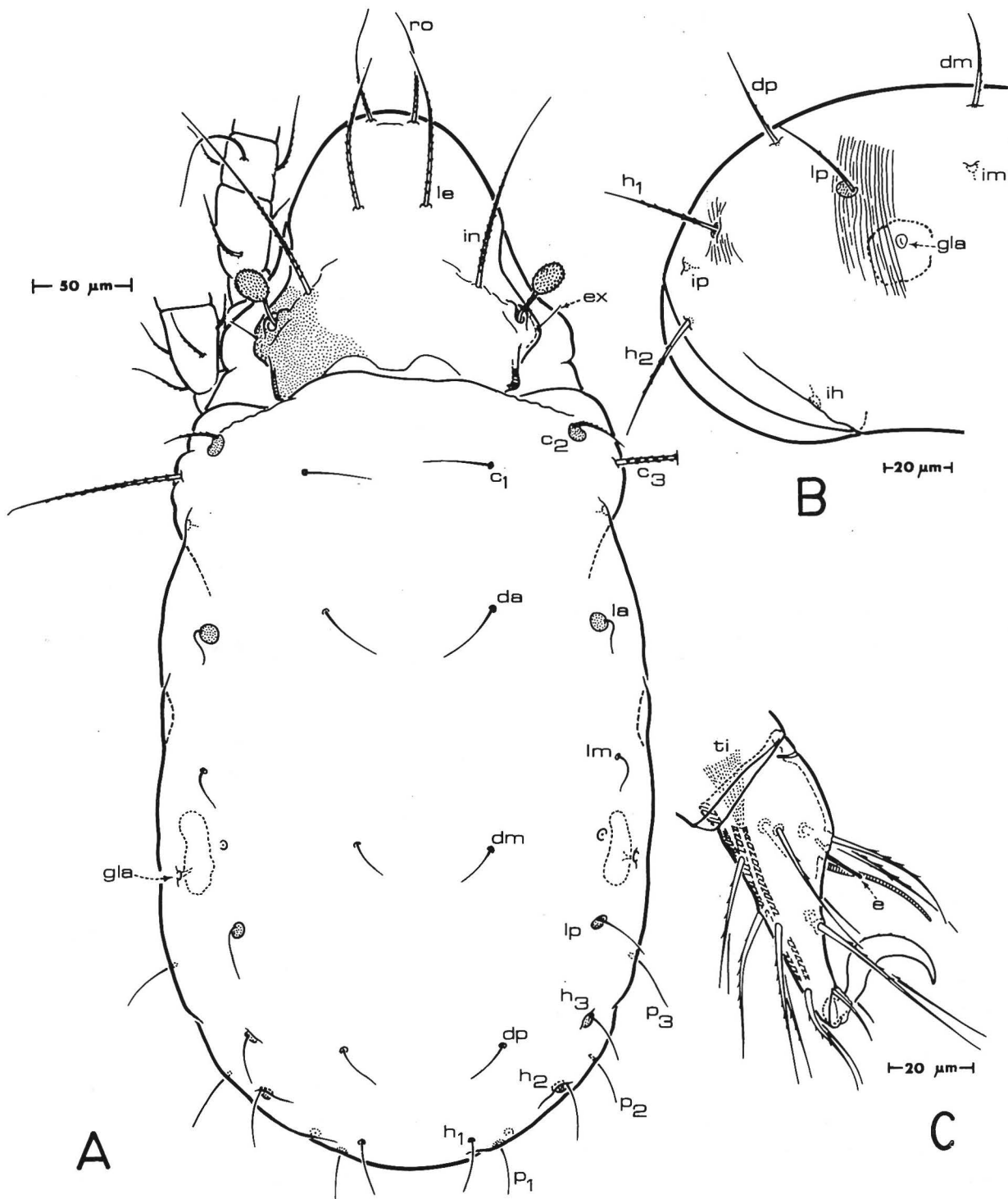
FIG. 4 : *Cryptozetes usnea* n. sp.

A. — Tritonymph, dorsal aspect. B. — Larva, posterior opisthosoma, lateral aspect. C. — Larva, tarsus I, abaxial aspect.

TABLE 1

Ontogenetic appearance of leg setae in *Cryptozetes usnea*, n. sp.

		Troch.	Femur	Genu	Tibia	Tarsus
LEG I	LA	-	d, bv''	l', l''	l', l'', v'	(p)(u)(pv)(pl)(a)(tc)(ft) s, e
	PN	-	-	-	-	-
	DN	-	l'	-	-	-
	TN	v'	l''	-	v''	(it)
	AD	-	v'	v'	-	v'
LEG II	LA	-	d, bv''	l', l''	l', v'	(p)(u)(pv)(a)(tc)(ft) s
	PN	-	-	-	-	-
	DN	-	l'	-	-	-
	TN	v'	l''	-	l''	(it)
	AD	-	v''	-	v''	-
LEG III	LA	-	d, ev'	l'	v'	(p)(u)(pv)(a)(tc)(ft) s
	PN	-	-	-	-	-
	DN	v'	-	-	-	-
	TN	-	-	-	v''	(it)
	AD	l'	l'	-	l'	-
LEG IV	PN	-	-	-	-	(p)(u)(pv) ft''
	DN	-	d, ev'	d	v'	(tc)(a) s
	TN	-	-	l'	v''	-
	AD	v'	-	-	l'	-

MATERIAL.

The holotype and about 125 paratypes are preserved in alcohol, and 18 paratypes are slide-mounted. The holotype and two paratypes will be kept in the Museo de Historia Natural de la Ciudad de México, México ; two adult paratypes in alcohol and two on slides will be sent to the following collections : Canadian National Collection, Ottawa, Canada ; Field Museum of Natural History, Chicago, Illinois, USA. Ten paratypes on slides and about 100 in alcohol will be kept by the second author, four paratypes on slides and 25 in alcohol will be kept by the first author. All are from the following locality : México, Estado de México, Volcán Popocatépetl. All were collected from the lichens *Usnea subfloridana* and *Pseudovernia intensa*, mainly from 3,600 to 3,900 m elevation, J. G. PALACIOS-VARGAS col. This species was previously cited by PALACIOS-VARGAS (1985) as *Dometorina* sp. from this locality.

ETYMOLOGY. The name of this species reflects the lichen in which it is very frequently found, *Usnea subfloridana*.

SYSTEMATIC RELATIONSHIPS.

Both our familial and generic placement of this species can be questioned, considering past and present classification schemes in the taxonomically very difficult Oripodoidea [2]. It is clearly a mem-

2. We use this name in the sense of GRANDJEAN's (1959) 'Excentrosclerosae' to include Oribatuloidea Thor, 1929, *sensu* BALOGH (1972) and BALOGH & BALOGH (1984), over which Oripodòidea Jacot, 1925 has priority, plus other poronotic Brachypylina whose nymphs have microsclerites at the base of notogastral setae, such as Mochlozetidae and Parakalummidae.

ber of the Scheloribatidae in the sense of GRAND-
JEAN (1933, 1953, 1958), who distinguished the
family from the Oribatulidae using both adult and
ontogenetic characters. All the important defi-
ning character-states of Scheloribatidae are shared
by *C. usnea*, including : *a*) paraproctal atrichosy
in the larva, as well as the protonymph and deu-
tonymph ; *b*) coupling and fusing of the palpal
solenidion with eupathidium *acm* to form the
'double horn' in the larva, as well as later ins-
tars ; *c*) a distal, almost comb-like arrangement of
other palpal eupathidia ; *d*) the terminal position
of palpal seta *su* in the larva ; *e*) the presence of
a sternal groove in the adult ; *f*) a short prodor-
sum, relative to the notogaster. Arguments can
be developed for considering all of these to be
apomorphic, relative to states in the Oribatulidae,
although it is not our intent to do so here.

Recently, BALOGH & BALOGH (1984) have split
the Scheloribatidae, removing those taxa which,
for example, have no recognizable pteromorph
(e.g. *Hemileius*) or which have the octotaxic
system of the notogaster represented by porose
areas (e.g. *Liebstadia*), and proposing new
family-group taxa for them. The pteromorph
character in particular is often difficult to inter-
pret, since the antero-lateral ('scapular', or
'humeral') border of the notogaster may exhibit a
relatively large tectum, that is, a pteromorph
capable of protecting retracted legs (e.g. *Grand-
jeanobates*), or an almost non-existent tectum
which does not deviate from the general notogas-
tral curvature when viewed dorsally (e.g. *Dometo-
rina*), or virtually any condition in between. The
humeral tectum of *C. usnea*, for example, pro-
jects slightly beyond the notogastral curvature,
but can hardly be called a 'pteromorph'. GRAND-
JEAN (1953) has also mentioned this problem in
terminology. The distinction between BALOGH &
BALOGH's (1984) concepts of Scheloribatidae and
Hemileiidae rests only on the often subjective cha-
racter of the presence or absence of pteromorphs,
and until further characters are assessed, we treat
C. usnea as a member of the better-defined Sche-
loribatidae (*sensu lato*).

When first trying to determine the generic pla-
cement of this species, we were drawn immediately
to comparaisons with *Dometorina* and *Siculo-
bata*, based on similarities of adult facies. The
absence of noticeable pteromorphs, the short,
straight capitate sensillus, and the straight anterior
border of the notogaster all contribute to this
appearance. Also, none of these taxa contain
soil-dwellers ; they are principally arboreal or
saxicolous mites. Additional similarities with
known species of *Dometorina* include three
character-states which may represent regressive
synapomorphies (i.e., losses), since the missing
structures are widespread in the Scheloribatidae
(*sensu lato*) and oripodoid out-groups, such as
Mochlozetidae and some Oribatulidae, among
others. One is the absence of retrotecta on
femora I and II, another is the absence of ventro-
distal porose areas on the leg tibiae, and the third
is the loss of coxisternal seta *3c*. Both *C. usnea*
and *Siculobata* have a rostrum which is pointed, a
potential progressive synapomorphy, but they dif-
fer in structure and may be independently derived.

Despite these similarities, a number of the spe-
cialized, presumably derived character-states which
define *Dometorina* and *Siculobata* are not found
in *C. usnea*. These include the following : *C.
usnea* develops seta *ft'* on tarsus III in the larva
(as usual in the Oripodoidea), whereas *Dometo-
rina* species have lost it ; *C. usnea* develops seta *l'*
on genua III and IV in the larva and tritonymph,
respectively (as usual), whereas in *Dometorina*
they are both delayed until the adult ; *C. usnea*
has tarsi of normal length, all with the primiven-
tral pair of setae, whereas *Dometorina* species
have short tarsi and have lost one or both of
these setae on legs I-III ; *C. usnea* develops seta
v' on tarsus I in the adult (as usual), whereas it is
lost in *Dometorina* ; *C. usnea* retains both ventral
setae on the palp tarsus, whereas in *Dometorina*
one is lost ; *C. usnea* retains carina *kf*, whereas
Dometorina spp. do not have it (a probable loss).
Nor does *C. usnea* exhibit some specializations
which are characteristic of *Siculobata*, such as the
regular duplication of notogastral saccules (but
see Remarks) or the modified globular tip of the
tibial solenidion of legs III and IV. In both
Dometorina and *Siculobata* the bothridium has
secondarily moved to a position well below the

level of the lamella ; in *C. usnea* the ancestral position is retained, in which the dorsal wall of the bothridium is virtually confluent with the base of the lamella. It therefore would require the modification of existing concepts to include *C. usnea* in either genus.

An alternative possibility which we followed, involved recognizing a genus proposed by HAMMER (1962) but very quickly synonymized with *Dometorina*. In a revision of the Oribatulidae (*sensu lato*), COETZER (1968) proposed several new combinations under *Dometorina*, most if not all of which were unfortunately based on incomplete literature descriptions. The characters relied upon were apparently restricted to the presence of a straight anterior notogastral border ('dorsosejugal suture'), notogastral saccules, the ten pairs of notogastral setae, small humeral tecta ('scapular pteromorphae'), and a rounded rostrum. One of these species was *Cryptozetes chilensis* Hammer, 1962, the type of a monotypic genus, and *Cryptozetes* was therefore considered a junior synonym of *Dometorina*. This synonymy was followed by BALOGH (1972). Both *Dometorina* and *Siculobata* were omitted from BALOGH & BALOGH's (1984) recent revision (presumably they should have been included under Hemileiidae), and no opinion on *Cryptozetes* was expressed. Although HAMMER's (1962) description of *Cryptozetes chilensis* is incomplete, it is clear from her illustrations that no regression has affected the primiventral setae of the leg tarsi, as it has in *Dometorina*, nor are the tarsi very short. Without a careful redescription, we do not know if other characters, such as the position of the bothridium or the presence of femoral retrotecta, are also different. It therefore seems unwise at present to recognize COETZER's synonymy, and we consider *Cryptozetes* to be a valid nominal genus in the Scheloribatidae (*sensu lato*).

Cryptozetes was not separately defined by HAMMER (1962), but it appears that the first paragraph of the description had this purpose. Thus, the absence of a well-defined pteromorph, the ten pairs of notogastral setae, and the hidden bothridium (covered by the humeral tectum of the notogaster) can be considered to constitute her generic diagnosis. As COETZER (1968) implied, these characters are shared with *Dometorina*, so HAMMER's diagnosis is not effective if they are not considered synonyms. We will not propose a new diagnosis here, without having studied representatives of the type-species, but clearly the presence of primiventral setae on all leg tarsi should be added. The presence of cuticular spurs or angular projections in the proximoventral region of the tibiae can also be noted from HAMMER's illustrations ; these are also known in a few *Scheloribates* species, and the apparently related genus *Nannerlia* (COETZER, 1968), but are absent from *Dometorina, Siculobata* and *Hemileius*. The distribution and polarity of this character is as yet uncertain. Our inclusion of *C. usnea* as the second known species of *Cryptozetes* is thus based on HAMMER's 'diagnosis' plus the presence of all primiventral setae, the normal tarsal length, and the presence of proximoventral cuticular spurs on the leg tibiae.

It is possible that *C. usnea* represents an earlier derivative of the scheloribatid lineage which gave rise to *Dometorina*. The latter genus exhibits a long list of regressive character-states, part of which is shared by *C. usnea*, as discussed above. Other species, apparently related to this group and also epiphytic, are known only from our collections, and a careful reevaluation of generic concepts awaits their description, along with redescriptions (including ontogenetic data) of other pertinent scheloribatid genera.

MISCELLANEOUS REMARKS.

1. Study of HAMMER's illustration (1962 : Fig. 5 C) might lead to the suggestion that another character, the presence of a pair of anteriorly directed spines (like the spinae adnatae of the Damaeidae) on the anterolateral margin of the notogaster, near the bothridia, might be useful in the generic diagnosis of *Cryptozetes*. However, these are almost certainly illusory. The spine-like structure is simply the base of the lamella (Fig. 3 F, *LAM*), between the bothridial wall and its junction with the sublamella, where it presents a separate contour when projected against the back-

ground of the sublamella in dorsal aspect. The notogastral margin, while complete, is very inconspicuous in many scheloribatids, and was apparently omitted from the illustration.

2. The frequently bilobed structure of the anterior notogastral saccules in *C. usnea* suggests a mechanism for the evolution of augmented numbers of saccules in *Siculobata* (GRANDJEAN, 1953) ; it may have been accomplished by the complete separation of lobes into separate saccules with independent tubes and surface pores, followed by their disjunction. One specimen of *C. usnea* exhibits such a division unilaterally ; *Sa*, on the right, is composed of two clearly independent simple saccules. The tube of the larger, anterior saccule opens via a long slit ; that of the smaller, posterior saccule has a minute pore (Fig. 1 D). This conditions is obviously rare in *C. usnea*, but the same evolutionary progression may have resulted in the more fixed duplication of saccules in *Siculobata*.

3. The polarity of the gradation between large and small (or absent) humeral tecta of the notogaster in the Scheloribatidae is unresolved. Are small tecta precursors to pteromorphs which are large enough to cover retracted legs, or are they vestiges of pteromorphs which have undergone regressive evolution ? NORTON (1983) espoused the second hypothesis when discussing a similar problem in the Mochlozetidae, another family of Oripodoidea, and this is the position followed here ; we are considering the small humeral tectum to be simply one more regressive state among many exhibited by this group, just as among the Mochlozetidae *Mochloribatula* apprently has lost the pteromorph. GRANDJEAN (1953) suggested that the first hypothesis was more probable, that pteromorphs are secondary within the Scheloribatidae. It seems likely that his thinking was influenced by the absence of pteromorphs in the Oribatulidae (*sensu stricto*), and this would also be an appropriate conclusion in a cladistic analysis, if one were to consider the latter family as the closest out-group of Scheloribatidae. However, if another family of Oripodoidea were hypothesized to be the nearest out-group (for example, the

Mochlozetidae, in which almost all members have pteromorphs, or the Haplozetidae, all with pteromorphs, or the Oripodidae, in which pteromorphs are present or absent), the results might differ. The question clearly has yet to be resolved, but a careful analysis of phylogenetic pattern among the families of Oripodoidea is a needed step.

4. The deep paired rostral emarginations of *C. usnea* correspond perfectly with the positions of the chelicerae, and it is interesting to speculate that they may be adaptations to allow feeding in a plane closer to horizontal than is usual in this group. GRANDJEAN (1956) found that female *Pirnodus detectidens* Grandjean (Oripodidae) have a regressive tectum which allows horizontal cheliceral movement ; they feed in cavities in crustose lichens, whereas the surface-feeding males have a normal rostrum which restricts chelicerae to the usual oblique movements. Unfortunately, no living specimens of *C. usnea* were observed *in situ*, so we know nothing of its feeding habits.

ECOLOGICAL NOTES

Six oribatid mite species were commonly represented in the epiphytic mosses and lichens of Popocatépetl : *Camisia* if *horrida* (Hermann), *Belba clavasensilla* Norton & Palacio-Vargas, *Scapheremaeus* sp., *Cryptozetes usnea* n. sp., *Trichoribates ocotlicus* Palacios-Vargas & Norton, and *Mycobates* sp. These species exhibit specificity for these microhabitats, as opposed to the underlying soil and leaf litter, as indicated by the following three types of data :

a) *Percent of permanence* (PP) (*sensu* RAPOPORT and NAJT, 1966). This indicates the duration of a given species' occurence during the observation period, and is expressed as the percentage of months sampled during which the species was represented at a particular station.

b) *Coefficient of frequency* (CF) (*sensu* CHRISTIANSEN, 1964). This is the percentage of the total number of samples tacken in which a given species was represented ; like PP, it always relates to a particular station and a particular microhabitat.

c) *Abundance.* Numbers of specimens from the three replicates were summed when comparing mite abundances among microhabitats ; pooled data are used because of the very high standard deviations encountered. Only general comments are made below, relating especially to months of peak and low abundance.

Scapheremaeus sp. PP : station I, soil (0).2 litter (7), mosses (92) ; station II, soil (0), litter (0), lichens (30) ; station III, soil (0), litter (15), lichens (46). CF : station I, soil (0), litter (0), litter (2.5), mosses (46.1) ; station II, soil (0), litter (0), lichens (10.2) ; station III, soil (0), litter (5.1), lichens (28.2). Abundance was low at all stations ; 5 to 10 individuals ; the maximum (50) was in mosses at station I, during July.

Camisia cf. *horrida*. PP : station I, soil (0), litter (15), mosses (69) ; station II, soil (7), litter (0), lichens (84) ; station III, soil (0), litter (0), lichens (92). CF : station I, soil (0), litter (5,1), mosses (35.8) ; station II, soil (2.5), litter (0), lichens (48.7) ; station III, soil (0), litter (0), lichens (53.8). Abundance was generally low in stations I and II, with 5-10 individuals, and similar (or slightly higher) at station III ; the maximum was 20 in the lichens of station III, during July & August.

Mycobates sp. PP : station I, soil (0), litter (0), mosses (23) ; station II, soil (7), litter (0), lichens (76) ; station III, soil (0), litter (30), lichens (69). CF : station I, soil (0), litter (0), mosses (10.2) ; station II, soil (2.5), litter (0), lichens (51.2) ; station III, soil (0), litter (10.2), lichens (35.8). Abundance was generally low, 5-10 individuals at all stations, except in December at stations II (50) and III (100).

Trichoribates ocotlicus. PP : station I, soil (7), litter (0), mosses (7) ; station II, soil (15), litter (15), lichens (30) ; station III, soil (23), litter (53), lichens (100). CF : station I, soil (2.5), litter (0), mosses (2.5) ; station II, soil (5.1), litter (7.6), lichens (15.3) ; station III, soil (7.6), litter (23), lichens (97.4). Abundance was low at stations I and II, but very high and constant in III, where more than 500 individuals were collected each month, except February and May (50 and 100, respectively).

Belba clavasensilla. PP : station I, soil (0), litter (0), mosses (7) ; station II, soil (0), litters (0), lichens (57) ; station III, soil (7), litter (15), lichens (92). CF : station I, soil (0), litter (0), mosses (2.5) ; station II, soil (0), litter (0), lichens (20.5) ; station III, soil (2.5), litter (5.1), lichens (61.5). Abundance was variable, very low at station I and between 5-20 at stations II and III.

Cryptozetes usnea n. sp. PP : station I, soil (0), litter (7), mosses (15) ; station II, soil (0), litter (7), lichens (84) ; station III, soil (0), litter (7), lichens (92). CF : station I, soil (0), litter (2.5), mosses (5.1) ; station II, soil (0), litter (2.5), lichens (53.8) ; station III, soil (0), litter (2.5), lichens (82). Abundance was low at station I, a maximum of 5-10 individuals during May and June, variable at station II (5-50) and moderate at station III, with from 50-100 individuals between April and December. Immatures were collected during January, March, May, July and October, and are probably present throughout the year.

According to the criteria of KARPPINEN (1972, 1977) and MORAZA *et al.* (1980), *fundamental* (or constant) species are those which have a CF greater than 51 %, *accessory* (or frequent) species are those with a CF between 26 and 50 %, and *accidental* species are those with a CF of 25 % or less. Even though all six species were represented at some time in soil or litter, their occurence there must be considered accidental. No two stations have identical fundamental or accessory epiphytic oribatid faunas, and station I mosses have no species which could be considered fundamental. Only *Cryptozetes usnea* is fundamental to lichen faunas at both stations II and III ; *Mycobates* sp. is fundamental at II, but accessory at III, whereas *Trichoribates ocotlicus, Camisia* cf. *horrida* and *Belba clavasensilla* are fundamental in station III lichens but only accidental in those of station II. The latter species was originally described from specimens collected from station I mosses, but is clearly more abundant in the lichens of stations II and III. *Scapheremaeus* sp. is never more than an accessory member of the epiphytic fauna (stations I & III) ; this unknown species is more associated with mosses than lichens, whereas at least one congener, *S. petrophagus* (Banks), is only known from lichens. If similar criteria were to be developed for percent permanence, the patterns would not be very different. One interesting general observation is that execpt for *Mycobates* sp., each species had higher PP and CF in station III lichens than in station II lichens ; we have no comparative data on moisture-levels of the epiphytes, but it is possible that substrate desiccation was more prevaleut at the lower altitude of station II. With regard to microhabitat specificity, it is important to realize that the bark-surface substrate was not sampled, and many species of some genera (e.g., *Camisia, Trichoribates*) are bark-dwelling and fungivorous

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