SOME NEW FORMS OF *PYEMOTES* (ACARINA: PYEMOTIDAE) FROM FOREST INSECTS, WITH REMARKS ON POLYMORPHISM

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----- ABSTRACT—Three new species of *Pyemotes*, *P. giganticus*, *P. tuberculatus* and *P. emarginatus* are described, as is the male of *P. dryas* (Vitzthum, 1923). Male *P. dryas* and both sexes of *P. giganticus* are polymorphic. A short, general discussion of polymorphism is presented which includes remarks on its mechanisms and possible ecological-evolutionary implications. -----

In an earlier paper, Cross and Moser (1975) discussed certain aspects of the taxonomy of the cosmopolitan parasitoid tarsonemine genus *Pyemotes* Amerling, 1861, and described an interesting polymorphic species, *P. dimorphus*. Since then, several new species and additional polymorphic forms have been found. In this paper 2 new species not known to be polymorphic are described, as are 2 polymorphic forms, one of which is only tentatively judged to be specifically distinct. We also present further information concerning tarsonemine polymorphism and offer a revised key to the species of *Pyemotes*.

A comparison of the types of *P. herfsi* (Oudemans, 1936) with various populations of *P. zwoelferi* Krczal, 1963 indicates these 2 forms are conspecific (new synonymy).

Terminology and measurements are the same as those used in Cross and Moser (1975) except that we follow the more conventional terminology with respect to leg segmentation (Fig. 9), also Lindquist's (1977) notation for dorsal opisthosomal setae.

POLYMORPHISM—Small size in animals may be negatively correlated with the ability to successfully disperse, i.e., successful niche relocation. This is because animal size is generally positively correlated with niche size and specialization but negatively correlated with the ability to disperse into these specialized niches. Probably, phoresy is the adaptation which maximizes the ability of small animals to disperse successfully under such conditions. Several authors (*vide* Dybas, 1978) have found "normal" (i.e. non-dispersing) morphs of various polymorphic invertebrates to be more fecund than dispersal forms, but no information in respect to this matter is presently available in mites.

Marked polymorphism in one or (usually) both sexes occurs in at least 2 genera (*Pyemotes* and *Siteroptes*) of Pyemotidae sensu Cross, 1965 (Moser and Cross, 1975). In all cases, the most obvious anatomical features of "heteromorphic" females are almost certainly adaptive for dispersion via phoresy, characteristically resulting in a more compact body form, enlarged legs and claws I, and darker, presumably thicker and/or denser cuticle. Differences between "normal" and "heteromorphic" females of the same species may be so great that many have been placed in different subfamilies or families by various authors. Only in *Siteroptes graminum* (Reuter) do both female morphs resemble one another closely. Polymorphism in males, who are not known to be phoretic, is also marked but largely restricted to differences in body and setal size, the latter correlated with slightly modified setal conformation, e.g., increasing spinosity (Figs. 7-8) and/or missing or supernumerary setae. Adaptive value of these characters is not obvious, but in male Rhizoglyphinae, certain male heteromorphs ("pleomorphs") live longer and sire more young earlier than "bimorphic" males (Timms et al., 1980).

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In pyemotids, males may show either a clear dimorphism (*Siteroptes* sp., *P. dimorphus*) or a more continuous series of intermediates may be present (*P. dryas, P. giganticus*). In the former case, polymorphism resembles that of certain rhizoglyphine mites, wherein the males may be short-haired ("homeomorphic") or long-haired ("dimorphic") (Woodring, 1967). Morphogenetic polymorphism in pyemotids usually involves both sexes in a given species; however, female *P. dryas* appear to be monomorphic while males are polymorphic.

In addition to morphogenetic differences, polymorphism in both sexes of many *Siteroptes* may include the presence or omission of a free-living larval stage. Such a larva is characteristic of most, if not all, pygmephorine and scutacarine mites but is normally absent in pyemotine and acarophenacine forms. A similar situation is noted in many astigmate mites in which a deutonymphal "hypopus" specialized for dispersion may be present or absent in developmental progression. In all of these cases, the omission shortens generation time, thereby enhancing r_m (the intrinsic rate of natural increase) and permitting the buildup of larger populations prior to the onset of limiting environmental degradation.

Experimental evidence shows the appearance of alternate morphs in many small invertebrates to be "environmentally cued" in the sense of Clark (1976). Parameters responsible for cueing may be known specifically [α-toxicopherol in certain rotifers (Gilbert, 1975); glycerol in the gall fly *Heteropeza* (Kaiser, 1967); yeast odor in astigmate mites (Poe, 1966, unpublished M.S. thesis)] or generally [pheromones in astigmate mites (Woodring, 1967; Timms et al., 1980); crowding in aphids (Dixon, 1977)].

Such polymorphism is sometimes erroneously called "nongenetic", since relatively constant proportions of morphs are usually not temporally predictable. This designation ignores the genetic matrix in which the developmental reactions are canalized and serves to obscure the basic genetic control of the resulting phenotypes. This genetic nature is clearly shown in pyemotids in its occurrence in clusters of closely-related species.

In pyemotine and pygmephorine mites, the extent of environmentally-cued polymorphism is not clear. Rack (1972), studying a time series of alcoholic specimens of *Siteroptes graminum*, found the same mother to produce a single morph and the population to consist exclusively of one morph at any point in time. Switch to the alternate morph was sudden and essentially complete. This may best be explained as environmentally-cued polymorphism and Rack in fact hypothesizes that the cue is the glycogen content of the fungus which serves as food. Košir (1975), studying a second species of *Siteroptes*, found both morphs to occur together in mushroom beds, but females specialized for dispersion (phoretomorphs) produced all "normal" morphs the first generation after being transferred to laboratory fungal cultures and continued to produce them throughout the course of the experiment. This also clearly suggests environmental cueing. Moser, rearing 2 species of *Siteroptes* and 3 species of *Pyemotes* (*dimorphus, dryas, giganticus*)found individual mothers to give birth to all morphs in laboratory cultures. However, the numbers of individuals concerned were usually small and the time frame was short so that morph frequencies and shifts in actual populations are unknown. Utida (1972) found direct selection as well as environmental cueing and genetic assimilation to be important in the regulation of polymorphism in the bruchid *Callosobruchus maculatus*. In pyemotids, selection in favor of phoretomorphs could be expected to occur in conjunction with deterioration of the microhabitat, but it is presently difficult to account for the reverse selection since dispersed phoretomorphs appear to produce "normal" daughters largely or exclusively in the few cases where they have been studied.

Dybas (1978) infers a correlation between small size and the occurrence of phenotypically plastic genotypes. The advantage of this type of system is obvious, since it would allow enhanced

population buildup in transient environments while providing maximum provision for successful dispersal to new ones via phoresy as argued previously. Presumably, this would be accomplished with a reduced genetic load. Another aspect of plasticity may be important. In at least one species of *Siteroptes* (*S. bennetti*), only the phoretomorph is known despite a long period of laboratory rearing by Moser. Also, the "normal" female of the form we have called *giganticus* has not been seen. This raises interesting questions as to the ease with which morphs may be fixed or lost in these populations. Perhaps phenotypic plasticity may also offer an unusually facile method for providing large amounts of evolutionary change over relatively short periods of time (Moser and Cross, 1975; Dybas, 1978).

Artificial key to the species of *Pyemotes*

1. Males 2
- Females 16

2. With all 4 pairs of prodorsal setae nearly in a transverse line; polymorphic species (Fig.6) ..... *dimorphus* Cross & Moser and *giganticus* n. sp.[4]
- At least 1 pair of prodorsals well anterior to the others; polymorphic or not 3

3. Prodorsals arranged in 2 rows, the first consisting of a single, small seta (#3), second row unevenly transverse with 3 setae; two lateral setae of second row usually distinctly larger than the innermost pair; polymorphic (Figs. 8, 10) ..... *dryas* (Vitzthum)
- Prodorsals not so arranged 4

4. Prodorsals arranged in 2 trasverse rows of 2 pairs each, posterior two pairs (# 3,#4) stout, similar to setae c_1 and c_2 of first hysterosomal plate ..... *parviscolyti* Cross & Moser
- Not as above 5

5. First and second hysterosomal terga separate and distinct; all 4 setae of 1st tergum subequal, very short, the laterals arising near the posterior margin of the sclerite ..... *scolyti* (Oudemans)
- First and second hysterosomal terga fused to form a plate; setae not as above 6

6. Hysterosomal setae c_2 large, similar to hysterosomals *d* or *e* in size 7
- Hysterosomal setae c_2 smaller, not much longer and sometimes shorter than setae c_1, and usually much smaller than *d* or *e* 10

7. Claw IV distinctly bulbose apically, appearing to be capped, its tip rounded or slightly acuminate (Figs. 18, 19) ..... *emarginatus*, n. sp.
- Claw IV saggitate and sharply pointed or tusklike and not bulbose apically 8

8. Seta c_1 short, less than half the size of seta *d*; claw IV elongate and tusklike, rounded apically; external tibial solenidium of leg IV very long, reaching to tip of claw or nearly so ..... *beckeri* Krczal
- Seta c_1 long, similar to *e* in size; claw IV saggitate and with a sharp point; external tibial solenidium of leg IV very short, not reaching much beyond base of claw 9

9. Third prodorsal seta shorter, not extending more than 1/2 its length beyond areolus of 4th prodorsal ..... *schwerdtfegeri* Krczal
- Third prodorsal longer, extending distinctly more than 1/2 its length beyond areolus of 4th prodorsal seta ..... (nr. *schwerdtfegeri*)

4. These 2 forms are not separable on male characters except for the presence of intermediates between "normal" and "heteromorph" forms, which are presently known only from *giganticus*.

10. With an anteromedian tubercle which bears prodorsals 1; [5] hysterosomal setae c_1 very large, subequal to 4th prodorsal; c_2 less than 1/4 as long as c_1 ..... *tuberculatus* n. sp.
- Without an anteromedian tubercle; setae c_1 and c_2 of various lengths 11

11. Setae *c* of femur IV short and slender, rarely reaching to tip of tarsus IV, less than half as long as opisthosomals *d* or *e*; claw IV appearing long and evenly fingerlike; solenidiu of tibia IV thin, elongate, reaching tip of claw or nearly so ..... *anobii* Krczal
- Seta *c* of femur IV long and stout, extending at least to, and usually beyond tarsus IV, more than 1/2 as long as dorsals *d* or *e*; claw IV and solenidium of tibia IV variable 12

12. Hysterosomal setae c_1 and c_2 subequal in length and thickness, or c_2 but slightly larger than c_1 13
- Seta c_1 distinctly larger than c_2 15

13. Fourth prodorsal long and narrow, distinctly thinner than hysterosomal setae *d* and *e*; internal presternal normally spinose, short, less than 1/2 the length of the 2nd axillary; 3rd prodorsal long, usually more than twice the length of the 2nd and usually extending well beyond areolus of 4th ..... *tritici* (LaGrèze-Fossat & Montagné)
- Fourth prodorsal long and stout, usually as thick as dorsal *d* and thicker than *e*. Other characters variable 14

14. Internal presternal short-setose, less than half the length of axillary 2; claw IV distinctly bulbose apically, appearing to be "capped" ..... *emarginatus*, n. sp.
- Internal presternal longer, half as long to equally as long as axillary 2; claw IV not or slightly bulbose apically, not appearing to be "capped" ..... *herfsi* (Oudemans)=*zwoelferi* Krczal

15. Hysterosomal setae *e* and *f* subequal in size ..... n. sp. "A" [6]
- Hysterosomal seta *e* several times longer and thicker than *f* ..... n. sp. "B" [6]

16. Internal ventrals II arising from or closely behind apodemes II; claw I usually large; mites often shorter, oval ..... *scolyti* group 17
- Internal ventrals II arising well behind apodemes II, usually in center of sclerite; claw I usually small-moderate in size; mites usually more elongate-fusiform ..... *ventricosus* group 20

17. Posterior margin of prodorsum distinctly emarginate ..... *scolyti* (Oudemans)
- Posterior margin of prodorsum rounded or (rarely) linear 18

18. Legs I immense (Fig. 4) ..... *giganticus*, n. sp. (Type II heteromorph)
- Legs I normal, less than twice as thick as legs II 19

19. Prodorsum and terga I-III with coarse, longitudinally parallel striae, heaviest on posterior 2/3 of these segments (Fig. 11) ..... *parviscolyti* Cross & Moser and *dryas* (Vitzthum)
- Prodorsum and terga I-III without marked longitudinal, parallel striae ..... *dimorphus* Cross & Moser and *giganticus*, n. sp. (Type I heteromorph)

20. Posterior margin of prodorsum distinctly emarginate medially ..... *emarginatus*, n. sp.
- Posterior margin of prodorsum rounded to linear medially ..... *ventricosus* group. [7]

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[5] This tubercle usually depressed during mounting, visible as creases or thickened lines.

[6] For collecting data, these species, see Cross and Moser (1975), p. 724.

[7] Includes the following females not separated in the key: *anobii*, *beckeri*, *herfsi* (=*zwoelferi*), *schwerdtfegeri*, "nr. *schwerdtfegeri*", *tritici*, *tuberculatus*, *ventricosus*, sp. A, and sp. B.

Pyemotes giganticus n. sp.
(Figs. 1-6)

This name is given to a form of *Pyemotes* discovered by D. Kinn and associated with at least 14 species of scolytid beetles in conifers in the western U.S. Both sexes are polymorphic in a manner similar to that of *P. dimorphus*, Cross and Moser 1975, but unlike the latter species, *giganticus* exhibits morphologically intermediate forms between the extremes. All male *giganticus* seen to date fall within the range between *dimorphus* "normal" and *dimorphus* "hetermorph", as given in the species description of the latter. In the case of females, the "normal" type females described for *dimorphus* have not been found in *giganticus*, but 2 *giganticus* morphs are known from collections in nature and laboratory rearings: (1) a form morphologically indistinguishable from the "phoretomorph" form of *dimorphus* and (2) a large "new" morph having immensely hypertrophied legs I. The first of these morphs is the most common, the second being known at present only in low frequency from Marin Co., California. Morphs are designated as heteromorph Type I (H) and heteromorph Type II (HH) respectively. One specimen thought to be an intermediate between H and HH females is designated in the type series (Paratype 4).

Males of *dimorphus* are indistinguishable as both "normal" and "heteromorphic" forms from respective forms of *giganticus* except that intermediate forms of the latter are known.

Because only HH females and intermediate males are presently morphologically separable from *dimorphus*, the specific status of *giganticus* is debatable. Two of the present authors (Moser and Rack) believe the 2 forms to be sibling species, based largely upon apparent ranges of hosts attacked and upon spatial distribution. Cross believes *giganticus* to be a third morph of *dimorphus*, his opinion based largely upon morphological similarity, especially of the males.

DIAGNOSIS—Type II (HH) females differing from all other *Pyemotes* in that legs I are enormously enlarged, usually more than twice as wide as those of Type I (H) females. Claw I reduced to a short, thick, only slightly curved spine. H females not separable from the "phoretomorph" female of *dimorphus* but distinguishable from all other *Pyemotes* because internal ventrals II arise on or immediately adjacent to apodemes II, in lacking dorsal longitudinal striae, and because the hind margin of the prodorsum is rounded. Males not separable from those of *P. dimorphus*, separable from all other species in the genus by the characters given in the diagnosis of *P. dimorphus*.

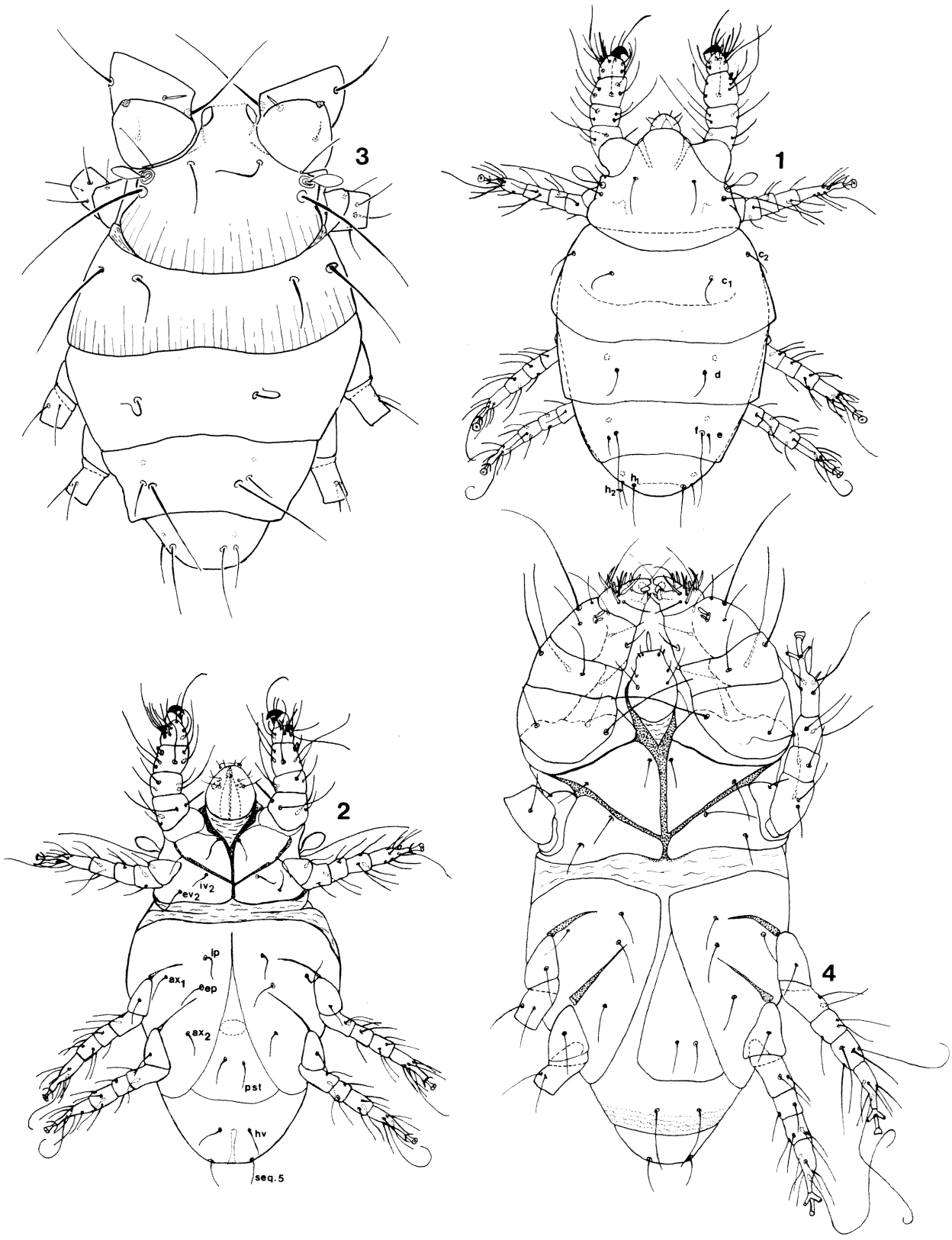
DESCRIPTION OF NON-GRAVID FEMALE, TYPE II (HH) HETEROMORPH (Figs. 3-4)—Large, length 257 (158[8]-298); width, 127 (85[8]-147); body oval as H female (or usually slightly rhomboidal); prosoma and 1st (to 1st 3) hysterosomal tergum with longitudinal, parallel striae[9]. All body setae thin, nude, flagellate.

GNATHOSOMA—33 (31-35) wide; more pyriform than that of H female.

PROPODOSOMA—DORSUM—As described for phoretomorph of *P. dimorphus*. VENTER—As *dimorphus* but internal ventrals II shorter, barely reaching hind margin of anterior ventral plate. Anterior ventral plate heavily (to moderately) sclerotized.

HYSTEROSOMA—DORSUM—Hind margin of segment I broadly and shallowly emarginate, margins of succeeding segments arcuate (to straight); setae c_1 distinctly shorter than c_2; *d* reaching well beyond hind margin of 2nd segment (or not); segment III with setae arising slightly behind *e* (or setae in a transverse line); *f* longest of hysterosomal setae (≅40), but shorter than posterior prodorsal; setae of segment IV in a transverse line, h_1 nearly twice as long as h_2. VENTER—As described for phoretomorph of *dimorphus* except opisthosomal ventrals longer than setae of segment 5.

8. This specimen (Paratype 4) may be an intergrade.
9. May be due in part to wrinkling of dorsal cuticle.



Figs. 1-4: *P. giganticus* n. sp. [Type I (H) ♀, paratype]-1, dorsal; 2, ventral. 3-4 [Type II (HH) ♀, holotype]-3, dorsal; 4, ventral.

LEGS—Leg I greatly enlarged, 57 (29^{8}-57, $\bar{X}$=48) wide; leg II 22 (14^{8}-22) wide; leg III 105 ($?^{8}$-105) long; leg IV 134 (98^{8}-134) long; length, ta IV, 28 (26^{8}-33). Claw I a thick, simple, slightly curved spine, sometimes blunted; setation of legs (with possible exception of ta I[10]) as described for phoretomorph of *dimorphus* [11].

DESCRIPTION OF NON-GRAVID FEMALE, TYPE I (H) HETEROMORPH ("PHORETOMORPH") (Figs. 1-2)—Agrees with the description of the phoretomorph of *dimorphus* except as follows: internal ventrals II not (usually) reaching hind margin of AVP; setae *d* extending beyond hind margin of segment II or not; *f* arising slightly anterior to *e*; position of h_1 variable with respect to h_2.

DESCRIPTION OF MALES (Figs. 5-6)—Agree with descriptions of male *dimorphus*, i.e., no specimens seen fall outside range of variability as described for the 2 morphs of that species. No "normal" males of *giganticus* were seen, all specimens being heteromorphs or intermediate forms.

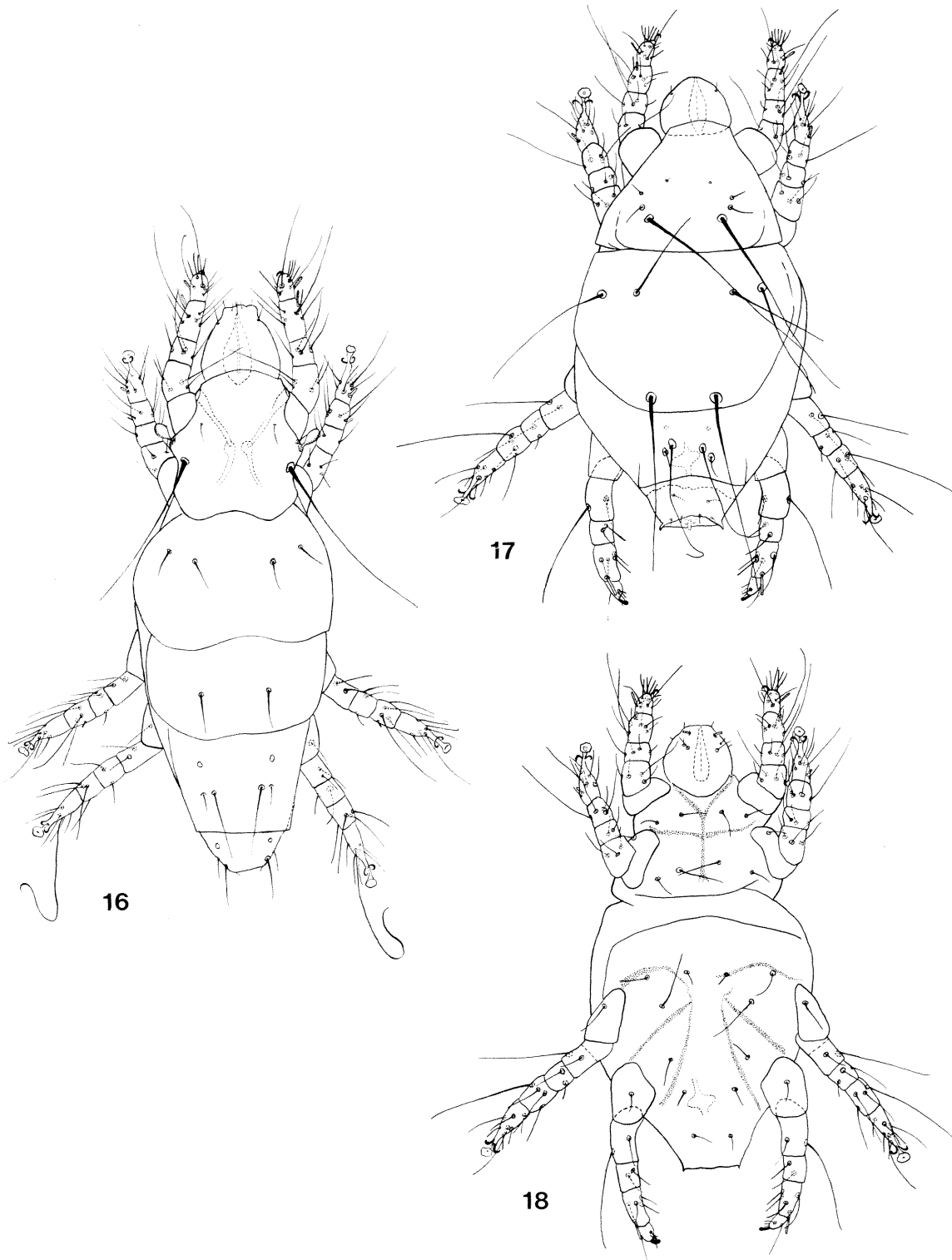
VARIABILITY—Type I females vary noticeably in degree of sclerotization, in setal length (absolute and, to a lesser extent, relative), and in leg thickness. Type II females vary in the extent of dorsal striation as well. One specimen (Paratype IV) appears to be intermediate between the two morphs. Males vary greatly in setal numbers, size, and placement in the same manner as those of *dimorphus*. Setae are more likely to be asymmetrical in size and placement in heteromorphic forms. Unlike *dimorphus*, which are presently known to occur in only two states, *giganticus* males occur in an array of forms which are not separable from *dimorphus* "normal" on one hand and "heteromorphs" on the other. No "normal type" *dimorphus* males were noted in our limited sample.

HABITS—Associated with galleries and adults of a variety of scolytid beetles in several western tree species (below). Progeny from 2 Type I females were reared by Moser in Louisiana. The mites were collected in Inverness, Marin Co., California in douglas fir (*Pseudotsuga taxifolia*). The first female produced 19 females and 1 male. Of the 19 females, 15 were Type I and 4 were Type II. The male was an intermediate close to "normal". One of these daughters (Type I) produced 11 males, of which 5 were close to "normal", 3 were more nearly intermediate, and 2 were "heteromorph". Both female morphs are probably phoretic, since Moser has found both to attach to several species of adult beetles in the laboratory. Moser (in press) has investigated the form as a possible beetle control agent.

DISTRIBUTION—CALIFORNIA-Blodgett Forest, El Dorado Co., ex galleries of *Scolytus ventralis* in "white fir"; Cone Peak, Monterey Co., ex *Scolytus dentatus* in *Abies bracteata*; Ft. Bragg, ex galleries of *Pseudohylesinus* sp. in "douglas fir" (reared); Hurtey Ck., P.C., San Jacinto Mtns. ex *Orthotomicus sabiniana*: galleries of *Pseudohylesinus grandis* in douglas fir; Nr. Inverness, Marin Co., ex *Taenioglyptes pubescens* in douglas fir; Nr. Middletown, Lake Co., ex *Phleosinus cristatus* in "sargent cypress"; Oakland Hills, ex galleries of *Phleosinus sequoia* in "coast redwood"; Oceanside, San Diego Co., ex *Phleosinus* sp. in "monterey cypress"; San Francisco, ex *Ips mexicanus* in *Pinus radiata*; Sequoia N.P., ex *Phleosinus rubicundulus* in *Sequoia gigantea*. OREGON—Keno, ex *Phleosinus chamberlini*; nr. Pinehurst, Jackson Co., ex *Phleosinus vandykei* in *Libocedrus decurrens*. UTAH: Mt. Timpanogos, Wasatch Co., ex "bark beetle". WASHINGTON — Mt. Rainier N. P., ex *Pseudohylesinus* (? *nobilis*) in "noble fir".

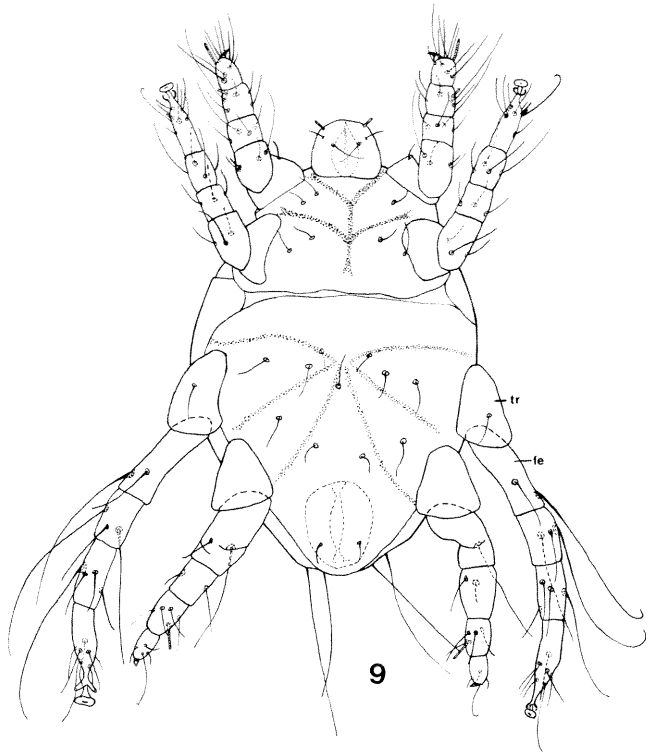
TYPE MATERIAL—Type II female holotype and male ("nr. normal") allotype reared in laboratory from galleries of *Pseudohylesinus* sp. in douglas fir, Ft. Bragg, Calif., Feb., 1976, G. Ferrell. Paratypes 1-5 (H♀, HH♀, HH♀, HH♀, H♀, respectively) from Inverness, Marin Co., Calif., ex *Pseudohylesinus nebulosus* in douglas fir. Paratypes 6-10 (N♂, NH♂, NH♂, H♂, H♂, respectively) reared in lab (H mother), same data as holotype-allotype. Paratype # 11 (H♀) from Mt. Timpanogos, Wasatch Co., Utah, ex "bark beetle".

10. Definitive view of the setation of this segment not possible from specimens in hand.
11. There are 7, not 6 setae on tarsi II-III, as stated in the description of that species.



Figs. 5-6: *P. giganticus* n. sp. ("intermediate", paratype 8, ♂)—5, ventral; 6, dorsal
Figs. 7-8: *P. dryas* (Vitzthum), (heteromorph, paratype*, ♂)-7, ventral; 8, dorsal.

* Paratypes of this species are left unnumbered since they are additions to the original type series.



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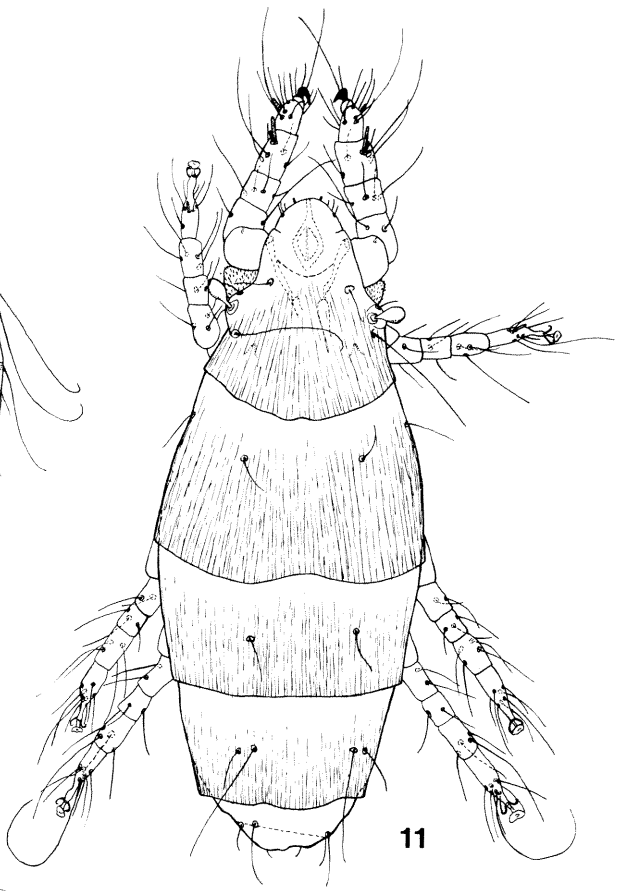

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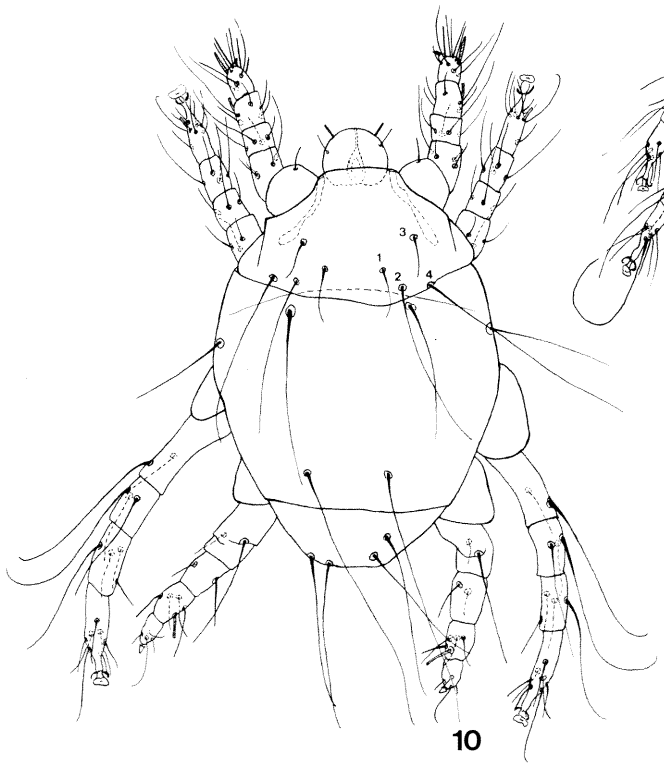

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Figs. 9-10: *P. dryas* (Vitzthum), [normal ♂(allotype)]-9, ventral; 10, dorsal. Fig. 11: *P. dryas* (♀)—dorsal (plesiotype).

TYPE REPOSITORIES—All type material to the U.S. National Museum except paratypes 2, 6, 8, 10, and 11, which are retained in the collection of the senior author.

Pyemotes dryas (Vitzthum)

Pediculoides dryas Vitzthum, 1923. Arch. f. Naturgeschichte, Abt. A, 89: 97-181.

The female of this species was described by Vitzthum in 1923, but we find no other record of it until its collection by Kielczewski and Balazy in Poland in 1966. It was originally taken from the scolytid *Pityogenes bistridentatus* Eichoff near Liebenau, Austria, but the present specimens were collected from *Polygraphus poligraphus* (L.) in *Picea abies* (L.) (=*P. excelsa* Link) in Wielkopolski National Park, Poland, and from *Pithopthorus pityographus* (Ratzeburg) near Krynica, Poland.

Morphologically, *dryas* belongs to the *scolyti* group and is closest to *parviscolyti*, females being monomorphic and indistinguishable from the latter. Unlike *parviscolyti*, male *dryas* are polymorphic, following the same pattern of variability as those of *P. dimorphus*. They lack the clear-cut dimorphism of that species, however, showing a series of intergrading forms between "normal" and "heteromorphic" males. Reciprocal crosses of *parviscolyti* X *dryas* were made by Moser in the laboratory and resulted in the production of only males in those cases where offspring were produced.

We describe the male here, but the female is not redescribed since it is not separable from *parviscolyti* and reference may be made to the description of the latter species. Also, since male variability is not sharply discontinuous, as in *dimorphus*, we make no effort to separately describe the 2 extremes, as in that form.

One of us (Rack) has compared females of the present series to those of the type and judged them to be conspecific, i.e., to belong either to *dryas* or *parviscolyti*. Since the latter is presently known only from the New World, we infer them to be *dryas*.

DIAGNOSIS—Females not separable from *parviscolyti*, separable from those of all others in the genus in that internal ventrals II arise on or immediately adjacent to apodemes II, because the dorsal plates are longitudinally striated, and in lacking hugely swollen legs I (Fig. 11). Males are separable from those of all others in the genus by the size, shape, and placement of the prodorsal setae (Figs. 8, 10).

DESCRIPTION OF MALE[12] (Figs. 7-10)—Length, 85 (83-121); all body setae flagellate, size variable according to specimen; dorsals mostly large, indistinctly and sparsely spiculate, ventrals smaller, nude; body oval (to rhomboidal) in dorsoventral aspect.

GNATHOSOMA—Dorsal setae small, ventrals large and conspicuous; palpal solenidium very long, cylindrical, 6 (6-9), subequal to (or longer than) the palpal seta immediately behind it.

PROPODOSOMA—DORSUM—Shape semicircular to subrhomboidal, dependent upon mount; 4 pairs prodorsal setae, numbers 1, 2, and 4 in a nearly transverse row (Figs. 8, 10), seta 3 well anterior and nearly directly in front of seta 2; prodorsal setae variable in size[13], but 2 and 4 always larger than 1 and 3, similar in size to setae of the 2 dorsal hysterosomal plates; seta 3 smallest, sometimes minute. VENTER—Internal ventrals I well separated, arising behind apodemes I; internal ventrals II (usually) distinctly larger than, external ventrals I distinctly smaller than other setae of plate.

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12. Description is of allotype male with variability shown in parentheses. See section on Variation for additional detail.
13. May also differ bilaterally.

HYSTEROSOMA—DORSUM—First hysterosomal plate with 3 pairs of large, elongate setae similar to prodorsals 2 and 4 in size, setae c_1 (Fig. 6) (usually) somewhat smaller than c_2 and d; second hysterosomal plate with 2 pairs of large, apical setae which may appear dorsal or ventral dependent upon mount. VENTER—Apodemes II-IV fused on each side; internal presternals variable, sometimes tiny, always the smallest setae of the plate; external presternals the largest setae of the plate.

LEGS—Leg II, 40 (40-53) long; leg IV, 52 (52-68) long. Leg II, 7. 5 (7. 5-11) wide; leg IV, 16 (14-21) wide. Ta I distinctly longer than wide; claw I small, arising from a well-developed petiole at inner apical margin of tarsus; tarsi II and III obliquely truncate apically when viewed from the side; tarsi I and II each with a very elongate, fingerlike solenidion, that of ta I, 10 (10-14), that of ta II, 7^{14} (7-14) long; fe III arcuate; solenidion of ti IV in apical 1/3 of segment, long and fingerlike, 0. 4 (0. 54-0. 67) times the length of ti IV; claw IV saggitate, apex sharp.

VARIATION—Variability in females is not unusual when compared to females of other species in the genus, and mainly concerns minor differences in size of body, setal lengths, etc., as well as artifact differences due to mounting, mite age, etc. "Heteromorph" males are distinctly larger, more rhomboidal in dorsoventral outline, and have much larger setae than more "normal" males. Their setae may appear spinose rather than setose. Heteromorphic males also tend to have abnormalities in the numbers and placement of setae. A degree of allometry in setal length and solenidial length is likewise evident in heteromorphs. For instance, the internal presternals of heteromorphs tend to be unusually long when compared to normal forms.

DISTRIBUTION—Known only from Austria and Poland on the hosts mentioned above and from Poland on the following additional hosts: *Pityogenes chalcographus* (L.), *Cryphalus asperatus* (Gyllenhall), and (laboratory cultures) *Leperismus varius* (Fabr).

TYPE MATERIAL—Allotype (normal) and 4 paratypes (normal to extreme heteromorph, unnumbered), reared in laboratory, Pineville, L A., USA, on *Dendroctonus frontalis* Zimmerman. Original stock from *Polygraphus poligraphus*, Wielkopolski National Park, Poland, in *Picea excelsa*, July 7, 1976, S. Bałasy. Female plesiotype, Wielkopolski National Park, May 29, 1976, S. Bałasy, same beetle and tree hosts.

TYPE REPOSITORIES—Entire type series to the U. S. National Museum, Washington, D. C.

Pyemotes tuberculatus, n. sp.
(Figs. 12-15)

This form belongs to the *ventricosus* group. Females are figured (Figs. 12-13) but indistinguishable from others of that group and are not described here. Males are distinctive. They are morphologically closest to *P. schwerdtfegeri* Krczal, 1959, but key to *P. anobii* Krczal, 1959, in Cross, et. al., (1975).

DIAGNOSIS—Males readily separable from those of all other species of *Pyemotes* in that setae c_1 are very stout, reaching well beyond the areolae of d while c_2 are very small, similar to external ventrals II in size, and in that the first prodorsals are close together, arising from a median tubercle (the latter not always clearly distinguishable, depending upon mount). In addition, it differs from *P. tritici*, *P. herfsi*, and from undescribed species "A" and "B" (Cross et. al., 1975) in that seta "c" of femur IV is short and slender.

DESCRIPTION OF MALE—Length 108 (99-118); width, 103 (90-110); body setae flagellate, large dorsals indistinctly spiculate, all others apparently nude; body distinctly oval in outline.

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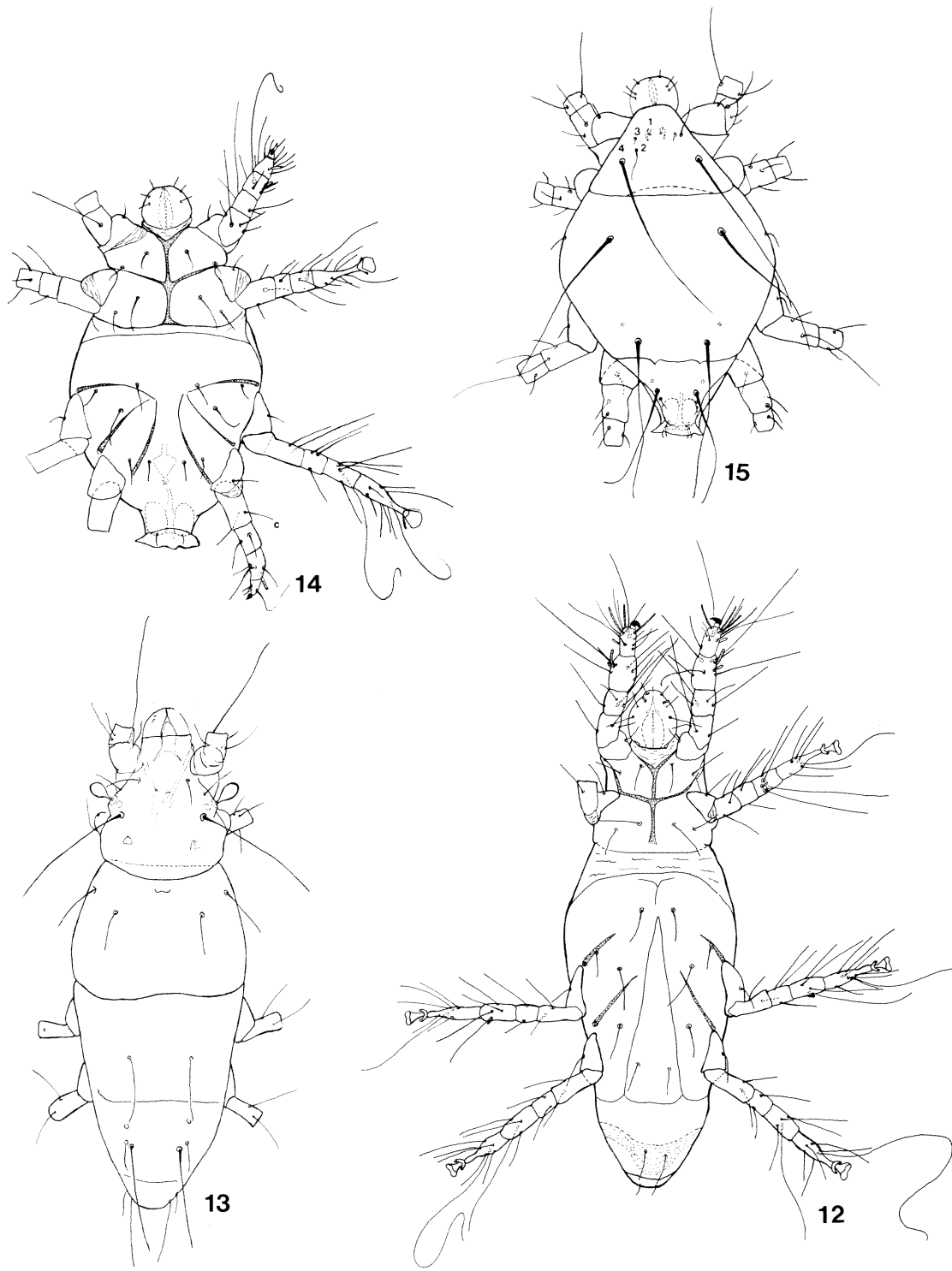
14. This structure is unusually short in this specimen.



Figs. 12-13: *P. tuberculatus* n. sp. (♀ allotype)—12, ventral; 13, dorsal. Figs. 14-15: *P. tuberculatus* n. sp. (♂ holotype)—14, ventral; 15, dorsal.

GNATHOSOMA—Dorsals short, marginal; palpal solenidium clavate, inconspicuous; ventrals fine, well separated, the anterior pair directly in front of (to slightly laterad of) the posterior.

PROPODOSOMA—DORSUM—Subtriangular in dorsal aspect; hind margin straight (to gently rounded); 4 pairs of prodorsals; first prodorsals tiny, close together, arising from a median eminence; prodorsals III well laterad and slightly posterior to prodorsals I, also tiny; second prodorsals well behind and slightly mesad of III, conspicuous and reaching well behind areolus of 4th prodorsal; fourth prodorsals greatly enlarged,reaching beyond hind margin of first hysterosomal plate, arising behind and laterad of all other prodorsal setae. VENTER—All ventral setae fine, internal ventrals II distinctly larger than the others, other three pairs subequal.

HYSTEROSOMA—DORSUM—First hysterosomal plate large and rounded; setae c_1 and *d* greatly enlarged, the latter slightly shorter than c_1 (Fig. 15); c_2 very small, similar in size to internal presternals; areolae of *d* removed from hind margin of first hysterosomal plate, 39 (37-40) apart; c_1 widely separated, 61 (55-66) apart; setae *e* of 2nd hysterosomal plate enlarged but distinctly shorter and thinner than those of 1st plate; setae *f* small and bristlelike, often hidden beneath *e*. VENTER—All ventral setae finely setose, varying somewhat in size but external presternals longest, 2nd axillaries next longest; internal presternals subequal to (to larger than) 1st axillaries, arising from apodemes III, overreaching apodemes IV only slightly.

LEGS—Leg I, 52 (50-53) long, 15 (13-16) wide; leg II, 15 (12-15) wide; leg III, 98 (90-103) long, 13 (13-14) wide; leg IV, 85 (77-85) long, 52 (50-53) wide, ta I as long as wide; claw I well-developed, arising from distinct pedicel; solenidia of ta I and ta II arising from middle of their segments; ta II not appearing sharply oblique or truncate apically when viewed from side; solenidium of ti I small, less than half the length of the adjacent blade seta; medial dorsal seta of ti II and III very large and flagellate, reaching well beyond claw, contrasting sharply with the remaining fine setae of the segment, this seta especially long on ti III; fe III not noticeably arcuate; dorsal solenidium of ti IV distal, reaching to middle of claw IV in profile; ta IV with a well directed, dorsal whip seta, a small but distinct median cuticular or membranous flap also present; claw IV sagittate.

DISTRIBUTION—Known only from Krefeld, West Germany.

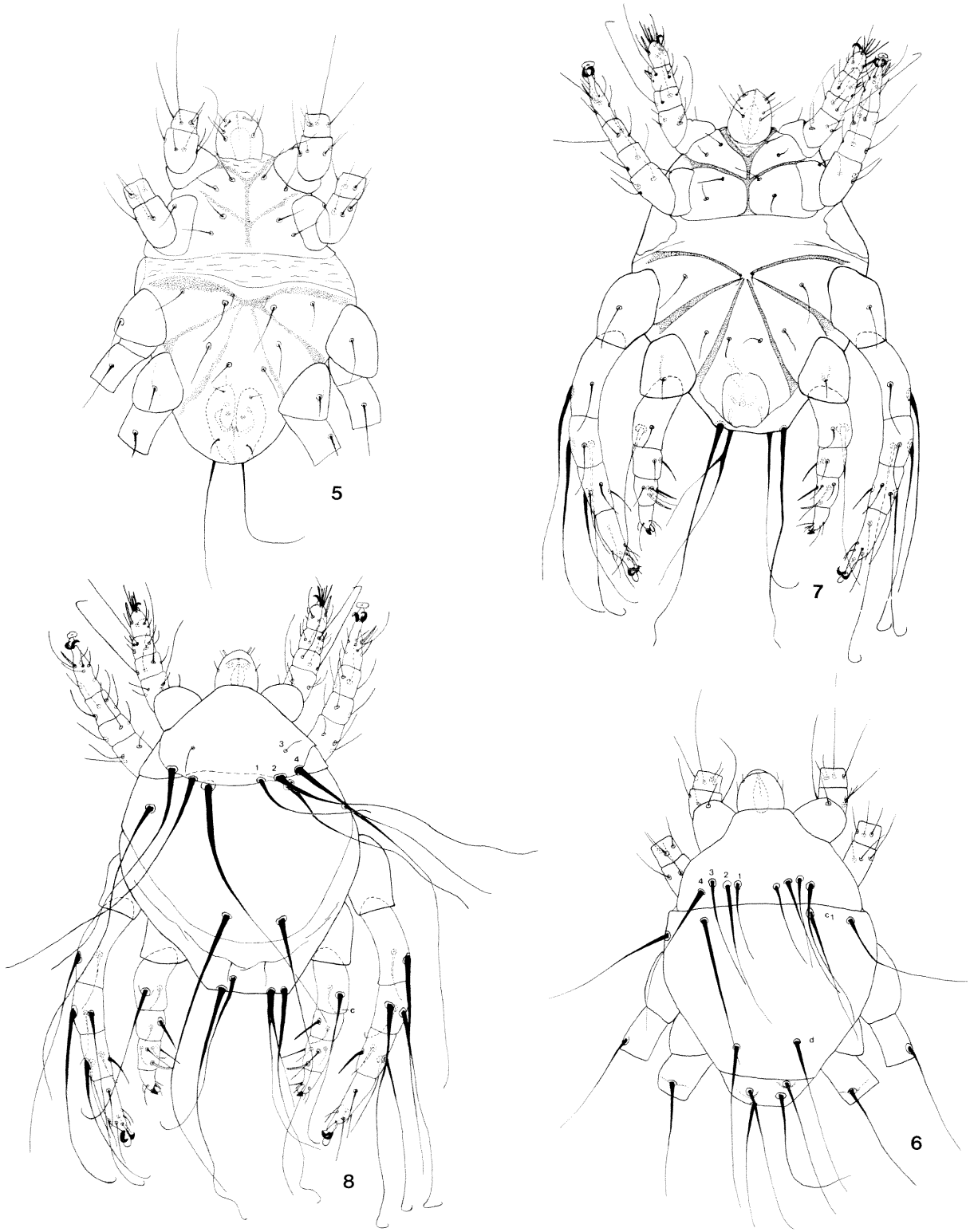
TYPE MATERIAL—Holotype male, allotype female, 15 paratypes (3 female and 12 male), all from Krefeld, West Germany, January 15, 1976, from *Oligomerus ptilinoides* (Anobiidae). S. Cymorek, coll.

TYPE REPOSITORIES—Holotype, allotype, paratypes 1 (female) and 4-6 (males) in the Zoological Museum, University of Hamburg. Paratypes 2-3 (females) and 7-8 (males) in the U. S. National Museum. Paratypes 9-10 (males) in the Snow Entomological Museum, The University of Kansas. Paratypes 11-12 (males) in the personal collection of the senior author.

No information concerning the habits of this distinctive species is presently available.

Pyemotes emarginatus, n. sp.
(Figs. 16-18)

This species, designated as "Species C" in Cross and Moser (1975) is known only from a single host and from one location in the southern United States. Both sexes, but particularly males, are morphologically variable, so that males are keyed in two places in the present key. Males also commonly show marked setal asymmetry, certain dorsal paired setae being different in size or lacking on one side. In the event of asymmetry in length, measurements were made on the longest seta.



Figs. 16-18: *P. emarginatus* n. sp.–16, ♀ dorsal aspect (allotype); 17, ♂ dorsal; 18, ♂ ventral (holotype).

DIAGNOSIS—Females separable from all species of the *scolyti* group in that internal ventrals II arise well posterior to apodemes II and in other characters. They differ from all members of the *ventricosus* group only in that the posterior margin of the prosoma is emarginate. In a few specimens, this margin is linear, in which case separation from certain *herfsi* and other *ventricosus* group females is not absolute. Males differ from all others in the size and conformation of claw IV, which is short and bulbose apically, appearing to be capped in most mounts. *P. tritici* males are similar in this respect but the claw appears longer.

They also resemble *tritici* in that the internal presternals are very short and bristlelike. Most male *emarginatus* may also be separated from *tritici* because the posterior prodorsals are thick basally and from *tritici* and *herfsi* because setae c_1 and c_2 are distinctly longer and stouter in *emarginatus*. (Fig. 17).

DESCRIPTION OF NON-GRAVID FEMALE—Length, 237 (216-237); width, 79 (75-85); body typically spindle-shaped, without coarse, parallel, longitudinal striae dorsally[15]; all body setae nude, thin, flagellate.

GNATHOSOMA—Wide and rounded, width 40 (39-42); palpal solenidium short, clavate.

PROPODOSOMA—DORSUM—Anterior margin straight, posterior margin with distinct median emargination (to posterior margin linear); anterior prodorsals short, not nearly reaching areoli of median or posterior prodorsals; posterior prodorsal very long and flagellate, reaching to hind margin of 2nd hysterosomal tergum (to posterior 1/4 of 2nd segment). VENTER—Apodemes II only moderately distinct (to indistinct); ventral setae well-defined, internal ventrals II distinctly longer than the others, arising from near center of ventrite II.

HYSTEROSOMA—DORSUM—Posterior margin of lst tergum broadly emarginate; setae c_1 slightly closer together than setae *d*; setae *f* longer than any other dorsal hysterosomals, 0.22 (0.13-0.23) length of posterior prodorsal; setae *e* very short, not reaching halfway to posterior margin of segment III, subequal to setae h_2; setae h_1 only slightly shorter than setae *f*. VENTER—First axillary setae longer than any others on posterior ventral plate; poststernals widely spaced, distinctly farther apart than either internal presternals or opisthosomal sternals.

LEGS—Leg I 13 (11-15) wide; leg II 13 (11-15) wide; length, leg III, 70 (66-72); leg IV, 94 (90-94) long; ta IV, 24 (20-24) long; ti I slightly attenuate towards apex, not wider than ge I; solenidium of ta I arising halfway down the dorsal face of the segment; the 2 solenidia of ti I in nearly a dorsal row, tubular, the smaller well basad of the longer; solenidium of ta II in basal half of the segment; solenidia of ti II and ti III present, arising in the basal half of segment near posterior margin (or these solenidia not visible -- lacking ??).

DESCRIPTION OF MALE—Length, 132 (129-139); width, 85 (80-88); all body setae nude, flagellate; body broadly spindle-shaped in dorsoventral aspect.

GNATHOSOMA—Broadly globose, width, 33 (31-35); palpal solenidium strobiloid, (usually) appearing to extend barely beyond margin of gnathosoma.

PROPODOSOMA—DORSUM—Subtrapezoidal, posterior margin broadly rounded; first (anterior) prodorsals minute, one of them (usually) lacking, arising slightly behind and mesad of 3rd prodorsal; 2nd prodorsal slightly laterad of (slightly mesad to-well laterad of) 3rd; the 4 prodorsals increase in size posteriorly, 4th prodorsal very long, reaching (nearly to-well beyond) areolae of dorsal setae *f*. VENTER—Internal ventrals II (about) twice as long as next longest pair (internal ventrals I) of anterior ventral plate.

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15. A few parallel wrinkles sometimes present.

HYSTEROSOMA—DORSUM—First hysterosomal plate broad, rounded posteriorly, setae variable in length and thickness; setae c_1 distinctly shorter than (to subequal to) c_2, lengths of both pairs variable; setae c_1 and c_2 arising in a transverse line; setae *d* reaching to base of ta IV (or at least to apical fourth of ti IV), 0. 75 (0. 5-0. 8) the length of the posterior prodorsal; setae *d* closer together than c_1, their areolae (usually) touching hind margin of plate; setae *f* subequal to c_2 (0. 7 length-nearly twice length of c_2); setae *e* relatively small, setose, arising well behind and barely laterad of setae *f*. VENTER—Apodemes III-V only weakly (or not) fused on each side; areolae of internal presternals on apodemes III, these setae very short, bristelike; external presternals longest setae of posterior ventral plate, nearly as long as distance between them (or, usually, distinctly shorter than this distance); external presternals arising well posterior to 1st axillaries; poststernals well behind and distinctly smaller than 2nd axillaries.

LEGS—Leg III, 72 (70-77) long; leg IV, 85 (83-87) long; leg II, 13 (13-17) wide; leg IV, 20 (19-22) wide. Ta I distinctly longer than wide; claw I small, arising from small, apicomesal pedicel; dorsal solenidium of ta I in middle of segment, moderately long, nearly rodlike, that of ta II slightly smaller, more clavate, in basal half of segment; fe III not arcuate; solenidium of ti IV rodlike, apicodorsal, in apical 1/4 of segment, reaching to base of claw IV; claw IV well-developed, relatively short, bulbose apically, (often) appearing to have an apical "cap"; inner, most apical seta of ta IV tiny, bristlelike (to subspinose); seta *c* of fe IV not (or barely) reaching claw IV.

HABITS—*P. emarginatus* is known only as a predator of the needle sheath midge *Contarinia* sp. (det. R. J. Gagné, Systematic Entomology Laboratory, USDA), which infests new growth of *Pinus taeda* L. The midge is always uncommon in normal forest stands, but may explode in numbers, apparently following spraying of foliage for seed and cone pests. One such outbreak occurred in 1972-74 at the Erambert Seed Orchard at New Augusta, Mississippi. Mites were found on two occasions feeding on midge larvae in August, 1973 and in September, 1975.

Because no midges were reared to adults and no adults were captured, phoresy was not observed. All progeny born to 10 "normal" females in the laboratory were "normal", i. e. , not phoretomorphs. Mated females fed readily on eggs, larvae, and pupae (preferred) of the southern pine beetle in the laboratory, suggesting that bark beetles, at least, may be an alternate host in the field. Alternate hosts may be essential to survival if the species is not phoretic. Unlike most species of the *ventricosus* group, females had little or no venom, single females taking 1-2 days to kill southern pine beetle larvae and pupae. Curiously, a yellow ring formed around the spot where females began to feed on pupae; the ring subsequently enlarged until the whole pupa became yellow in 24 hours , a phenomenon never observed in the feeding behavior of the other species of *Pyemotes* we have studied.

Of 10 fully-engorged females allowed to swell on pupae of the southern pine beetle, all began giving birth to progeny on the 10th day after feeding started. The birth sequence was typical for most *Pyemotes* . A male was always born first. He assisted in the birth of the females (born head first) and immediately mated with them. The average number of females born was 106 (extremes were 70 and 199), 64% of which were born by the 4th day. The average number of males was 3. 5 (extremes were 2 and 5); 51% were born on the first day. Birth persisted for an average of 12. 5 days (extremes were 7 and 20), the mother always dying from 2-9 days after the last individual was born.

DISTRIBUTION—Known only from the type locality.

TYPE MATERIAL—Holotype male, allotype female, female paratypes 1-6, and male paratypes 8-13 all from Erambert Seed Orchards, New Augusta, Mississippi, September, 1975. Female paratype 7, same data except collected August 20, 1973.

TYPE REPOSITORIES—Holotype, allotype, and paratypes 1-3, 8-9 and 13 to the U. S. National Museum. Paratypes 6 and 11 to the Snow Entomological Collection, The University of Kansas. Paratypes 7 and 12 in the collection of the senior author.

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