EVALUATION OF SEVERAL CHARACTERS BY WHICH FIVE SPECIES OF CHEYLETUS ARE DISTINGUISHED

(ACARINA: CHEYLETIDAE)

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ABSTRACT—Results of this investigation indicate that the distinguishing morphological characters or combinations of characters already attributed to five species of *Cheyletus* by their describers are trustworthy within satisfactory limits. In respect to measurement data, some of the items measured provided information useful for taxonomic judgments, others did not. A method was devised for tabulating the amount of overlap between the linear measurements obtained for each of several characters among five species when the species are compared two at a time. This procedure emphasizes the measurement data which give the clearest differentiation between species.

The observed frequencies with which various numbers of teeth occur on the claw and combs of the pedipalps show that these tooth counts are useful in species taxonomy. Attempts to distinguish species according to small differences in types of particular setae were virtually unprofitable—except that the general form of body and appendicular setae may be distinctive, as in *cacahuamilpensis*.

The character and distribution of dorsomedian setae provide satisfactory bases for species discrimination. The qualitative or quantitative variations observed among the dorsomedians of species which normally bear a complement of dorsomedian setae were not serious enough to impair the worth of judgments based on the features. Strangely, more variations in the pattern and dimensions of dorsomedian setae were encountered in the variants of *eruditus*, a species normally having no dorsomedian setae. In these cases, however, the kinds of dorsomedian setae found on the exceptional specimens were unique for the species; such variants were not confused with other species.

The rearing and examination of large numbers of individuals in clones and inbred cultures, have not produced atypical specimens which deviated seriously from the general range of fluctuating variations of their kind. No hybrids or off-type intermediates were observed. Instead of furnishing important new morphological criteria for separating species, the results of this investigation tend to affirm rather than to deprecate the worth of the features already in general use. Observations on mating, laying and nesting are reported briefly for one or another of the five species.

About ten years ago five species of *Cheyletus* were collected within a small area of the campus of the University of California at Davis. The specimens were taken from feed grain trash and vegetable matter in hay debris and manure scooped from the floors of various domestic animal barns and stock pens. The species of *Cheyletus* were: *C. eruditus* (Schrank), *C. malaccensis* Oudemans, *C. aversor* Rohdendorf,

C. cacahuamilpensis Baker, and *C. trouessarti* Oudemans. Samples collected from each kind of situation often yielded two species of *Cheyletus* in addition to species of other cheyletid genera, such as *Cheletomorpha* and *Acaropsella.*

Females of the five species of *Cheyletus* seemed to classify discretely, without confusing intermediate forms. Their distinguishing features are given in two recent publications (Volgin, 1969; Summers and Price, 1970). The characters by which they have been differentiated, although apparently serviceable for taxonomic purposes, are nevertheless minute, delicate and somewhat variable features. For example, the very tiny and hard-to-see dorsomedian setae are disposed differently or are absent on the different species. Among some of the more ornate species in other cheyletid genera, the dorsomedian setae are noticeably unstable in respect to number, location and, sometimes, conformation. One who copes with the differentiating characters described for *Cheyletus* species has to wonder about their reliability—whether all of the immediate descendants of an individual or a pair will classify as one species and not be confused with another. Since there appears to be some degree of intermingling of species within general habitats, is it possible that interspecific F_1 hybrids may appear (Edwards, in A. M. Hughes, 1960)? Another element of possible confusion may be introduced by the occurrence of two forms of males, homeomorphic and heteromorphic, as described for the ubiquitous species, *C. eruditus* (Hughes, 1960). What is their genetic or developmental significance in taxonomy?

In an effort to test the constancy or trustworthiness of the taxonomic characters already ascribed to the above-named species, the writers initiated the task of capturing live specimens of each one of these predaceous mites and rearing selected individuals and pairs under fairly constant, contrived conditions. The standardization of methods and materials ultimately proved to be less troublesome than the effort to capture and recognize living specimens of the mites.

The immediate objective of this study was to examine the currently recognized taxonomic features on significant numbers of these mites, to seek other criteria which may be useful for identifying species, and to record the kind or magnitude of deviations from the central tendencies of the populations observed. To this end, judgments on 40 possibly useful characters were made for samples of 100 slide-mounted females of each species; and many additional specimens reared from isolated pairs were examined for general conformity with our criteria of species. Involvement in a rearing program of the scope to be described inevitably has revealed other avenues of fruitful investigation; some of the side issues are reported here, others may be reported elsewhere.

Materials and Methods

Considerable information has been published about the relations of cheyletids to their prey organisms (Rodionov and Furman, 1940; Krantz, 1961; Soloman, 1962) and about the conditions under which the acarid prey organisms grow (Soloman, 1962; Sinha, 1962, 1968; Woodring, 1963). Thus the task of finding and rearing a suitable prey species did not entail much exploratory work. A good source of food organisms was found without much ado; this was a large sack of wheat bran stored in a cold room at 41°C, 70% RH. This material was heavily infested with *Acarus siro* Linn., *Glycyphagus destructor* (Schr.) and *G. domesticus* (DeG.), with the first species predominating. Although the preferences of these acarids for several other kinds of food were tested, as done by Radinovsky and Krantz (1961), the stock of *Acarus siro* growing on wheat bran was selected as a standard food supply for the cultures of *Cheyletus*. The cultures of food organisms and predators were incubated at 25°C and held within a humidity range of 80–85% RH. The culture vessels were stored on glass shelves in glass or plastic moist chambers the bottoms of which were flooded with saturated aqueous KCl.

The *Glycyphagus* species ultimately disappeared from the stock cultures of *Acarus siro* and, much later during the course of the work, another acarid, *Aleuroglyphus ovatus* (Troupeau), appeared and flourished in all of the laboratory stocks. The same food source, *Acarus siro* only, or *A. siro* and *Aleuroglyphus ovatus*, and the same procedures and culture vessels proved to be adequate for rearing each one of the five species of *Cheyletus*. The intrusion of *A. ovatus* in the food supply seems not to have had any noticeable effect on the vitality of the cultures as far as present purposes were concerned. The growth of the acarids was found to be appreciably stimulated when quick-cooking oat flakes were added to the bran, only a few flakes per culture tube.

Small mass cultures of acarids were reared in either of two kinds of containers. Most used were 4-oz screwcap glass baby food jars. One and one-quarter inch holes were punched in the metal screw-caps and bleached muslin was cemented over the openings. In practice, the jars were filled to half-volume with fresh bran, capped and preconditioned for about 24 hours in a humidifier before a substantial inoculum from an older culture was sifted in. Other mass cultures of acarids were cultivated in 100 × 100 × 15 mm square plastic Petri dishes. The venting tabs were trimmed from the bottom sections and the tops sealed on with 18 mm masking tape applied as circumferential strips. Insofar as the seals were nearly airtight, a small piece of wetted filter paper (about 1 × 2 cm) was included to boost the humidity of the enclosed air. Cobalt thiocyanate paper was used to monitor per cent R.H. where a rough check of the closed culture vessels was desired.

The Petri dish cultures were stackable and the condition of the acarids could be checked quickly with a dissecting microscope. Thriving mass cultures of the acarids were easy to produce but exceedingly difficult to keep confined.

Four types of containers were used for rearing *Cheyletus* species.

1. The supply stocks of different species were kept in the sealed square Petri dishes as described above. Some of these *Cheyletus* cultures survived long periods of neglect (5 months or more), depletion or disappearance of prey, and with humidities considerably lower than the optimum for *Acarus siro* (Solomon, 1962). Such stocks were refurbished or subcultured before mites were taken therefrom for experimental use.

2. Small "holding" cells were constructed by cementing 5 mm sections of thick-walled glass tubing (13 mm I.D.) onto molded flats of plaster of paris-charcoal mixture (Lipovsky, 1953). The plaster-charcoal slurries were cast in glazed ceramic dishes used for embedding tissues in paraffin. The upper, open ends of the cells were covered with 18 mm circular coverglasses "soldered" in place with paraffin. A pencil type of soldering iron was equipped with a slender screwdriver tip and dipped into a beaker of just-melted paraffin. A powerstat was used to reduce the temperature of the soldering iron to slightly exceed the melting point of the wax. Several touches of the iron to the margin of the coverglass usually sufficed to make a tight seal without overheating the glass cell. The breaking of the seal with a sliver of razor blade was troublesome and the covers often cracked. Small squares of thin plastic film were also used to cap the cells. The film was sealed onto the end of the cell with a very small amount of vaseline. This closure proved to be quite satisfactory when the amount of vaseline was properly adjusted.

The principal use of these small cells was to confine isolated pairs with a few food organisms so that the survival of both mates could be confirmed after a short period of exposure to each other. This was especially helpful when males were confined with female deutonymphs for the duration of the final molting period of the latter. The plaster flats bearing the cells were preconditioned in a moist chamber for at least 12 hours prior to use.

3. "Rearing" tubes were made of 18 mm O.D. pyrex glass tubing sawed into lengths of 60 mm. One end was closed with cigarette paper affixed with warm, dilute gelatin; a plastic snap-cap was used to close the other end of each tube. These tubes were used for rearing the progeny of isolated females and, sometimes, for starting cultures with selected pairs. Each tube was normally filled to about one-quarter of its volume with bran and acarids. Prepared tubes were stored horizontally on racks in moist chambers or placed upright with paper ends

down and resting on a wire grid. Although the parent cheyletids were not easily found in the mass of bran within the tubes, the finding of immature forms later sufficed to indicate survival of the female parent. The acarids sometimes multiplied to form dense masses which soon depleted the vegetable food supply after which they declined quickly. The heavy buildup may have affected the propagation of the cheyletids. When humidification failed, the prey organisms diminished quickly and additional bran and acarids had to be added. Increasing the volume of the bran added appreciably to the labor of harvesting the progeny of the selected cheyletids.

4. "Harvesting" cages were made of 50 × 10 mm circular, plastic Petri dishes. The venting tabs were trimmed from the edges of the bottom sections and the lids fastened down with 4 radial strips of narrow masking tape. The contents of the rearing tubes were transferred to these cages so that the progeny of the individuals originally isolated could be recovered and classified. The transfer of mites and food substrate from tubes to dishes could be done effectively by first dumping the bran and mites and then sharply tapping the up-ended tube with a pencil-like wand. The reverse transfer, dish to tube, was rarely done because some of the tiny immature cheyletids were usually lost or overlooked. Additional amounts of bran and acarids plus wetted paper strips were added at this time or at any time thereafter when unfavorable conditions prevailed.

Living specimens were recovered from bulk field samples with a Tullgren-type funnel extractor, and the extracted specimens were trapped on the surface of water or in a dry tube taped to the stem of the collecting funnel. Live or floating *Cheyletus* species were difficult to identify even when water-mounted specimens were temporarily immobilized with a coverglass. Female specimens suspected of being desired species were isolated in rearing tubes until F_1 female progeny matured and some of them sacrificed for specific determinations.

A routine was established for assessing the reproduction habits of each species. As soon as the first mass cultures permitted, approximately 20 rearing tubes were set up with one nymph each. Another 20 tubes were set up with one mature female each. If males were noticed in the stocks, an additional 20 cultures were established from attempted matings. One male and an active or a moulting deutonymph were caged together in small holding cells or sometimes seeded directly into prepared rearing tubes. The size of the nuptial cage—whether tube or cell—appeared not to affect the outcome of the mating attempt, but the use of the small cells for a short confinement gave a better check on the outcome of the final molt of the selected nymph. Much labor was expended in the setting up of intended matings because many of the isolated nymphs transformed into males instead of females.

At a much later date, the authors attempted to separate species in mass cultures of *C. malaccensis* (arrhenotokous) accidentally contaminated with *C. eruditus* (thelytokous) through the food supply. We noticed that the males of the former identified for us the moulting deutonymphs of its own species and, at the same time, the preoccupation of the males with only certain of the moulting deutonymphs identified these as females. Thereafter only such "identified" moulting forms of *malaccensis* were selected for mating trials.

Mature F_1 progeny from isolated individuals or from attempted intraspecific crosses were harvested by hand at irregular intervals between the third and fifth weeks or were harvested once with a Tullgren apparatus at the end of the fifth week. We believed that a growing period of five weeks yielded most of the brood of first generation adults without appreciable intrusion of mature individuals of a second generation. The estimate of five weeks was based on a 19 to 30 day cycle reported for *C. eruditus* (Beer and Dailey, 1956).

The progeny of attempted intraspecific crosses were sexed and counted but not minutely examined for phenotypic variations. In the case of attempted interspecific crosses, all individuals reared from each isolated pair, to a maximum sample of 20, were preserved and mounted for microscope examinations.

The length of leg I (Table 1) was measured as the distance between the coxo-trochanteral articulation and the tip of the tarsal claws. Tarsus I was measured from its proximal end to the distal face of the rounded elevation which bears the paired addorsal setae *tc'* and *tc''*. The mesal (paraxial) addorsal seta on tarsus I is noted as *Tc'* in Table 1. The gnathosoma was measured in the dorsal midline, from the arched apodeme which supports the hind margin of the stylophore to the apex of the rostrum. Macro. IV refers to the unusually long dorsolateral seta of tibia IV. In *cacahuamilpensis* the seta in this location is a short blade, not longer than its opposite companion. Post. Coxa I and Ant. Coxa III refer to lengths of the posterior or anterior setae on the coxae indicated.

Analysis of Taxonomic Characters

Forty characters were selected as possible criteria for distinguishing between the five species of *Cheyletus* available for study. Twenty of these were continuous variates selected to yield reasonably precise measurement data. For example, the distance between the two setae on the same sclerite could be determined to the accuracy limit of the micrometer whereas dimensions subject to severe parallax or distortion due to mounting were avoided. The other twenty characters were qualitative, some requiring judgment of degree or condition (e.g., form of setae), others were meristic or discontinuous variates (e.g., number of setae on podomeres).

Table 1. Means and standard deviations obtained for measurements of 20 characters in 5 species. Each mean represents 100 specimens. Two lots of *Cheyletus eruditus* were processed.

Characters	*eruditus* (lab. clone)	*eruditus* (wild)	*trouessarti*	*cacahuamil-pensis*	*malaccensis*	*aversor*	Mean Coef. Var.	LSD 1%
* Leg I	411.0 ± 19.4	417.4 ± 31.4	285.2 ± 26.6	277.2 ± 25.9	443.0 ± 32.1	365.4 ± 16.9	7.1	9.41
* Gnathosoma	189.3 ± 7.9	186.1 ± 14.8	141.0 ± 11.1	153.9 ± 9.3	207.9 ± 13.4	174.6 ± 8.1	6.2	4.03
* Tarsus I	115.0 ± 5.9	119.0 ± 7.3	88.3 ± 7.2	94.7 ± 6.3	136.3 ± 8.6	103.5 ± 4.8	6.2	3.11
Tibia I	87.2 ± 5.2	89.7 ± 9.0	54.1 ± 6.2	41.8 ± 4.0	92.9 ± 8.8	66.1 ± 3.8	8.7	
Sol. *w* I	26.0 ± 2.3	27.2 ± 3.0	16.5 ± 1.5	12.7 ± 1.8	23.6 ± 2.0	26.7 ± 2.7	10.3	
* Guard Seta	—	—	35.9 ± 3.8	59.2 ± 3.8	—	50.3 ± 3.8	8.2	2.23
* Ve	70.6 ± 4.8	68.9 ± 6.7	49.7 ± 4.7	45.3 ± 3.2	73.6 ± 7.3	60.8 ± 4.9	8.5	2.28
* Ve-Ve	130.7 ± 7.5	130.2 ± 12.9	94.8 ± 9.4	111.0 ± 10.9	181.0 ± 16.7	129.7 ± 8.4	8.5	3.44
Dl4	67.6 ± 5.0	65.3 ± 6.6	41.7 ± 3.9	41.2 ± 3.8	74.1 ± 7.7	60.2 ± 4.8	9.0	
Dl6	66.0 ± 4.6	62.0 ± 5.9	41.2 ± 4.4	39.4 ± 3.6	82.2 ± 8.5	66.4 ± 5.5	9.2	
* *Dl6-Dl6*	158.3 ± 9.1	150.7 ± 16.3	123.6 ± 17.0	141.5 ± 17.0	172.0 ± 14.7	142.6 ± 10.8	9.8	5.25
Dl6-Dl7	92.3 ± 5.5	91.9 ± 7.2	64.1 ± 9.6	58.3 ± 8.8	103.1 ± 9.4	77.2 ± 7.9	10.5	
Subcap.—Subcap.	69.4 ± 3.4	71.7 ± 6.1	50.3 ± 5.8	49.1 ± 4.5	63.8 ± 4.5	65.5 ± 4.1	7.9	
D.Plp.Fem.Seta	136.8 ± 7.2	134.9 ± 12.4	90.8 ± 8.3	47.8 ± 3.4	156.8 ± 13.3	109.7 ± 7.6	7.7	
D.Plp.Gen.Seta	89.3 ± 5.0	92.6 ± 9.9	61.7 ± 6.4	41.6 ± 3.5	103.3 ± 7.9	82.8 ± 5.8	8.3	
Humeral Seta	140.9 ± 8.1	144.4 ± 13.2	68.5 ± 7.4	48.2 ± 3.9	147.1 ± 21.0	100.2 ± 7.8	9.3	
* Macro. IV	141.6 ± 8.3	157.3 ± 16.0	84.6 ± 9.7	—	176.1 ± 13.7	106.4 ± 8.4	8.6	4.18
Post. Coxa I	88.5 ± 6.1	87.9 ± 8.8	61.3 ± 7.2	65.5 ± 6.6	104.9 ± 8.9	83.4 ± 5.7	9.0	
Ant. Coxa III	57.8 ± 3.6	60.0 ± 5.1	40.7 ± 6.0	35.4 ± 3.4	62.4 ± 6.4	52.5 ± 4.7	9.7	
Tc′ I	126.0 ± 6.7	127.0 ± 8.8	86.5 ± 8.6	75.3 ± 6.8	128.0 ± 8.6	93.2 ± 6.2	7.4	
Mean for Coef. of Variation	6.0	9.1	10.7	8.8	8.8	8.6		

Table 2. Comparisons of different combinations of five species in per cent overlap for measurements of eight characters.

Characters	1	2	3	4	5	6	7	8
	Lengths						Distances	
Species	Macro-Seta IV	Leg I	Tarsus I	Guard Seta	Gnatho-soma	*ve*	*ve-ve*	*dl6-dl6*
malaccensis	0	0	1		0	12	0	12
trouessarti	† 0	† 0	† 1		† 0	25	† 0	28
cacahuamil.		0	0		0	1	3	61
malaccensis		† 0	† 0		† 0	† 3	6	65
trouessarti	1	3	14		39	51	37	55
eruditus	† 1	† 3	30		18	26	14	77
malaccensis	0	11	1		16	36	6	53
aversor	† 0	61	† 5		65	96	53	75
cacahuamil.		0	41		78	8	82	93
eruditus		† 0	4		27	3	61	98
cacahuamil.		97	93	0	99	99	62	72
trouessarti		97	97	† 0	92	94	90	87
aversor	34	28	47	14	26	77	7	99
trouessarti	51	5	27	10	13	51	2	57
cacahuamil.		1	69	82	54	8	38	93
aversor		6	72	58	33	21	69	100
malaccensis	97	93	57		72	95	8	94
eruditus	91	97	86		74	99	59	81
aversor	14	85	94		100	100	100	100
eruditus	6	30	29		57	61	98	95

† Used to mark couplets in which neither value exceeds 5%.

Each of the 40 characters were examined on 100 specimens of each species. Items occasionally missing on one specimen were supplied from spare specimens or from the opposite (spare) side of the next specimen processed.

The use of laboratory-reared specimens was inimical to the purpose of this phase of the study because interest was focused on variations within species rather than within clones or families. Unfortunately, series from samplings of numerous localities in California were available only for *eruditus* and *trouessarti;* otherwise the scarcity of "wild" individuals required that the sample of 100 species be reared from one or a few wild specimens, or that all of the wild individuals be recovered from bulk material obtained in one or two locations. All of our data, therefore have the limitation of representing somewhat related clones or inbred families of each species rather than representing species in their broadest sense.

A. Continuous Variates.

The means and standard deviations for measurements of lengths or distances between two parts are given for 6 lots of 100 specimens each (Table 1). Coefficients of variation were calculated for the pairs of parameters (Mean ± Std. Dev.) and averaged for columns (species) and rows (characters). The individual coefficients are omitted from the table.

Eight of the 20 characters were subsequently judged to be more useful for taxonomic purposes (marked *) than the others and these were further analyzed for least significant difference (L.S.D.) values. Two lots of *eruditus* were processed. One lot comprised a clone reared in our laboratory (lab. clone) and included only females of four consecutive generations. The other lot of 100 specimens (wild) included females taken from at least 20 localities scattered throughout Northern California.

Although only small differences between the means of comparable measurements for the several species are required for statistical significance, the data of Table 1 are difficult to assimilate for taxonomic judgments. The means and deviations are probably more useful for comparing samples of populations within species whereas estimates of degree of overlap may better indicate the worth of such data for discriminating species. In an effort to reveal more clearly the utility of these measurements in taxonomy, a different presentation of the same data was devised. In Table 2, the amount of overlap in measurements is shown in per cent for the ten dissimilar combinations of five species taken two at a time. The lab-reared clone of *eruditus* was omitted from these comparisons. Each separate value in the table represents the frequency with which the measurements of a structure on one species lie within the observed range of the corresponding structure on another species. For example (Table 2, upper right), 12 per cent of the measurements of distances between setae of the pair *dl*6 on *malaccensis* overlap 28 per cent of the corresponding measurements on *trouessarti*. These percentages of overlap were obtained from frequency distributions of each character plotted over a common base line for each of the five species, approximately as done in Tables 3 and 4. The numbers are percentages because the sample size was 100 in each case.

In respect to most structural features, *trouessarti* is the smallest species in this series and *cacahuamilpensis* is but slightly larger; the largest of the five is *malaccensis*. Table 2 shows that some of the quantitative characters observed do not overlap when large and small species are compared (e.g., *trouessarti* vs. *malaccensis*) whereas species similar in general body size tend to show great overlapping in linear dimensions of various parts (e.g., *trouessarti* vs. *cacahuamilpensis*, or *aversor*

vs. *eruditus*). If some arbitrary value is fixed as a level of tolerance for overlap, then it is easier to identify some quantitative characters as more serviceable than others for species identification. If the tolerance for overlap is limited to 5% or less for either value of a couplet the possibilities for distinguishing between species in each couplet according to several characters (rows), or the usefulness of each character for distinguishing several couplets of species (columns) can be roughly quantified.

Table 2 is arranged to show these discriminating critera in approximate diminishing order of value reading down and left to right. It therefore appears that, according to the samples tested, characters 1–4 should be of greater service in specific descriptions than others included in the table. A character such as the distance between setae *dl*6 and *dl*6 (Fig. 1) can be measured with precision but the information would be of dubious assistance when comparisons are being made between a few specimens.

The coefficients of variation averaged for species and characters (Table 1) appear to demonstrate several other tendencies of the samples observed. The means of the coefficients for 20 items (Mean ± Std. Dev.) in each column differ little between species. There is. however a large difference in these means for the two lots of *eruditus*. The mean C.V. of 6.0% for the reared clone versus 9.1% for the lot of wild specimens, indicates greater uniformity among the 100 individuals of the reared clone. The coefficients computed for items in the column for the lab-reared clone were consistently smaller than the coefficients (not shown) for the corresponding items obtained for the lot of wild specimens.

The coefficients averaged for rows appear to show that deviations observed for measurements of length of certain setae—verticals (*ve*) and second dorsolateral hysterosomals (*dl*6)—are not appreciably smaller than the coefficients averaged for distances separating the setae of each of these pairs (*ve-ve* on the propodosomal and *dl*6-*dl*6 on the hysterosomal plate). In other words, the amount of stretch between pairs of alveoli on each of these plates attributable to pressures of mounting appears to introduce no unusual source of variation. The greatest average coefficient was obtained for measurements of distance between setae *dl*6-*dl*7 on one or the other sides of the hysterosomal plate. This variability is probably related to developmental anomaly because *dl*7 is frequently not set opposite its mate.

B. Qualitative Characters.

The frequencies of variation—any noteworthy deviation from normal—among 20 qualitative or meristic characters are summarized in Tables 3–5 inclusive.

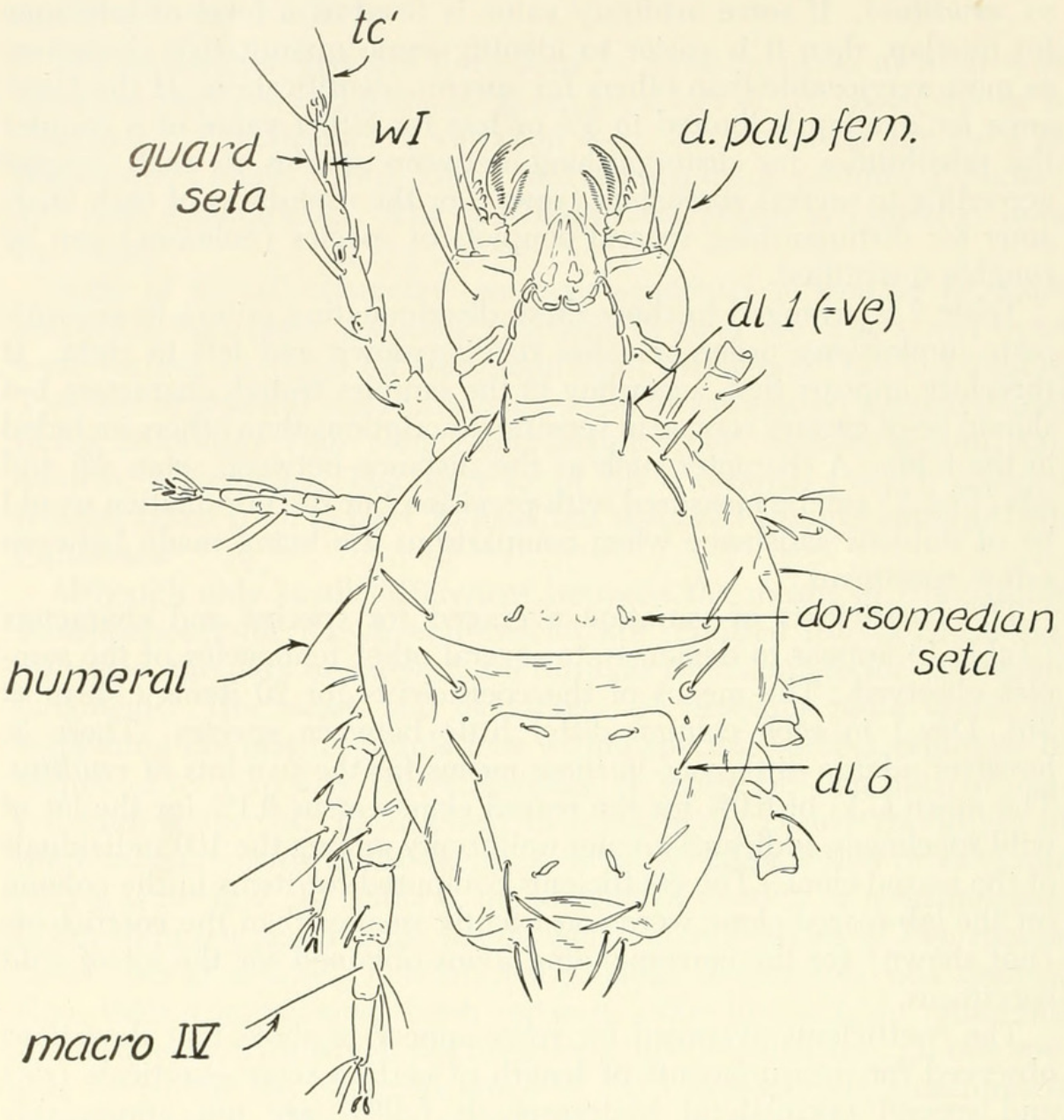

Fig. 1. Female of *Cheyletus trouessarti* Oud. Most of the dorsal setae mentioned in the text are labeled on the drawing.

The number of teeth on the base of the palp claw gives a tentative identification only of *trouessarti* (Table 3). The modal number of teeth on the claw of this species is 3. The teeth, or cusps, are very nearly equal (isodont). The other four species are not separable according to number of these teeth. The coalescence of the several basal teeth into one large apophysis occurs so rarely among these five species that the single apophysis on the palp claw of *fortis* Ouds. may be a reliable spot character on that species.

The form of the teeth on the palp claw (Fig. 2) gives an identifier important assistance in distinguishing *eruditus* from *malaccensis*, *cacahuamilpensis* and *aversor*. In the first species, the cusps are con-

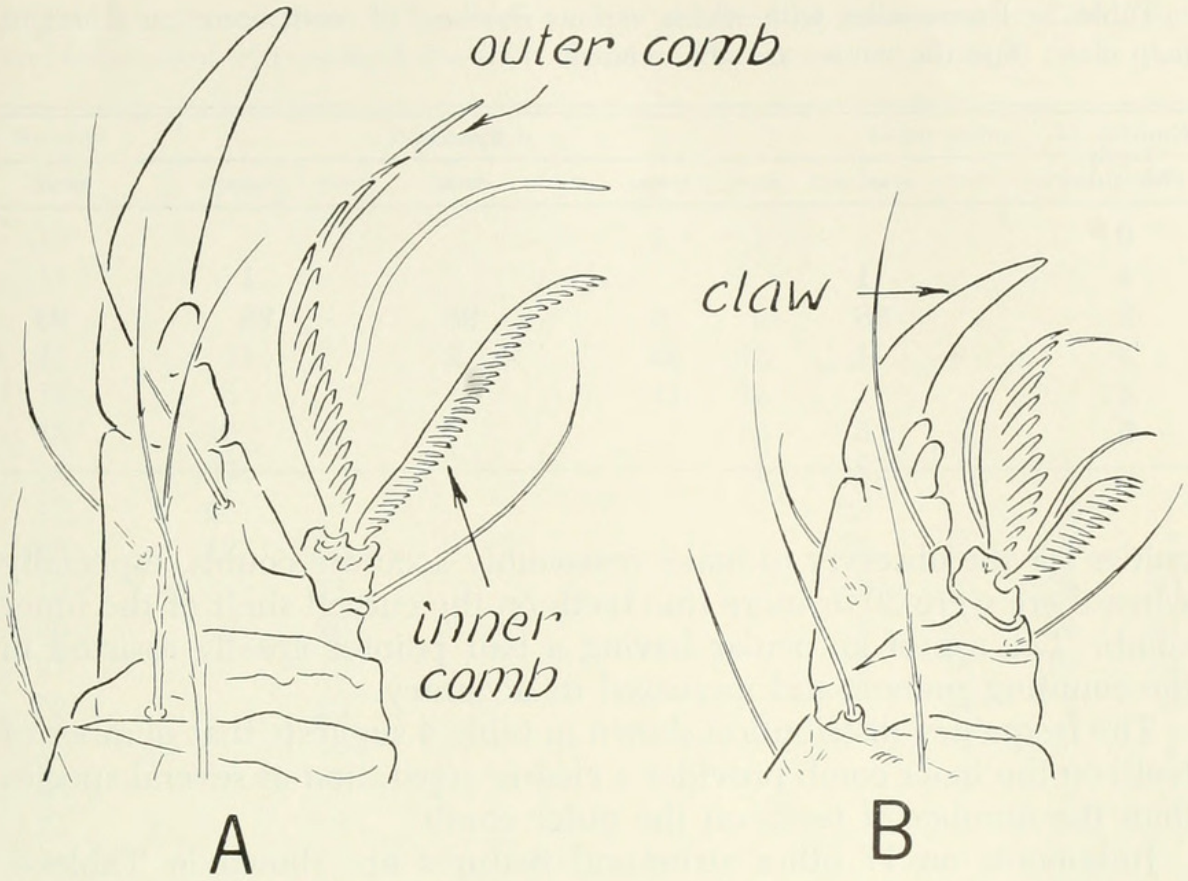

Fig. 2. Illustration of the terminal segments of the palps of *Cheyletus malaccensis* Oud. (A) and *C. eruditus* (Sch.) (B) to show shapes of the teeth on the tibial claws.

ical, very nearly alike in size and their long axes are almost parallel. In the others the two basal teeth are dissimilar, one is conical, the other flat-sided. A common deviation is incompletely separated teeth—*eruditus* (5%), *cacahuamilpensis* (5%), *malaccensis* (18%) and *aversor* (1%). In such instances the basal excrescence of the claw is a sort of dental ridge having a faint notch approximately in its midregion. In many specimens of *malaccensis*, *cacahuamilpensis* and *aversor*, the basalmost cusp appears to be flat-sided when viewed in one plane but it appears to be conical when viewed from another. It is appressed tightly against distal tooth so that the axes of the two lie in different planes. The appearance of the flattened tooth cannot be relied upon to differentiate *malaccensis* from *cacahuamilpensis* and *aversor*.

The numbers of teeth (or tines) on the inner and outer comb-like setae on 100 specimens of each of the 5 species are given in table 4. Of this group, only *eruditus* has both combs with relatively few, coarse teeth. The teeth on both sensilla may be counted with relative ease. In 5% of the *eruditus* individuals observed, the inner comb possessed 1 to 4 additional spurious teeth on its off side (bipectinate). The larger number of teeth on the combs of the other species created diffi-

Table 3. Frequencies with which various numbers of teeth occur on the right palp claw. Specific names are abbreviated.

Number of Teeth (Rt. side)	Species				
	erud.	*trou.*	*caca.*	*mala.*	*aver.*
0		1			
1	1			1	
2	98	6	98	98	95
3	1	82	2	1	5
4		11			
5					

culties for the observer to make reasonably accurate counts, especially when there were 30 or more fine teeth on the curved shaft of the inner comb. The use of an ocular having a hair pointer greatly assisted in the counting process and increased its accuracy.

The frequency distribution shown in table 4 suggests that number of teeth on the inner comb provides a clearer separation of several species than the number of teeth on the outer comb.

Judgments on 17 other structural features are shown in Table 5. Some of the features selected for observation seem to have no evident worth for distinguishing these particular species. Several of the characters proved to be stable or uniform within the range of species studied (Nos. 1, 7, 8). For example, the four pairs of dorsolateral setae on the propodosomal plate (No. 1) deviated from the common condition only three times in 500 observations. Another stable character, the disposition of dorsolateral setae on the hysterosomal plate, assuredly distinguishes *cacahuamilpensis* (No. 17). Setae of the fifth pair of dorsolaterals are set on the hysterosomal plate only in this species; this pair of setae is interscutal in the other four species. The numbers of dorsolaterals on the hysterosomal plate are shown to be highly variable because the hindmost one or two pairs—mostly the 8th pair—show many irregularities in location, and the posterior portion of this plate is frequently deficient on one side or both.

The numbers, kinds and disposition of dorsomedian setae have critical value in species recognition. Lack of dorsomedian setae heretofore has been thought to be characteristic of *eruditus* and *malaccensis*. No exceptions have been noticed in our samples of *malaccensis*. However, this character is now known to vary appreciably in *eruditus*; superfluous dorsomedians occur on both plates and even between the plates (interscutal). The superfluous dorsomedians do not really confound the matter of identification because, when they occur, their structure is peculiar to the species. They are acicular, smooth and small, sometimes so minute that they are classifiable as microsetae; they are also

Table 4. Frequencies with which various numbers of teeth occur on the inner and outer comb-like setae of the palp tarsus.

Number of Teeth	Inner comb					Outer comb				
	erud.	* *trou.*	*caca.*	*mala.*	*aver.*	*erud.*	*trou.*	*caca.*	*mala.*	*aver.*
10						1				
11										
12						6				
13	3					37				
14	5					42	1			
15	19					13	5	1		
16	33					1	18	1	1	
17	26						23		9	7
18	12	4					25	14	29	7
19		11					22	30	28	30
20	2	20					4	27	19	30
21		18					2	18	10	19
22		23						4	4	6
23		13						4		1
24		7						1		
25		2		2	2					
26				13	9					
27		1		21	21					
28			1	24	18					
29			3	16	21					
30			7	11	14					
31			9	7	7					
32			16	5	3					
33			29	1	3					
34			14		2					
35			8							
36			7							
37			5							
38			1							

*/ n = 99

unpredictable as to symmetry of position on the body. Records from some of the attempts to breed *eruditus* suggest that a certain complement of dorsomedian setae is inherent in the genetic organization of each species but the genic control over phenotype somehow varies during the final molt of females so that superfluous setae or deficient pairs occasionally appear.

Another noteworthy phenomenon was encountered in *aversor*. The female of this species normally has two pairs of very small, saccular dorsomedians, one pair on the propodosomal, another on the interscutal membrane in front of the hysterosomal plate. The deviations in num-

Table 5. Results recorded for judgments made on several kinds of characters selected for possible use in identifications. The quality norm for each character is indicated and the number of deviations per 100 specimens is shown in parentheses.

Characters			*erud.*		*trou.*		*caca.*		*mala.*		*aver.*	
1		Laterals on propodo. pl.	four	(0)	four	(0)	four	(0)	four	(2)	four	(1)
2	Number of dorsal setae	Laterals on hystero. pl.	three	(29)	three	(4)	four	(5)	three	(3)	three	(11)
3	(pairs)	Medians on propodo. pl.	zero	(11)	one	(1)	one	(1)	zero	(0)	one	(8)
4		Medians on hystero. pl.	zero	(2)	two	(6)	one	(1)	zero	(0)	zero	(2)
5		Medians interscutal	zero	(1)	zero	(2)	zero	(0)	zero	(0)	one	(3)
6	Number	On femora I–IV	2222	(1)	2221	(2)	2221	(3)	2221	(1)	2221	(1)
7	of leg	On genua I–IV	3222	(2)	3222	(4)	3222	(1)	3222	(1)	3222	(2)
8	setae	On tibiae I–IV	6444	(3)	6444	(2)	6444	(1)	6444	(0)	6444	(0)
9		Dorsolat. No. 1 (*ve*)	C	(0)	D	(20)	D	(0)	C	(0)	C	(0)
10	Types	Dorsolat. No. 4	C	(0)	D	(17)	D	(0)	C	(0)	C	(0)
11		Dorsolat. No. 5	C	(0)	D	(16)	D	(0)	C	(0)	C	(1)
12	of	Humeral	B	(0)	C	(35)	D	(0)	B	(29)	D	(0)
13		Macroseta IV	B	(0)	B	(0)	—		B	(0)	B	(0)
14	setae	Ant. s. of coxa III	B	(0)	B	(0)	C	(0)	B	(0)	B	(0)
15		Dors. s. of palp femur	B	(0)	B	(0)	C	(8)	B	(0)	B	(0)
16	Guard seta shorter (s) or longer (l) than *w* I		s	(0)	l	(0)	l	(0)	s	(0)	l	(0)
17	Location of dorsolat. No. 5—on/off hystero. plate		off	(0)	off	(0)	on	(0)	off	(0)	off	(0)

ber of dorsomedian setae in *aversor*, as indicated in table 5 (Nos. 3, 5), represent unilateral deficiencies of one side or the other. The form of the dorsomedians in *aversor* presents an interesting aspect of its chaetotaxy. In numerous other cheyletid genera, the form of the dorsomedians is sex-linked. All of the dorsomedians of males and all juveniles are indistinguishable structurally from their neighboring dorsolaterals. The dorsomedians of females in these genera are transformed into aberrant or peculiar setae during the final molt. In females of *aversor* these setae may or may not become aberrant; those which change become small and saccular. The dorsomedians of *aversor* females may show aberrancy (27%) or orthodoxy (73%) for both pairs. In only one specimen (1%), the individual setae of the pair of interscutals were heteromorphic, one orthodox and one aberrant.

The numbers of setae on three segments of legs I–IV do not vary sufficiently to confuse species identification (Table 5, Nos. 6, 7, 8). On the other hand, among the five species examined, only femur IV of *eruditus* females provides a differentiating feature. An interesting point arises in this connection. Oudemans (1906) and Hughes (1961) described males of *eruditus* from European localities. But no males of this species have been reported in North America (Beer and Dailey, 1956; Summers and Price, 1970). We suppose that wherever males of *eruditus* occur, their femora IV should bear two setae. The present descriptions of *eruditus* males do not cover this point.

The types of setae located on various parts of the body (Table 5, Nos. 9–15 incl.) seem to provide no novel or useful criteria. Small deviations from the normal types are not discernible or they are too subjective to be reliable. Also, the amount of rotation or angle of view seriously affects judgments of fine differences between lanceolate and narrow spatulate classes. The attempted classification of unspecialized setae encountered within this group of species was as follows: A = acicular, smooth; B = acicular, barbed; C = lanceolate, narrow, fringed; D = spatulate, fringed, with 1–3 barbed ribs on blade.

Character No. 16, guard seta longer (l) or shorter (s) than solenidion *w* on tarsus I, is most helpful and definitive for the species in question because judgments are easily made; the guard seta either is much longer or much shorter. Other species intermediate in this respect could introduce complications in this judgment.

Observations on Reproduction

1. Parthenogenesis and Sex Ratios.

The intended program of experimentation with intraspecific and interspecific mating trials was considerably disrupted when the nature of reproduction by each species became clear. All five species are parthenogenetic. Two of them, *eruditus* and *aversor*, are thelytokous

types and the strains dealt with developed no males. We have reared very large numbers of *eruditus* from juveniles and females under a wide range of conditions and have not encountered males. Beer and Dailey (1956) also reared clones of this species and found no males. We have not discovered males of *eruditus* or *aversor* among numerous cheyletid samples collected in Northern California.

Females of *aversor* were easy to transfer and their growth requirement presented no special problems. Since all individuals became females and produced only females, we merely seeded 45 isolation cultures with stock females and counted the number of mature daughters harvested on or close to the 35th day in isolation. The 45 females produced 1,633 daughters or 36.3 mature progeny per mother.

Cheyletus cacahuamilpensis also proved to be thelytokous but the strain propagated did produce males. It had a peculiarity in its sexuality, however. As far as known, the strain reared in our laboratory was propagated from a single wild female. The first stock cultures had males but these were notably few in number. It seems probable, therefore, that she had previously mated. Mature F_1 progeny were counted and sexed for 69 isolation cultures established to provide information about the sex ratios. Eleven of the cultures were seeded with nymphal stadia, 34 were seeded with females picked randomly from mass cultures and 24 were started with confirmed pairs. The latter averaged 21.9 matured, progeny per parent. Matured progeny harvested from the isolated pairs comprised females only, and the assumption is that there was no functional mating. Male progeny appeared in only two of the 69 cultures, both of which had been seeded with females picked from general stocks. The peculiarity is the fact that the male-producing females produced males only, 21 males by one parent, 31 males by the other.

The taking of males for mating attempts somewhat depleted the population of males in the stocks of *cacahuamilpensis*. Since we failed to breed males intentionally, the male line became depleted and was eventually lost. The stocks then became clones of thelytokous females.

It has been noted in phytoseiids that conspicuous absence of males may characterize highly inbred lines (Poe and Enns, 1970). The duration of the period of inbreeding of our strain of *cacahuamilpensis* was probably not more than six months, time enough for a few generations only. This cheyletid is thelytokous and it could be possible, though not established, that its males may not be haploid.

Routine rearings of isolated individuals and pairs of *trouessarti* and *malaccensis* clearly established that these are arrhenotokous species having plentiful males. The bisexual condition of their colonies was easily maintained in laboratory stocks.

Although numerous juveniles of *trouessarti* were isolated in culture

vessels, only eight of these survived to maturity and became reproducing virgin mothers. These produced only males; 136 males were harvested from these isolates. Two cultures, each initially containing a proved pair yielded 23 progeny, 9 males, 14 females. The term "proved" pair is employed to indicate that an isolated deutonymph is known to have transformed into a female in the presence of an active male. Forty-four females picked at random from mass cultures and reared in isolation tubes produced offspring of both sexes. Males only were produced by 11 of these 44 females; these were presumed to have been virginal when isolated. The other 33 isolated females produced F_1 progeny of both sexes, 233 males, 402 females. At this stage of technical capability in the rearing operations, the conditions of the cultures were somewhat erratic and many of the offspring were victims of cannibalism. Possibly the real reproductive capability of *trouessarti* exceeds that which was demonstrated.

In the case of *malaccensis*, one group of 20 isolated deutonymphs became reproducing females and these gave rise to males only. This group of females produced 213 males. Twenty-one cultures started with mature females randomly selected from stocks produced 487 progeny harvested as adults, 130 males, 357 females. All of these 21 females reproduced. Twenty-two cultures seeded with proved pairs yielded 572 progeny, 200 males, 372 females. Six of the isolated pairs failed to reproduce. More progeny were harvested from this group of 16 cultures than were taken from cultures initially established with females picked randomly from stocks. The latter probably included older, partly expended individuals. The mated females of *malaccensis*, like those of *trouessarti*, tended to weight the sex ratio appreciably in favor of females. How the sex ratio may have been affected by cannibalism or by the restricted period of the harvesting is not known at present. In all of our culture vessels, the number of eggs observed has greatly exceeded the number of mature progeny harvested later.

2. The Mating Process.

Deutonymphs of presumptive opposite sexes are not easily distinguished by their gross features and apparently identifiable associations between them have not been noticed—except when one feeds upon the other. Males begin to attend molting deutonymphs destined to become females shortly after the onset of the final quiescent period. One male usually becomes the dominant suitor and, having established an enduring association, hovers about, mostly in contact with the transforming nymph. The portent of approaching ecdysis is an increased mobility of the male. He quickens his assiduous ministrations—the moving of her body or legs, palpations and even possibly the puncturing of her integument with his stylets, until her exuviae is shed.

Very soon thereafter he backs beneath the front part of her somewhat elevated body and copulation ensues, with female over male in a rear to rear posture. When the mates separate, the constancy of the association is broken and mates no longer can be identified as such. This account of copulation conforms closely with Robertson's (1952) description of the process in *eruditus* and with the description of mating given by Beer and Dailey (1956) for the species which they named *Cheletophyes knowltoni.*

3. Conditions for Mating.

It has been possible to investigate only a few of the factors involved in the breeding processes of *malaccensis.* One question concerned the size of the vessel within which potential mates were confined. It is our common experience that the probability of fruitful matings was not perceptibly affected by our choice of the kind of isolation culture vessels employed or, within reasonable limits, by the quantity of prey mites present at the critical time of mating. The confinement of a moulting nymph and the male within a small "holding" cell did not increase the number of successful matings as compared with pairs seeded into the larger vessels having greater numbers of acarids and more of their cereal food materials.

Twenty-two cultures with proved pairs were set up in vial-like rearing tubes and their mature progeny harvested 30 days later. Sixteen of these females mated successfully and produced F_1 progeny of two sexes—about 72% mating—and six produced only males. Another lot comprising 20 cultures was set up with one moulting nymph (potential female) and 10 males per vessel. Only 60% of these virgins mated and produced progeny of both sexes; the unsuccessful cultures contained only a few hold-over males but no females. Our attempts to mate couples or to mate virgin females by confining them with several males have demonstrated that mating is difficult to induce or control in captive populations.

Gravid or ovipositing females (virgin or mated) of *malaccensis, aversor, cacahuamilpensis* and *eruditus* exhibit a kind of nesting behavior, protecting their nests or broods of eggs against other encroaching mites, including males of their own kind. They may therefore repel all potential mates for the duration of the brooding periods or, possibly, for the entire period of oviposition.

Evidence from trials with *malaccensis* suggests that successful matings in this species occur very soon after the female deutonymph molts but less frequently thereafter. In one battery of tests, virgin females reared from isolated deutonymphs were exposed to males at various intervals after they attained adulthood. Two males were placed with virgin females 2, 4, 6, 8 and 14 days of age. In the trials with younger virgins,

2–8 days inclusive, the males were allowed to remain with the females for 2 days only after which they were removed from the nuptial cages. There were 10 replicates for each age to 8 days and 25 replicates for the 14-day isolates. In the final series, the isolated females were transferred at 7-day intervals to new cages with new food in order to cast off their own male progeny prior to the actual mating attempts. Two strange males were introduced when the females were transferred on the 14th day. In this series, the numbers of progeny produced before and after the introduction of males were recorded. Most of the progeny were produced from eggs laid before the 14th day (288 males harvested) and only a few were produced from eggs laid after males were introduced (46 males harvested). Female progeny appeared in only one of the 65 culture vessels; culture #3 among the 4-day isolates yielded 44 males and 2 females other than the mother mite. Otherwise there were no other indications of mating among virgins 2 days of age or older. The 64 other females produced male progeny exclusively.

The question of whether mating may occur much later than the teneral period was approached in a different way. Isolated virgin females were confined for long periods with their accumulated male progeny. Thirty-five such cultures were set up and inspected regularly for periods ranging to 81 days. Most of the cultures developed only males and then died out. However, 12 of the isolated females ultimately produced daughters; these cultures were discarded when at least four females were found. That approximately one-third of the females appeared to have mated with their sons late in the reproductive period may relate to the intermittency of brooding. Females may lose their broodiness and accept males in the brief intervals between oviposition cycles.

4. Oviposition.

As mentioned before, females of the species *eruditus*, *aversor*, *cacahuamilpensis* and *malaccensis* exhibit pronounced nesting habits. The progeny of *eruditus* are especially difficult to harvest from cultures containing bran flakes because the young brooding or laying females secrete themselves within the rolled or cupped flakes. They do not move about freely on the walls of the containers and they are quite difficult to dislodge from their nests. The nesting species accumulate sizeable clutches of eggs on which they perch. Invaders are attacked by the nesting mothers. A few strands of silk have been observed only in the nests of *eruditus*.

C. trouessarti does not seem to deposit eggs in obvious clusters. It was necessary to isolate and hatch some of the eggs of this species in order to demonstrate that its females are oviparous. In thriving cultures the eggs of the acarids complicate the matter of identifying those of the predator.

A special study of oviposition was made for *malaccensis*. In this study, 30 females were reared to maturity in isolation cultures and their production of unfertilized eggs recorded daily for the first 11 days of adulthood. The nests were removed daily from each culture vessel so that yields could be determined. It is probable that the taking of the nests each day affected to some extent the progress of oviposition. All of these females reproduced. First eggs were laid on the second to sixth days, with 23 individuals beginning to lay on the third or fourth days. This lot of virgin females averaged slightly more than 19 eggs on the initial laying day and 5 females actually laid 50 eggs on the first day of the laying period. They averaged 83.7 eggs during the first 11 days of adult life.

A second series of 22 isolates was established to estimate total egg production and to provide information about the duration and intermittency of laying. These females were virginal and their nests were taken daily for the first 15 days and thereafter only when sizeable lots of eggs appeared. One of these females was unproductive; she died on the 11th day. The remaining 21 females average 133.1 eggs during their laying periods.

Twenty of the females survived at least 38 days and 8 survived 48 days. Oviposition peaked on the fifth day and approximately 75% of the eggs were deposited during the first 15 days. Individual protocols showed that laying was intermittent, one large burst of ovipositional activity followed by 2 to 3 minor flurries at variably spaced intervals, the last of which ended on the 40th day. Insofar as the females were virgins and their nests were repeatedly taken, we do not know how the eggs would have been laid under undisturbed circumstances or in the presence of males.

5. Attempts to Cross Species.

Attempts to produce interspecific F_1 hybrids were begun when laboratory stocks included but three species: *eruditus*, *trouessarti* and *cacahuamilpensis*. The only males in good supply were those of *trouessarti*. At this stage of the operation, many attempted matings aborted because some of the molting deutonymphs isolated and placed with males transformed into males. Without relevant genetic or cytological information with which to anticipate outcome, we attempted to mate the males of an arrhenotokous species (*trouessarti*) with females of thelytokous species (*eruditus*, *cacahuamilpensis*).

Fifty-five culture tubes containing proved couples of *eruditus* females × *trouessarti* males produced 351 matured progeny, all parthenogenetically generated females of *eruditus*. These were mounted in Hoyer's fluid and individually examined. In similar fashion, 46 culture tubes containing proved couples of *cacahuamilpensis* females ×

trouessarti males were established. Many of these failed to reproduce; 21 females produced 241 matured progeny. All were mounted and judged to be parthenogenetically produced females of *cacahuamilpensis*.

Later on, attempts were made to obtain F_1 hybrids from the two arrhenotokous species, *malaccensis* females × *trouessarti* males and *trouessarti* females × *malaccensis* males. Only male progeny were harvested from 20 proved couples of the attempted crossing of the first combination. All of these females reproduced; 376 *malaccensis* males were harvested from the cultures. Thirty-seven attempts to test the reciprocal cross, *trouessarti* females × *malaccensis* males, aborted because moulting deutonymphs or young virgin females of *trouessarti* were attacked or devoured by the much larger males of *malaccensis*.

The 121 attempts to cross species produced no evidence of hybridization in respect to morphology or change in the sex ratios of the progeny examined. In virtue of the reluctance of *Cheyletus* females to accept mates, at least when reared in captivity, the issue of whether interspecific F_1 hybrids occur is not clearly resolved by these trials.

One noteworthy phenomenon was recorded for some of the progeny generated in attempted matings of *eruditus* females × *trouessarti* males. Systematists have described *eruditus* females as having no dorsomedian setae. Actually a small percentage of them do have one or more pairs of inconspicuous dorsomedians (Table 5). A few of the females used in the attempted interspecific matings gave progeny having one or more pairs of dorsomedian setae. In two cases out of 55 observations, the daughters from each of the two mothers varied in this respect, some daughters of each one showed dorsomedian setae in several patterns whereas other daughters had no dorsomedians. In a third case, an *eruditus* mother produced 15 daughters all having dorsomedian setae among which there were 15 variations in the numbers and symmetry of the scutal or interscutal setae. Otherwise, however, the daughters were indistinguishable from *eruditus* females generally. The dorsomedian setae, when present were also observed to vary in size, from mere dots in the center of alveoli to substantial acicular, smooth setae about 30 microns long.

This appears to present a situation in which a character—a complement or dorsomedian setae—is expressed variably. We suppose that the mother's genotype governs the development of dorsomedian setae as a group but that something in the nature of organizer control during later periods of differentiation becomes feeble or inhibited and regionally spotty.

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