KARYOTYPES AND DEVELOPMENTAL STAGES OF HARPYRHYNCHUS NOVOPLUMARIS SP. N. (ACARI: CHEYLETOIDEA: HARPYRHYNCHIDAE), A PARASITE OF NORTH AMERICAN BIRDS

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ABSTRACT: Descriptions are given of karyotypes, developmental instars, and host associations of the cheyletoid mite Harpyrhynchus novoplumaris sp. n. The karyotypes strongly suggest the haplo-diploid method of sex determination, with n=2. There is a strong possibility that the species is arrhenotokous. The developmental stages for both sexes of the mite consist of egg, larva, protonymph, deutonymph, and adult; all stages subsequent to the egg exhibit sexual dimorphism and are easily distinguishable from each other. Adult females and female deutonymphs are relatively immobile and occur at the bases of feathers, in the region of the head, neck, and breast; the other stages move freely over the skin of the host. Oviposition occurs at the base of a feather, the eggs being laid serially and enclosed in a semifibrous sheath that envelops the female as well. A brown creeper examined thoroughly for degree of infestation had 85 attached female mites; the maximum number of eggs per female was 48. Lack of success in collecting ovipositing females at seasons other than the spring suggests that the parasite's reproductive season is correlated with that of its hosts. On two separate occasions both H. novoplumaris and H. brevis were collected from the same host specimens. H. novoplumaris has to date been taken from the type host (the brown creeper, Certhia familiaris), and from six additional host species, representing four families of passeriforms. The mite occurs across North America, from Maryland to California.

The cosmopolitan mite family Harpyrhynchidae includes the two genera Harpypalpus Dubinin and Harpyrhynchus Mégnin, containing about two dozen described species of avian parasites. The most recent general references to the family are those of Fritsch (1954), Dubinin (1957), and Lawrence (1959a, b, c). Most harpyrhynchids appear to be host-specific, but some (e.g., Harpyrhynchus nidulans [Nitzsch], H. brevis Ewing, H. plumaris Fritsch, and the new species herein described) are found on a variety of hosts. This paper represents a first step toward a monographic revision of the world fauna of the family, providing a description of karyotypes, developmental stages, and some aspects of the biology of a harpyrhynchid, Harpyrhynchus novoplumaris sp. n.

MATERIALS AND METHODS

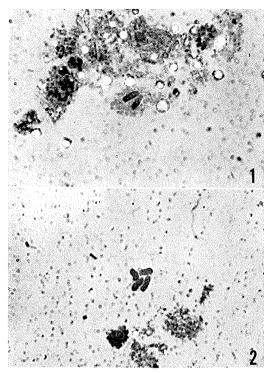
Birds were collected with a .22 caliber rifle using dust shot, or a .410 gauge shotgun using various shell sizes, placed individually in polyethylene bags, and kept overnight in a refrigerator at 5 to 7 C. The following morning the birds were removed from the bags and examined under a dissecting microscope for the presence of ectoparasites. When a bird was found to harbor Harpyrhynchus, the area and intensity of infestation were noted. The intensity of infestation per host of attached females was categorized as light (1 to 10), medium (11 to 50), or heavy (>50); in one case a complete count of females was obtained. Feathers bearing attached females with associated eggs and embryos were removed from the host and placed in a petri dish with moist filter paper. Embryos of appropriate age were then dissected for chromosome study. Chromosomal preparations were made on differently aged embryos via the squash technique and aceto-orcein stain (Oliver, 1965). Embryos of yellow-orange color were generally too far advanced for useful chromosomal analysis, but white, opaque eggs containing young, relatively undifferentiated embryos gave adequate preparations. Chromosome data are based on hundreds of cells from many embryos.

Numerous postembryonic specimens were preserved in 70% ethyl alcohol for subsequent mounting and determination.

Each positive host was also examined thoroughly for cysts and immature harpyrhynchid developmental stages, and then washed with detergent. Washings were strained through a Büchner funnel and the mites collected were preserved in 70%

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FIGURES 1-2. Harpyrhynchus novoplumaris sp. n., karyotypes. 1. Haploid chromosome complement. 2. Diploid chromosome complement. Note: length of longer chromosome = 3.5μ ; shorter = 3.0μ .

alcohol, cleared in Nesbitt's solution, and mounted in Hoyer's medium. Examinations were made by means of phase contrast microscopy.

Measurements of chromosomes and mites were obtained with a filar micrometer eyepiece. Pictures of chromosomes were taken with Kodak Verichrome Pan film VP120; illustrations of developmental stages were prepared with the aid of a microprojector.

Nomenclature of avian hosts follows Wetmore. 1961.

DESCRIPTIONS

Karyotypes

All cells examined with either two or four chromosomes per cell, but only one ploidy level per embryo (Figs. 1, 2, respectively). Chromosome lengths variable, depending on stage of mitosis; typical prophase chromosomes from 5.0 to 6.5 μ , metaphase chromosomes from 2.2 to 3.6 μ . One pair (or one chromosome in the haploid cells) approximately 0.5μ shorter than the other.

No consistent morphological features were found on the chromosomes to enable us to distinguish the chromosomes of this species from those of other known harpyrhynchids (Oliver and Nelson, 1967). No primary or secondary constrictions were seen,

and thus it appears likely that the chromosomes are either cephalobrachial or holocentric.

Eggs

About 200 μ in diameter, surface smooth, white when first laid, later becoming yellowish. Laid in compact string, two eggs wide, in manner illustrated by Fritsch (1954) for H. plumaris Fritsch.

Female

Larva: Setal terminology either new or that of Dubinin (1957); citation given where appropriate.

Gnathosoma dorsally (Figs. 3, 19) with subcylindrical basal region bearing peglike supracoxal seta anterolaterally on each side, as well as pair of movable, medially flanged, enlarged palpal segments. Peritreme of this and succeeding stages prominent, chambered, situated near dorsal juncture of gnathosoma and idiosoma.

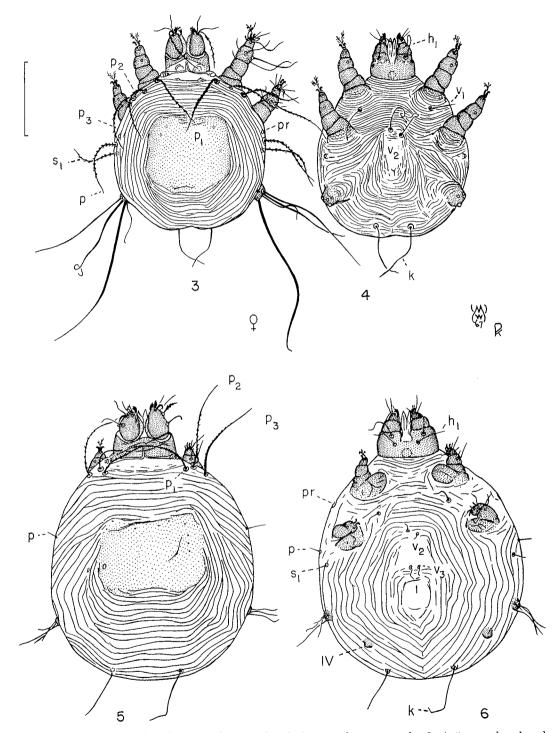
Gnathosoma ventrally (Figs. 4, 31) with basal area bearing faint median line and pair of hypostomal setae (h_1) ; palps with two free, sclerotized segments and membranous terminal segment; pair of medioventral, membranous cheliceral sheaths (cs) enclosing cheliceral stylets, extending almost to tips of free palpal segments; palpal spur (sp), arising from penultimate palpal segment, wellsclerotized, two-pronged, and curving laterad; two whiplike setae, t_1 and t_2 , situated respectively on terminal and penultimate sclerotized palpal segment. Position of pharynx (ph) shown by dotted

Palps dorsally (Fig. 19) with two modified palpal setae; the more anterior (g1) stout, somewhat flattened, bearing row of lateral, lobelike teeth; the more posterior (g₂) prominent, whiplike and slightly bipectinate, extending at least as far as posterior margin of gnathosoma.

Idiosoma dorsally (Fig. 3) subcircular in outline, with prominently striated integument surrounding weakly sclerotized, roughly rectangular dorsal shield, slightly concave anteriorly and slightly convex posteriorly. Dorsal idiosomal setae p, p_{1-3} , and s_1 (terminology of Dubinin, 1957: 77) subequal in length and pectinate.

Idiosoma ventrally (Fig. 4) with two pairs of ventral setae, v_1 and v_2 , located respectively at base of leg I and just anterad of median unsclerotized, unstriated area. Three pairs of legs: legs I and II with five obvious segments (most basal partially fused with body) plus terminal segment (pretarsus) composed of claws and bifid, pectinate empodium. Leg III reduced to two-segmented stub (or with only one obvious segment, basal segment being completely fused with idiosoma), and bearing four apical, whiplike setae, one about half as thick as other three; of these latter, the most posterior somewhat thicker than others, and approximately as long as idiosoma.

Single pair of subterminal, posterior idiosomal setae (k; Dubinin, 1957) present, in contrast to condition in male larva (Fig. 12) where two pairs of posterior idiosomal setae are present. Porelike opening (pr), often difficult to observe, present dorsolaterally or laterally, posterad of leg II.



FIGURES 3-6. Harpyrhynchus novoplumaris, female larva and protonymph. 3, 4. Larva, dorsal and ventral view. 5, 6. Protonymph, dorsal and ventral view. Abbreviations (Figs. 3-18): h₁, first hypostomal seta; IV, leg IV; k, posterior idiosomal seta; p1-8, p, and s1, dorsal and lateral idiosomal setae; pr, idiosomal pore; v₁₋₃, ventral idiosomal setae. Scale line represents 100 µ in this and all succeeding illustrations.

Table I. Harpyrhynchus novoplumaris sp. n. Table II. Harpyrhynchus novoplumaris sp. n. Measurements of developmental stages.

Instar and character	n	Max	Min	Mean	SE ¹	C.V.
FEMALE						
Larva						
A	4	65	57	61.0	1.65	5.40
В	5	214	162	192.9	10.91	12.64
$\overline{\mathbf{C}}$	5	221	151	190.5	14.11	16.56
D	5	122	110	113.1	2.23	4.40
E	5	100	97	99.4	0.60	1.36
Protonymp		100	0.	00.1	0.00	1.00
A	. 5	87	80	83.9	1.24	3.30
В	6	276	213	255.8	10.17	9.74
Č	6	298	218	277.6	12.15	10.72
D	6	158	141	$\frac{277.0}{146.7}$	2.56	4.28
E	6					
	_	116	99	107.9	3.18	7.21
Deutonymr		101	00	1750		0 = 1
A	9	121	99	115.3	2.59	6.74
В	9	381	267	337.5	13.16	11.70
C	9	485	296	397.9	20.87	15.74
D	9	245	179	208.8	7.38	10.60
E	9	184	116	151.7	7.65	15.13
Adult						
A	9	141	114	130.9	3.26	7.46
В	9	402	325	363.6	6.73	5.56
C	9	485	344	431.0	12.70	8.84
D	9	332	274	299.2	6.08	6.09
\mathbf{E}	9	235	206	222.5	3.25	4.38
MALE						
Larva						
A	1	_	_	61	_	-
В	1	-	-	187	-	_
C	1		_	170	_	_
D	1	_		118		-
\mathbf{E}	1	-	_	102		
Protonymp.	h					
A	3	77	66	71.8	3.19	7.69
В	3	245	206	220.6	12.44	9.77
C	3	238	183	210.3	15.63	12.87
D	3	146	132	138.9	3.84	4.80
E	3	114	105	110.5	2.78	4.36
Deutonymp	-		100	11010		1.00
A	8	81	64	71.3	2.08	8.25
В	8	265	214	230.9	5.79	7.09
Č	8	250	201	225.0	6.18	7.77
D	8	167	138	150.5	3.48	6.54
E	8	120	102	111.9	$\frac{3.48}{2.57}$	
Adult	O	120	102	111.9	2.57	6.50
	1			70		
A	1	_		73	-	
В	1	****		192		-
C	1		_	182		-
D	1	-	-	165		-
E	1			138		-

¹ SE = Standard error of the mean; C.V. = Coefficient of variability. Character measurements (in microns) are coded as follows: A = Greatest width of gnathosoma; B = Greatest width of idiosoma; C = Length of idiosoma, from level of peritreme to posterior margin; D = Greatest width of dorsal shield; E = Greatest length of dorsal shield. Large standard errors for body size measurements (B and C) are due to the inclusion of both engorged and unengorged specimens.

Ratio of character means for each developmental stage to mean larval measurements.1

Character	Instar	Female	Male
	L	1.00	1.00
A	P	1.38	1.18
	D	1.89	1.17
	A	2.14	1.20
	L	1.00	1.00
В	P	1.33	1.18
ь	D	1.75	1.23
	A	1.88	1.03
	L	1.00	1.00
C	P	1.44	1.24
C	D	2.64	1.32
C	A	2.85	1.07
	L	1.00	1.00
15	P	1.30	1.18
D	D	1.85	1.28
	A	2.64	1.40
	L	1.00	1.00
E	P	1.08	1.08
	D	1.53	1.10
	Λ	2.24	1.35

¹ Coding of characters as in Table I; L = larva, P = protonymph, D = deutonymph, A = adult.

Remarks

Some measurements of this and all succeeding developmental stages are given in Table I. The striking sexual dimorphism in body size that occurs during the course of development is evident from Table II, which gives the ratio of five character means to mean larval measurements for each postlarval stage.

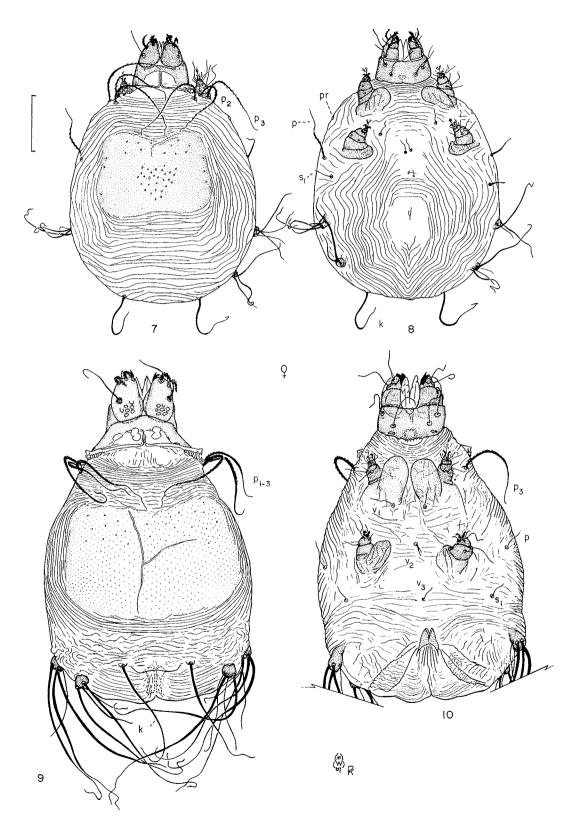
Protonymph: Gnathosoma dorsally (Figs. 5, 20) basically similar to that of larva, with addition of two modified palpal setae, g_3 and g_4 ; palpal seta g_1 unchanged, g_2 considerably shortened, pectinate and subequal in length to g3; g4 whiplike, with few fine pectinations, slightly longer than palpal segment from which it arises.

Gnathosoma ventrally (Figs. 6, 32) similar to that of larva, with addition of second pair of hypostomal setae (h_2) posteromediad of h_1 .

Idiosoma dorsally (Fig. 5) suboval in outline, dorsal shield somewhat broader than in larva, with number of small pores. Dorsal idiosomal setae p_1 , p_2 , and p_3 unchanged from larval condition, but p and s1 greatly reduced in size, subequal and devoid of pectinations.

Idiosoma ventrally (Fig. 6) with additional pair of small ventral setae, v_3 , situated posterad of v_1 and v_2 , in advance of second unsclerotized, un-

FIGURES 7-10. Harpyrhynchus novoplumaris, female deutonymph and adult (holotype). 7, 8. Deutonymph, dorsal and ventral view. 9, 10. Adult, dorsal and ventral view.



striated area. Four pairs of legs: legs I and II similar to each other and reduced from larval condition, with tendency toward fusion of leg segments, particularly in leg II, and with prominent lobe arising from basal segment of leg I. Leg III reduced to single segment, partially fused with idiosomal integument; leg setae reduced in length and thickness, almost as long as gnathosoma. Leg IV barely visible: lightly sclerotized stump without setae. Posterior idiosomal setae (k) and lateral pore present as in larva.

Deutonymph: Gnathosoma dorsally (Figs. 7, 21) and ventrally (Figs. 8, 33) basically similar to that of preceding stages, with g2 and g3 rela-

tively thicker.

Idiosomal shape (Fig. 7) as in protonymph, with further slight widening of dorsal shield, further tendency toward anterior and posterior median concavity, and addition of numerous pores. Dorsal idiosomal setae as in protonymph, but p may be thickened, elongate and pectinate, as shown in illustration.

Idiosoma ventrally (Fig. 8) with same setation as in protonymph but v_3 somewhat more reduced. Legs I and II similar to those of protonymph, leg III with four setae a little more strongly developed, the most posterior slightly longer than gnathosoma. Leg IV better developed, located more laterally than in protonymph, with two to four setae (usually four), the longest slightly longer and stouter than those of leg III. Posterior idiosomal setae (k) thicker and longer than in protonymph: lateral pore present.

Adult: Gnathosoma dorsally (Figs. 9, 22) and ventrally (Figs. 10, 34) basically similar to that of preceding stages. Small, weakly sclerotized platelet (Fig. 34, plt) appearing on terminal palpal segment. Prominent muscle attachments visible on dorsal wall of idiosomal base and on modified palpal segments.

Idiosoma pear-shaped (Fig. 9), with further widening of dorsal shield, which often has prominent creases as illustrated for holotype. Dorsal idiosomal setae p_{1-3} thickened and pectinate; s_1 and p_1 reduced in size, smooth. Idiosomal striations anterodorsally and posterodorsally less well connected than in preceding stages.

Idiosoma ventrally (Fig. 10) with same setation as in deutonymph, although one member of setal pair may be lost and both may arise from same socket, as illustrated for holotype. Ventral unsclerotized areas less distinct than in preceding stages. Legs I and II similar to those of deutonymph, although lobe may project from base of leg II. Legs III and IV with four setae strongly developed, longest setae of leg IV slightly longer than those of leg III; leg IV situated dorsally, instead of ventrally or laterally as in protonymph and deutonymph. Lateral pore lost in this stage; posterior idiosomal setae (k) further thickened and shifted dorsally to lie on either side of median, transverse hump.

Reproductive aperture a longitudinal slit, situated posteroventrally. Genital armature consist-

ing of dorsal and ventral sclerotizations at either end of reproductive aperture. Ventral armature (Fig. 10) comprising two median anteriorly diverging sclerotized arms covered by membranous flap. Dorsal armature, subintegumental, consisting of pair of tubelike structures extending posterad from Y-shaped support (shown dotted in Fig. 9). Integumental folding evident posterad and laterad of genital area.

Male

Larva: Gnathosoma dorsally (Figs. 11, 23) and ventrally (Figs. 12, 27) similar to that of female larva (cf. Figs. 3 and 19), with modified palpal seta g1 stout, flattened and laterally lobed, g2 long and whiplike, extending backward to or slightly beyond posterior margin of gnathosoma.

Idiosoma somewhat more compact than that of female larva, legs and body setation identical to that of female with exception of posterior idiosomal setae (k), of which two pairs present (cf. female larva, Fig. 4); these setae prominent and approximately equal in length, located terminally and slightly ventrally, respectively. Paired k setae found in all succeeding instars except adult male, in which both lost. As in female larva, pore situated dorsolaterally, just anterad of seta s1 and slightly posterad of leg II.

Protonymph: Gnathosoma dorsally (Figs. 13, 24) and ventrally (Figs. 14, 32) as in female protonymph, g2 reduced in size, with g3 and g4 appearing anterolaterally.

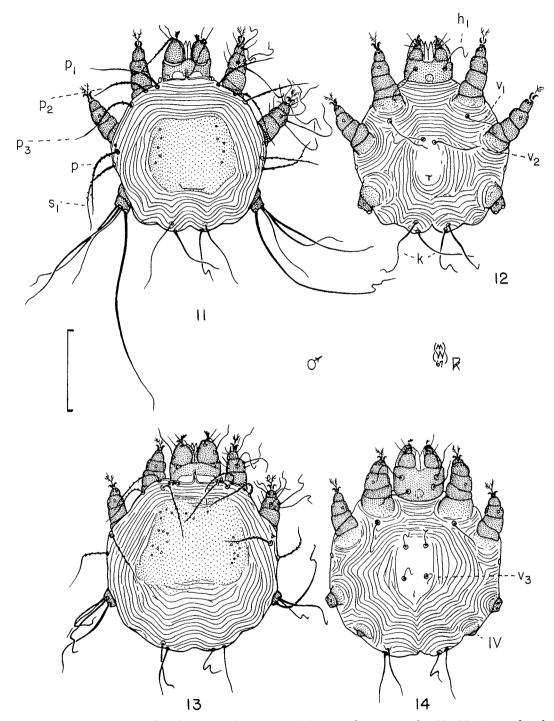
Idiosomal shape (Fig. 13) similar to that of male larva, and strikingly different from that of female protonymph (cf. Fig. 5). Idiosoma ventrally (Fig. 14) with single unstricted area, v_3 added as in female protonymph. Legs I and II lacking basal lobe. Leg III better formed than in female, two segments visible and setae longer and stouter. Leg IV a stump, with basal segment barely visible. Posterior idiosomal setae (k) and lateral pore as in male larva.

Deutonymph: Gnathosoma dorsally (Figs. 15, 25) and ventrally (Figs. 16, 33) similar to that of preceding stages.

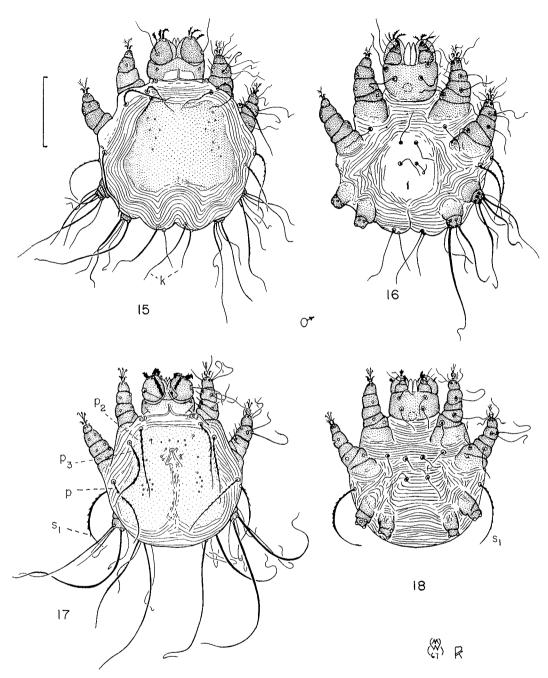
Idiosomal shape (Fig. 15) as in male protonymph, dorsal shield with tendency toward posterolateral widening and anterior and posterior concavity. Body setation as in male protonymph. with all idiosomal setae well developed. All legs well developed in comparison with female deutonymph (cf. Fig. 7): leg I not lobed basally, similar to leg II; legs III and IV with strongly developed complement of setae, usually with six setae on leg III and four on leg IV; setae of leg III often better developed than those of leg IV (although not in specimen illustrated).

Ventrally (Fig. 16) setation as in protonymph, with single unstriated area. Posterior idiosomal setae (k) and lateral pore as in protonymph.

Adult: Gnathosoma dorsally (Figs. 18, 26) with slight relative shortening and rounding of movable palpal segment, modified palpal setae g_{1-3} (especially g2) considerably hypertrophied over condition in deutonymph.



FIGURES 11-14. Harpyrhynchus novoplumaris, male larva and protonymph. 11, 12. Larva, dorsal and ventral view. 13, 14. Protonymph, dorsal and ventral

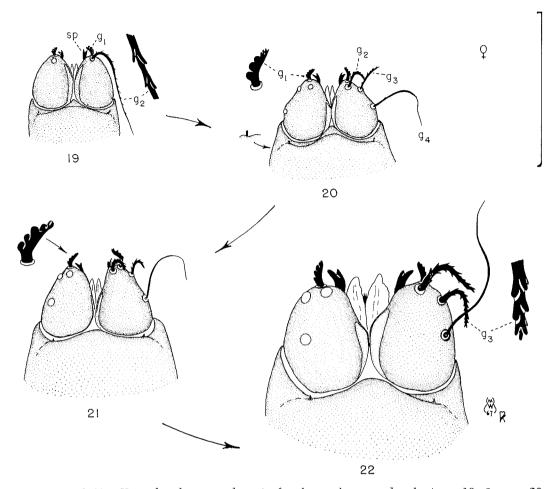


FIGURES 15-18. Harpyrhynchus novoplumaris, male deutonymph and adult (allotype). 15, 16. Deutonymph, dorsal and ventral view. 17, 18. Adult, dorsal and ventral view.

Idiosoma dorsally (Fig. 18) almost covered by dorsal shield, considerably broadened posterolaterally and posteriorly incised.

Genital opening located in dorsal shield at about

and whiplike. Genital opening flanked by inverted-V-shaped support and three pairs of minute setae. One pair of anterior p series (probably p_1) reduced to microsetae and situated on dorsal shield near anlevel of base of leg II. Aedeagus eversible, tubular, terior margin; other idiosomal setae somewhat en-



FIGURES 19-22. Harpyrhynchus novoplumaris, female gnathosoma, dorsal view. 19. Larva. 20. Protonymph. 21. Deutonymph. 22. Adult. Abbreviations (Figs. 19-26): gi-i, modified palpal setae; sp, palpal spur or clawlike seta.

larged relative to their condition in male deuto-

Ventrally (Fig. 17), idiosomal setation as in deutonymph, but ventral unstriated area lacking. Legs similar to those of deutonymph, but somewhat better developed. Legs I and II with five or six segments plus terminal segment (pretarsus), increase in segmentation apparently brought about by partial or complete subdivision of basal segment. Leg III may have two or three segments; leg IV two-segmented. Terminal setae of legs III and IV more strongly developed than their counterparts in deutonymph.

Lateral pore and posterior idiosomal setae (k)lacking.

Adult male allotype illustrated in Figures 18 and 19 somewhat reduced in size from male deutonymph of Figures 16 and 17; this reduction normal, or perhaps host-influenced, as allotype taken from different host than remainder of type series (see

below under "Allotype" in Taxonomic Data section).

TAXONOMIC DATA

Type host

The brown creeper, Certhia familiaris L., AOU p. 401 (Aves: Passeriformes: Certhiidae).

Holotype

Adult 9, Hopland Field Station, Mendocino Co., California, 26 March 1965 (B. C. Nelson; Host No. BCN 539); No. 3248 in the USNM Collection, Washington, D. C.

Allotype

Adult &, 11 mi SE of Nebraska City, Nebraska, 25 January 1960 (N. Braasch; Host No. 600125-1), from cardinal, Richmondena cardinalis L., AOU p. 546 (Aves: Passeriformes: Fringillidae); de-

FIGURES 23-26. Harpyrhynchus novoplumaris, male gnathosoma, dorsal view. 23. Larva. 24. Protonymph. 25. Deutonymph. 26. Adult.

posited under the same accession number as the holotype in the USNM.

Note: Two male deutonymphs in the process of molting into adults were present in the series from the brown creeper, but no fully molted adult males were available from this host; rather than designate an incompletely formed, teneral specimen as an allotype, a well-sclerotized adult male from the cardinal was chosen.

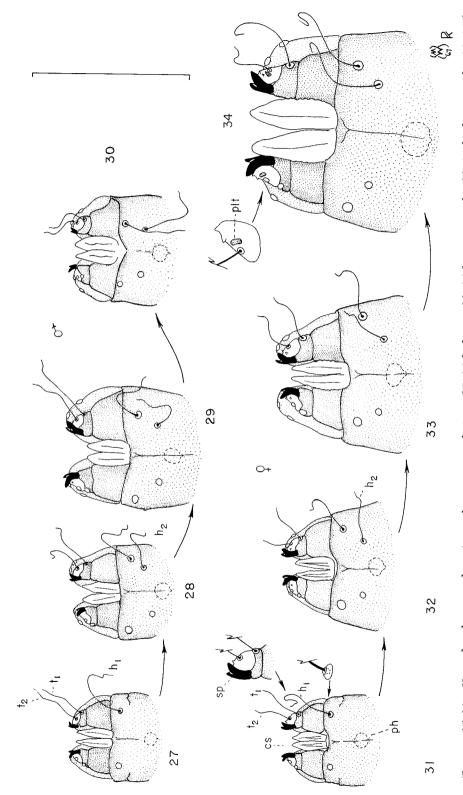
Paratypes

These include 3♀ larvae, 4♀ protonymphs, 5♀ deutonymphs, 69 adults, 18 larva, 38 protonymphs, and 73 deutonymphs, all from the same locality and host species as the holotype. In addition, four adult of paratypes, Laurel, Maryland, 20 March 1961 (W. W. Moss; Host No. WM-1), from cardinal.

Material is deposited in the collections of the Academy of Natural Sciences of Philadelphia (19); the Bernice P. Bishop Museum, Hawaii (19); the Canadian National Collection, Ottawa (19; No. 9556); the Institute of Acarology, Columbus, Ohio (19); the Snow Entomological Museum, Lawrence, Kansas (1♀ larva, 1♀ protonymph, 19 deutonymph, 19 adult, 18 protonymph, 13 deutonymph); the Zoological Institute of the Academy of Sciences, Leningrad, USSR (1 \circ). Remaining material is in the collections of the authors.

The type series is mounted in Hoyer's medium and the cover slips are ringed with Zut lacquer.

Of the species of Harpyrhynchus described to date, H. novoplumaris sp. n. is most similar



morphologically to H. plumaris Fritsch, a European form, but differs from the latter in having one of the modified palpal setae (g_1) of the female thickened and distinctly shorter than the other two modified setae (all three are long, unthickened and similar to each other in H. plumaris). In addition, the lobes at the bases of legs I and II of the female are more prominent in H. novoplumaris, and the male aedeagus is closer to the anterior margin of the dorsal shield. According to Fritsch's 1954 descriptions and illustrations, legs I and II of female H. plumaris lack the empodium, a structure that is present in H. novoplumaris; however, due to the poor preservation of the specimen of H. plumaris examined, the absence of an empodium in this species cannot be confirmed at this time.

The type host of *H. novoplumaris* (the brown creeper, *Certhia familiaris*) also occurs in Europe, in the range of birds parasitized by the Palearctic *H. plumaris*. Accordingly, it would be of interest to sample European creeper populations to determine which (if either) of these two closely similar mites is present on this host in Europe.

BIOLOGY OF HARPYRHYNCHUS NOVOPLUMARIS

Virtually nothing is known of the biology of harpyrhynchids, aside from their host records and the tendency of a few species to induce the formation of host cysts (Mégnin, 1877; Morley and Shillinger, 1937). The first complete description of the developmental cycle of a harpyrhynchid is given above for *H. novo-plumaris*; no data are yet available on the duration of each stage for this or any other harpyrhynchid.

The following observations, although incomplete, are a first contribution toward our understanding of the natural history of these mites.

Chromosome complement

No animal or plant has been reported to possess a smaller number of chromosomes than that found in *Harpyrhynchus novoplumaris* sp. n., and not many species have been reported to have as few. Oliver and Nelson (1967) found *Harpyrhynchus brevis* Ewing to have the same number, and listed several taxa that share this number in at least some

cells during some part of the individual's development. For example, certain species of insects (coccids of the tribe Iceryini) display a haploid number of two chromosomes, with unfertilized haploid eggs developing parthenogenetically into males; fertilized eggs develop into females (Hughes-Schrader, 1948). Two species of water mites, $Eylais\ rimosa\ Piersig\ and\ E.\ setosa\ Koenig,\ were found to have <math>n=2$, but were not arrhenotokous (Sokolov, 1954).

The presence of haploid and diploid embryos suggests that arrhenotoky may be present in Harpurhunchus novoplumaris and in other species of the family (e.g., H. brevis Ewing, where a similar situation exists (Oliver and Nelson, 1967). Obviously, the mere coexistence of haploid and diploid embryos is not definitive proof of arrhenotoky. In the diaspidine scale Pseudaulacaspis pentagona (Targ.). male embryos begin as diploids, but the paternal chromosomes are eliminated during late cleavage stages, the male embryos developing thereafter as true haploids (Brown and Bennett, 1957). Nevertheless, this type of chromosome behavior is rare and the finding of haploid and diploid embryos, plus the fact that arrhenotoky is common in many trombidiform mites (Oliver, 1962), argues strongly in favor of arrhenotoky in this species.

Location on host and oviposition

Mites such as H. novoplumaris remain in close contact with the host throughout their developmental cycle and, accordingly, belong to the host-dwelling ecological category of Audy (1948, 1958) and Camin (1963, 1964). Most cheyletoid mites in this category scatter their eggs or young loosely over or within the body or feathers of the host (e.g., Cheyletidae; Syringophilidae; Psorergatidae; Demodicidae; Ophioptidae: Fain, 1964), or lay their eggs singly on stalks (e.g., some Myobiidae: Grant, 1942). In the case of H, novoplumaris (and in H. plumaris and H. pilirostris Berlese and Trouessart), the eggs are laid in a string, and the female herself serves as the "stalk" or site of attachment (see fig. 11a of Fritsch, 1954).

The slightly mobile female deutonymph of *H. novoplumaris* can be found at the base of the calamus of a feather, oriented parallel to the length of the shaft, with mouthparts at the

surface of the host's integument. In this position the subsequent molt to the adult stage occurs, when copulation presumably takes place (as in a closely similar species of Harpurhunchus from the cowbird: Moss, unpubl.). The female attaches to the calamus of the feather by means of a semifibrous sheath that eventually comes to envelop both her and her eggs. The latter are arranged serially, and remain attached to each other. The eggs will separate from each other, however, if placed in water and agitated. Eggs laid most recently are white, situated closest to the female, and contain early stage embryos suitable for chromosome study. Older eggs are vellow, farther from the female, and contain advanced embryos. Finally, the oldest eggs are followed by the collapsed, empty chorions from which larvae have hatched. Females apparently die in situ after the completion of oviposition.

Adult females of *H. novoplumaris* occur chiefly on the contour feathers of the head, neck, and upper breast. Mites may be found on the auricular, gular, and malar feathers, as well as on those of the lores and occiput (feather topology that of Pettingill, 1956). Females are restricted to the ventral surface of the auricular feathers. On feathers other than the auriculars, the ventral surface is usually utilized, but some females attach to the dorsal surface. Attachment sites are normally in areas that cannot be preened effectively, and it is possible that ventral attachment is an additional adaptation to prevent dislodgement of the mite by its host.

An exhaustive count was made of the number of attached females and their eggs on a brown creeper (BCN 552). Of 85 attached females, five had no eggs; and one female and her eggs were covered with a fungus so that an accurate count could not be made. Egg production of the 84 females for which counts could be made is presented in Table III. The presence of white eggs suggested that a female was still ovipositing. Obviously, as counts were made before all females had completed oviposition, the figures of Table III do not represent the actual biotic potential of the species, but only the reproductive picture at one point in time.

Seventy-one females had one to three white eggs. Seventy-four females had yellow eggs

Table III. The number of eggs laid per female by Harpyrhynchus novoplumaris sp. n. on various areas of a brown creeper (BCN 552).

No. of eggs per female	Site of oviposition: Number of females					
	Auriculars	Head feathers	Neck and breast feathers			
0	0	2	3			
1-10	4	4	4			
11-20	5	6	4			
21 - 30	7	8	14			
31-40	1	3	13			
over 40	0	0	6			
Totals	17	23	44			

with advanced embryos; the maximum number of advanced embryos per female was 12. The maximum number of eggs laid by one female was 48 (two white eggs, 10 yellow eggs, and 38 empty chorions).

The maximum number of eggs laid per mite varied considerably among eight females presumed to have ceased oviposition: five females with only empty chorions had laid 15, 24, 28, 34, and 40 eggs, while three females with only advanced embryos and empty chorions had laid 13, 19, and 26 eggs. Further counts must be made in order to determine if this variation was typical, or perhaps only the result of mite mortality due to the death of the host. The latter alternative is possible, although some mites remained alive up to 10 days subsequent to their removal from the host under the conditions mentioned above. Loss of empty chorions from the egg strings would be a source of counting error. However, although the empty chorions are easily broken by direct contact with forceps, the chorions remain intact when the feathers are removed and mounted on slides; further, a study skin of a brown creeper collected in 1863 and deposited in the University of California Museum of Vertebrate Zoology (No. 6429) still has many H. novoplumaris females with relatively long strings of empty chorions. Unfortunately, accurate counts of the eggs could not be made without damaging the skin.

Discrimination of developmental stages

The developmental stages of *H. novoplu-maris* may be distinguished from each other by a few easily observed characters. The larva may be identified by its three pairs of legs,

one pair of hypostomal setae (h_1) , only two pairs of ventral idiosomal setae $(v_1 \text{ and } v_2)$, and by its modified palpal setae g_2 which extend back almost to the base of the gnathosoma. Protonymphs may be recognized by their possession of a stublike leg IV that lacks setae, by the presence of a second pair of hypostomal setae (h_2) , and the third ventral idiosomal setae (v_3) , as well as the addition of two palpal setae $(g_3 \text{ and } g_4)$ accompanied by a reduction in length of g_2 . Deutonymphs possess setae on leg IV, but lack a reproductive aperture. Adult males lose their posterior idiosomal setae (k) and ventral unsclerotized area, and possess an aedeagus that opens via the dorsal shield. Adult females exhibit a dorsal migration of leg IV, with a considerable hypertrophy of the setae of legs III and IV. and possess a ventral genital opening situated posterad of setae v_3 . Males and females of all stages prior to the adult may be distinguished from each other on the basis of the number of posterior idiosomal setae (k): two pairs are present in males, one pair in females.

Relatively few species of acarines are known from all developmental stages and few, if any, exhibit sexual dimorphism in all instars subsequent to the egg (see Moss and Funk, 1965, for a description of a laelaptoid that exhibits such dimorphism in all stages subsequent to the larva). It is, unfortunately, an extremely difficult task to maintain harpyrhynchid mites in colonies. If this difficulty could be overcome, the mite described in the present paper, H. novoplumaris, would be an ideal organism for use in population studies of the dynamics and possible causes of shifts in sex ratios.

Apparent seasonality of reproduction

Although harpyrhynchids may be collected at almost any time of the year, actively ovipositing females of H. novoplumaris have been found by us so far only during the months of March through June, a period corresponding roughly to the breeding seasons of its hosts. Intensive year-round collections of H. novoplumaris are needed to confirm this observation, but it would seem reasonable that a synchronization of the reproductive seasons of the mite and its hosts would be of advantage to the mite, in assuring transfer from host to host. In addition, it would be disadvantageous

for ovipositing female mites to attach to feathers that would be shed during the host's postnuptial molt. As these molts generally occur during the late summer in temperate North America, mite reproduction should occur before or after this time. We have as yet no evidence that reproduction occurs in the autumn or winter.

Interestingly, an examination of a large series of newly molted house sparrows (Passer domesticus L., collected by R. F. Johnston) showed an almost complete absence of Harpurhynchus pilirostris, a mite that is commonly found on the house sparrow during the spring and early summer. Subintegumental nymphs of H. pilirostris were collected from these sparrows, and it is possible that such forms also occur in H. novoplumaris, enabling a nucleus of the mite population to survive the host molt.

Evidence for the concurrence of the breeding cycles of H. novoplumaris and its hosts is of interest in view of the findings of Camin et al. (1967) who demonstrated the likelihood of a similar correspondence in two species of cloacarids, members of a newly discovered family of chevletoids parasitic in the cloaca of turtles.

Host list

Harpyrhynchus novoplumaris has been collected from seven passeriform host species in four different families:

(1) Parus bicolor L.: Tufted Titmouse [Paridae], AOU p. 390 (Kansas: Vergil, 13 April 1963, B. Gilbert, M-180).

(2) Certhia familiaris L.: Brown Creeper [Certhiidael, AOU p. 401 (CALIFORNIA: Mendocino Co., Hopland Field Station, 26 March 1965, B. C. Nelson, BCN 539; same locality and collector, 18 April 1965, BCN 552; Napa Co., 23 March 1941, Univ. Cal. Mus. Vert. Zool. 83282; Santa Clara Co., 17 March 1863, UCMVZ 6429; MISSOURI: Columbia, 1 April 1954, M. C. Grabau, M-289).

(3) Campylorhynchus brunneicapillus (Lafresnaye): Cactus Wren [Troglodytidae], AOU p. 416 (New Mexico: 30 mi NE of Portal, Arizona, 5 April 1965, W. W. Moss, M-239).

(4) Richmondena cardinalis (L.): Cardinal [Fringillidae: Richmondeninae], AOU p. 546 (Kansas: Jefferson Co., 2 mi E, 6 mi N of Lawrence, 19 April 1952, E. H. Kardos, EK520419-2; MARYLAND: Laurel, Patuxent Wildlife Research Refuge, 20 March 1961, W. W. Moss WM-1; Nebraska: 11 mi SE of Nebraska City, 25 January 1960, N. Braasch, 600125-1 and -2).

(5) Pipilo fuscus Swainson: Brown Towhee [Fringillidae: Emberizinae], AOU p. 582 (New 1965, W. W. Moss, M-259 and M-260).

(6) Amphispiza bilineata (Cassin): Blackthroated Sparrow [Fringillidae: Emberizinae], AOU p. 603 (New Mexico: 30 mi NE of Portal, Arizona, 5 April 1965, B. I. Jump, M-240).

(7) Spizella passerina (Bechstein): Chipping Sparrow [Fringillidae: Emberizinae], AOU p. 613 (California: Mendocino Co., Hopland Field Station, 16 May 1965, B. C. Nelson, BCN 593 and 594; same locality and collector, 16 June 1966, BCN 768; Wyoming: 15 mi S of Sundance, 2 September 1962, W. W. Moss, M-109).

A congeneric association

On two occasions, harpyrhynchid eggs were found attached singly by a tiny stalk to the skin of the occiput and neck (i.e., the cervical apterium) of chipping sparrows, Spizella passerina (BCN 593 and 594) positive for H. novoplumaris. A female harpyrhynchid observed in the process of laying a stalked egg was subsequently identified as Harpurhunchus brevis Ewing, a species that also occurs on a wide variety of hosts (at least 25 species of North American passeriforms; Moss, unpubl.). Females of H. brevis retain their locomotory ability and wander freely over the surface of the host; this mite was implicated in cyst formation by Morley and Shillinger (1937).

It is interesting that two species of Harpurhynchus, H. novoplumaris and H. brevis, were found together twice on two separate hosts. The presence on the same host of two species of the same parasite genus is not rare among host-dwelling ectoparasites, and may be of common occurrence among species of the related cheyletoid family Cloacaridae (e.g., at least three species of *Cloacarus* Camin et al. have been found in the box turtle, Terrapene ornata (Agassiz); Camin, pers. comm.). We have no data on possible competition for food and living space between these two harpyrhynchids, although competition for ovipositional sites is obviously avoided as described above.

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Mexico: 30 mi NE of Portal, Arizona, 13 April Atyeo of The University of Nebraska enabled the collection of additional specimens of H. novoplumaris from western North America. Mite material was loaned to us by Wilbur R. Enns of The University of Missouri, and Wilhelm Fritsch provided specimens of H. plumaris for comparative purposes. We are especially grateful to A. B. Amerson for permission to use his unpublished observations on the condition of the posterior idiosomal setae in the developmental stages of Harpurhunchus.

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