

ATHYREACARIDAE, A NEW FAMILY OF MITES  
(ACARI : HETEROSTIGMATA) ASSOCIATED WITH SCARAB BEETLES  
OF THE GENUS *NEOATHYREUS* (COLEOPTERA : SCARABAEIDAE)

BY Evert E. LINDQUIST \*, Marek KALISZEWSKI \*\*  
and Gisela RACK \*\*\*

INSECT MITE  
ASSOCIATION  
NEOATHYREUS  
ATHYREACARUS  
PLEIOTRETUS  
MEXICO  
CENTRAL AMERICA  
SOUTH AMERICA

ABSTRACT : A new family of heterostigmatic mites, Athyreacaridae, is described on the basis of a group of 9 species whose adult females are phoretic on adult geotrupine scarab beetles of the genus *Neothyreus* Howden and Martínez from Mexico, Central America, and South America. *Athyreacarus* new genus is described as the type genus of the family, based on material representing the type species, *A. pleiotretus* new species, and 3 undescribed species ; it is differentiated from a group of 5 other undescribed species which are thought to represent another, undescribed, genus. These mites evidently live symbiotically in the burrows of their beetle host ; however, their feeding habits and life cycle are unknown.

ASOCIACIÓN  
INSECTO  
CON ÁCARO  
NEOATHYREUS  
ATHYREACARUS  
PLEIOTRETUS  
MÉXICO  
CENTROAMERICA  
SUDAMERICA

RESUMEN : Se describe una nueva familia de ácaros heterostigmáticos, Athyreacaridae, basada en un grupo de 9 especies cuyas hembras adultas están foréticas sobre escarabajos adultos del género geotrupino *Neothyreus* Howden y Martínez de México, Centroamérica, y Sudamérica. Se describe *Athyreacarus* gen. n. como el género tipo de esta familia, basado en material representando la especie tipo, *A. pleiotretus* sp. n., tan bien como 3 especies que no están descritas ; se diferencia este género de otro grupo con 5 especies que no están descritas y que se piensa representar otro género no aún descrito. Al parecer, estos ácaros viven como simbioses en los túneles de sus huéspedes escarabajos ; sin embargo, sus hábitos y ciclo de vida aún son desconocidos.

#### INTRODUCTION

Substantial research has been devoted to mites of various of the more derived, or advanced, families of Heterostigmata, particularly those in the super-families Pyemotoidea, Pygmephoroidae (as distinct from Scutacaroidae sensu KALISZEWSKI, in prep.) and Tarsonemoidae, which contain a diversity of species of economic importance as plant and fungus feeders and as parasites or parasitoids of insects.

However, mites of the more early derivative groups of this subcohort are poorly known, both systematically and biologically. Among the few of these groups for which some knowledge of their ways of life is available, we find a surprising array of highly specialized associations, behaviors, and life cycles. An example is the three-way symbiotic association between trochometridiid mites, certain fungi whose spores they propagate and whose hyphae they consume, and ground-nesting bees on which both

\* Biosystematics Research Centre, Agriculture Canada, Research Branch, Central Experimental Farm, Ottawa, Ontario, Canada K1A 0C6.

\*\* Department of Biology, University of Alabama, Tuscaloosa, Alabama 35486 U.S.A. Present address : Department of Zoology, Brigham Young University, Provo, Utah 84602 U.S.A.

\*\*\* Zoologisches Institut und Museum, Martin Luther King Platz 3, 2000 Hamburg 13, Deutschland.

the mites and fungi depend for dispersal and for sites to undergo their life cycles (CROSS and BOHART 1979, LINDQUIST 1985). Moreover, systematic and biological information on these early derivative taxa provide important knowledge and better perspective concerning the origins and evolutionary trends of more recently derived groups, and permit more refined and predictive hypotheses concerning the phylogenetic relationships among the family-level taxa of Heterostigmata.

Material of several unusually interesting, undescribed species representing new family-group taxa have become available to one or the other of us during the last few years. It is our intention to publish a series of papers which will describe these taxa and introduce them to researchers who may be stimulated to investigate them ecologically. In the present case, one of us (E.E.L.) has material of 9 species representing apparently 2 genera of a new family-group taxon. All of these have been used in description of the new family proposed herein, but due to time constraints material of only one species, which becomes the type species of the new genus on which the family is based nomenclatorially, is formally described.

Our interest in these mites was initiated in 1983 when we received from Dr. R. W. HUSBAND slide preparations of several adult females removed from a geotrupine beetle, identified as *Athyreus excavatus* Laporte, from Honduras. Subsequently, one of us (E.E.L.) examined several substantial collections of geotrupine beetles, as noted in the acknowledgment, for additional specimens of these mites. This investigation led to realization that (a) *excavatus* is now a member of the genus *Neoathyreus*, in accord with the concepts of HOWDEN and MARTINEZ (1963); (b) determinations of *excavatus* prior to the revision of *Neoathyreus* by HOWDEN (1985) are doubtful and may actually be *N. mexicanus* (Klug) (H. F. HOWDEN, personal communication 1988); and (c) these mites are found associated with beetles of a variety of species of the genus *Neoathyreus* but not, so far, with beetles examined of the genus *Athyreus* or of other genera of Athyreini. Mites representing 9 species of this new family have been recovered from beetles representing 12 species of *Neoathyreus*; host specificity is evident for some

of the mite species, but insufficient material is available to assess this at present. Nevertheless, as some 60 species of *Neoathyreus* have been described, we anticipate that a substantial number of additional species of this family of mites exist that have as yet not been collected from their hosts. Heterostigmatic mites of apparently related families (e. g., Trochometridiidae and Carabacaridae as discussed below) were not found on any of the athyreine beetles examined.

#### MATERIALS AND METHODS

Adult athyreine beetles in curated museum collections were examined for the presence of mites. Adult female athyreacarid mites were found on the exposed undersurfaces of beetles' thoraces and abdomens, where they were usually attached to one of the host's hairs by means of the enlarged claw in apposition to the spinelike unguinal setae of tarsus I (Figs. 8, 11). They were also found in abundance in the deep cleft, or recession, ventrally between the metasternum and base of the abdomen on one beetle; this cleft is rarely exposed to view, and perhaps is a more common refuge for these mites than may be realized. The mites were removed, dry, from the beetles by means of a fine needle tipped with a droplet of Hoyer's medium, and mounted directly into Hoyer's medium on a microslide. An initial strong warming of the slide preparation for about a half minute sufficed to eliminate air bubbles from the preparation peripherally and to clear the specimen sufficiently for preliminary observation. Slide preparations were then placed in a warming oven at about 40°C for 2 or 3 days, for further clearing and setting; their coverslips were sealed with Glpt insulating varnish a couple of weeks later.

Systematic observations, measurements, and line illustrations were made using compound microscopes equipped with differential interference contrast optical system. All measurements, given as micrometres, were made with a stage-calibrated ocular micrometer. Scanning electron micrographs, taken with an ETEC Autoscan S.E.M., were obtained

using dried mite specimens removed from beetles in museum collections. These specimens were first relaxed and cleaned in 50 % ammonium hydroxide for 30 min, then placed in 25 % ethanol for 20 min; they were subsequently dehydrated in a series of 6 increasingly concentrated solutions of ethanol, from 40 % to 95 %, ending in 2 changes of 100 % ethanol, with 15 min in each solution. The specimens were then dried in a critical point dryer,

mounted on stubs using double-stick tape, and sputter coated with gold.

In the descriptions, the terminology of structures and application of the systems of setal notation of GRANDJEAN for the idiosoma and legs follow those of LINDQUIST (1977, 1986). Unless otherwise noted, the specific identities of host beetles were based on determinations by Dr. H. F. HOWDEN, a world authority on the systematics of geotrupine beetles.

#### ATHYREACARIDAE NEW FAMILY

Figs. 1-12

*Type genus* : *Athyreacarus* new genus. Family based on adult females representing 9 species (8 undescribed) in 2 genus groups (1 undescribed).

*Diagnosis*. Adult females (the only instar known) of this family group are distinguished from those of other families of Heterostigmata by the following combination of characters : Gnathosomal capsule with 1 pair of dorsal setae, 2 pairs of ventral setae ; cheliceral stylets stout, strongly curved ; pharyngeal musculature smooth-walled, not subdivided ; palpi prominent, extending beyond apex of stylophore. Idiosoma fusiform, widest at level of tergites C, with plate PS formed into a caudal capsule bearing 3 pairs of prominent pseudanal setae and a protruding, bivalved opening ; idiosomal setae all setiform, smooth or barbed. Prodorsum with a pair of circular stigmata widely spaced anterolaterally and a well developed tracheal system, and with 2 or 3 pairs of setae but lacking bothridia and bothridial setae  $sc_1$ . Tergite C tripartite ; tergite EF with setae  $e$  and  $f$  aligned longitudinally ; tergite H with setae  $h_1$  and  $h_2$  aligned transversely. Coxisternal plates I and II each with 3 pairs of setae ; prosternal apodeme and apodemes 1 and 2 fully developed. Coxisternal plates III and IV separated medially by soft cuticle ; plates III with 3 pairs of setae, plates IV tripartite, each side with elements of 2 pairs of setae, 3rd pair on triangular midsternal plate ; apodemes 3 and 4 well developed, 5 reduced. Aggenital plate expansive, with 2 or 3 pairs of prominent aggenital setae, completely covering primary genital opening ; genital setae absent. All legs 5-segmented,

with ambulacra. Leg I markedly thicker than legs II to IV, with single, enlarged sessile claw in apposition to enlarged spinelike unguinal setae ; subunguinal seta setiform ; femur I and genu I each with 5 setae. Trochanter IV differing in form from trochanter III in being subquadrangular rather than subtriangular. Legs II to IV each with well developed, paired claws and prominent, stalked empodium, with all setae setiform ; tarsi II and III each with 7 setae, including  $pl''$  and elongated  $tc'-tc''$  but lacking proral seta  $p'$  ; IV also with 7 setae, including  $pl''$  and elongated  $tc''$ , but lacking  $tc'$  and with short, stiff, apical proral seta  $p'$  instead (this different combination of 7 setae on tarsus IV, versus those on tarsi II and III, is unique to this group). Legs with dorsal seta  $d$  ultralong on femora I to IV and tibiae I to IV.

*Description of Adult Female*. With the character states of the subcohort Heterostigmata as described by LINDQUIST and KETHLEY (1975), and of the group Tarsonemina as described by LINDQUIST (1976), but restricted and augmented as follows :

*Gnathosoma* (Figs. 1, 2, 9). Stylophore coalesced with subcapitulum to form gnathosomal capsule ; prognathous. Dorsal face of stylophore with 1 pair of simple cheliceral setae,  $ch_1$  ; palpcoxal setae  $e$  inserted laterally, at bases of palpi. Ventral face of subcapitulum with 2 pairs of setae inserted on its anterior half ; adoral setae absent. Cheliceral stylets stout, strongly curved, retractable, attached to conspicuous, closely-set levers. Pharynx surrounded

by smooth-walled, moderately enlarged but weakly defined musculature, not subdivided as in pygme-phoroid-scutacaroid families. Palpi projecting freely anteriorly of apex of stylophore, somewhat convergent but well separated apically; palpi 2-segmented, femorogenu with 2 setae dorsolaterally (1 femoral, 1 genual), tibiotarsus with a rodlike solenidion ventroproximally, a reduced tibial "claw" distally, and a minute rodlike eupathidiform seta (optically birefringent) and a minute setiform seta paraxially, lacking the second, non birefringent organ beside the solenidion that is characteristic of some pygme-phoroid-scutacaroid taxa.

*Idiosomal dorsum* (Figs. 1, 7, 8). Idiosomal length 250-650  $\mu\text{m}$ ; body fusiform in dorsoventral aspect, widest at midlevel near posterior margin of tergites C. Dorsal setae simple, attenuated, smooth or barbed. Prodorsal shield subtrapezoidal, its anterior margin broadly truncated, covering only base of gnathosoma, and lacking any apodeme medially. Stigmata subcircular, not on hornlike projections and lacking guttate peritrematal extensions, positioned on dorsal surface near anterolateral angles of prodorsum, laterad of vertical setae; tracheal trunk of each stigma directed medially to sagittal plane, where the two together are then directed posteriorly, each to an unsclerotized atrium, from which many (10-12) small tracheal branches issue at level of coxisternal plates I. Prodorsum lacking bothridia and their setae  $sc_1$ , only their alveolar vestiges remaining; vertical setae  $v_1$  and scapular setae  $sc_2$  well developed, setae  $v_2$  present or vestigial;  $v_1$  inserted well anteriorly of alveoli of  $v_2$ . Tergite C subdivided into a pair of lateral plates, each bearing seta  $c_2$ , and a middorsal plate; setae  $c_1$  present on this plate or absent. Tergites D, EF, H each entire, well developed, wider than long, successively overlapping the next plate posteriorly; posterior edges of each tergite smooth, and straight or gently curved. Tergite D with paired setae  $d$ , cupules  $ia$ , and a pair of porelike structures usually evident medially of  $d$ . Tergite EF with paired setae  $e$  and  $f$  in oblique or longitudinal alignment, cupules  $im$  and  $ip$  usually evident laterad of these setae, respectively, and a pair of porelike structures usually evident medially of each pair of these setae;

lateral margins of tergite EF not extended sufficiently ventrally to overlap anterolateral margins of aggenital plate. Tergite H with paired setae  $h_1$  and  $h_2$  aligned transversely, with cupules  $ih$  on lateral curvature of tergite (often difficult to discern), and lacking porelike structures. Pseudanal plate PS a terminal caudal capsule with a protruding, bivalved opening (uropore?); plate with 3 pairs of prominent setae of which  $ps_1$  inserted dorsoapically,  $ps_2$  lateroapically, and  $ps_3$  ventrosubapically and usually shorter than  $ps_{1,2}$ ; plate lacking cupules or porelike structures.

*Idiosomal venter* (Fig. 2). Ventral setae simple, attenuated, smooth or slightly barbed. Coxisternal plates I and II united to each other medially where forming a prosternal apodeme that extends from its union with apodemes 1 to posterior margin of plates II; apodemes 1 greatly thickened, U- or V-shaped; apodemes 2 fully developed united with prosternal apodeme; sejugal apodeme variably reduced, at least with lateral remnants on either side. Posterior margin of coxisternal plates II usually desclerotized or emarginated along medial half of its extent. Coxisternal plates I and II each with 3 pairs of setae; setae  $1a$  widely spaced from each other, inserted near lateral extremities of apodemes 1; setae  $1b$  and  $1c$  transversely or obliquely aligned in middle of field of plates I; setae  $2a$  and  $2b$  transversely or obliquely aligned in middle of field of plates II, and  $2c$  similarly aligned with  $2a-b$  or inserted posterolaterad of this alignment. Coxisternal plates III and IV well separated from plates I and II by broad, transverse band of finely striated, soft cuticle, which evidently allows for considerable idiosomal distension; plates III and IV separated from each other medially by soft cuticle, which bears a separate triangular midsternal plate (tegula); poststernal apodeme thus absent. Anterior margins of plates III not overlapping sejugal furrow; medial margins of plates III and IV closely approaching but not overlapping each other medially, and only narrowly overlapping midsternal plate; lateral margins of plates III and IV not expanded dorsally to overlap lateral margins of tergite EF; posterior margins of plates IV and midsternal plate only narrowly overlapping expansive aggenital plate. Coxisternal plates III with

3 pairs of setae, plates IV with 2 pairs, excluding 3rd pair on midsternal plate; setae *3a* inserted anteriorly of transverse alignment with *3b* and *3c*; setae *4b* on midsternal plate inserted posteriorly of transverse alignment with *4a* and *4c*. Apodemes 3 well developed, extending medially from anterior condyle of trochanters III and weakened or interrupted near insertions of setae *3a*, sometimes continuing posteromedially of these setae to unite with apodemes 4; apodemes 3 also extending short distance laterad of these condyles; apodemes 4 fully developed, directed anteromedially from anterior condyle of trochanters IV to level slightly medial of insertions of setae *3b*; apodemes 5 abbreviated, not approaching insertions of setae *4a* or union with apodemes 4 medially. Metapodosomal and opisthosomal venters lacking invaginations designed for carrying fungal spores (sporothecae). Single expansive aggenital plate entirely covering primary genital opening, whose soft elongate valves are discernible underneath and attached to short crescentic genital apodeme anteriorly; aggenital plate with 2 or 3 pairs of well developed aggenital setae; genital setae absent; lateral margins of aggenital plate extended dorsally to approach but not overlap lateral margins of tergite H; posterior margin of aggenital plate nearly straight or slightly concave, narrowly overlapping base of caudal pseudanal capsule PS.

*Legs* (Figs. 3-6). Legs I to IV with ambulacra; leg I more massive than legs II to IV; leg IV longer than leg III, which in turn is longer than legs II and I. Leg I 5-segmented, with tibia longer than tarsus; single claw of tarsus I nearly sessile, greatly enlarged and tightly incurved, its apex fitting between enlarged spinelike unguinal setae *u'-u''* (Fig. 11). Legs II to IV each 5-segmented, with femur and tarsus subequally the longest segments, and with genu and tibia subequal in size on each leg; pretarsi II to IV short, thick, unsclerotized, each with paired claws and an empodium with long stalk and smooth, expanded apex (Fig. 10). Femora III and IV retain vestiges of sutural delineation between basi- and telo-femora; femora I and II with these sutural remnants effaced. Leg IV similar in shape to leg III except that its trochanter appears more subquadrangular than subtriangular due to slightly more

extensive development of its posterolateral surface. Segments of all legs lacking spurlike or flangelike outgrowths, and lacking spinelike setae other than *u'-u''* on tarsus I.

Number of setae (and solenidia in parentheses) on segments of legs I-II-III-IV, respectively, trochanters: 1-1-1-1; femora: 5-3-2-2; genua: 5-3-3-2; tibiae: 6(2)-4(1)-4(1)-4(1); tarsi: 13(2)-7(1)-7(0)-7(0); homologies of leg setae denoted in Figs. 3-6. Number, size, shape and position of setae similar on equivalent segments of legs II to IV, though femur II retaining 1 more seta, *l'*, than femora III and IV, genu IV with 1 less seta (lacking *l'*) than genua II and III, and tarsus IV with same number of setae, including *pl''*, as tarsi II and III but with proral seta *p'* present apically, which is short, stiff and finely barbed, instead of tectal seta *tc'*, which on tarsi II and III is subapical and long, flexible, smooth and shaped like *tc''*. Femur I with all setae setiform; seta *d* ultralong, attenuated on each of femora I to IV. Genu I with seta *d* moderately long, attenuated but less than half as long as *d* of femur I and tibia I; other setae of genu I and setae of genua II to IV not elongated. Tibia I with eupathidial seta *k''* setiform, long, tapered, at least as long as tibial segment, inserted closely proximad of solenidia  $\varphi_{1-2}$ , these short, rodlike; tibia II to IV with solenidion  $\varphi$  short, rodlike; seta *d* ultralong, attenuated on each of tibiae I to IV, similar to *d* on femora; other than *k''* and *d*, setae of tibia I short, except *l'* moderately long; other than *d*, setae of tibiae II to IV moderately long, though *l'* somewhat shorter on tibia II. Tarsus I with solenidia  $\omega_{1-2}$  short, rodlike, inserted proximally near  $\varphi_{1-2}$  of tibia (Fig. 12),  $\omega_1$  slightly larger than  $\omega_2$ ; tarsus I with setae *pl'-pl''* slender, attenuated, clearly the longest of tarsal setae *pv'-pv''* and *s* similarly short and setiform, *u'-u''* greatly thickened, spinelike, and with eupathidia *ft'-ft''* and *tc'-tc''* of moderate lengths, *p'-p''* shorter. Tarsus II with solenidion  $\omega$  short, rodlike, inserted proximally near setiform *pl''*; tarsi III and IV lacking  $\omega$ ; tarsi II and III with setae *tc'-tc''* elongated, with attenuated or narrowly spatulate tips, tarsus IV with *tc''* similarly shaped, but *tc'* absent; proral seta *p'* absent on tarsi II and III but present as a short, stiff, slightly barbed seta apically on tarsus IV; other setae of moderate

length on tarsi II to IV,  $u'-u''$  inserted symmetrically, setiform, similar to each other in size;  $pv'-pv''$  similar to each other in size, sometimes slightly stouter than  $u'-u''$ ,  $pv'$  inserted slightly more proximally than  $pv''$  on each leg, and  $pl'''$  on tarsus IV sometimes longer and stouter than  $pl''$  on tarsi II and III.

**Remarks.** Adult females of Athyreacaridae resemble those of Trochometriviidae Mahunka (1970) in having a tripartite tergite C and tripartite coxisternal plates IV, the same complement of setiform setae on coxisternal plates I to IV, all legs with 5 segments and ambulacra, leg I thickened, with 5 setae each on its femur and genu and with an enlarged, nearly sessile claw, leg IV with subquadrangular trochanter, legs I to IV with dorsal seta  $d$  ultralong on the femur and tibia, and tarsus IV with 7 setae including  $pl'''$ ,  $tc''$  and  $p'$  but lacking  $tc'$ . Trochometriviid females differ markedly from the former in having the idiosoma elliptical, the prodorsum with bothridia and capitate bothridial setae  $sc_1$  and with closely set stigmata and surface peritremes, the setae of tergite EF transversely aligned, the pseudanal tergite PS small, largely overlapped by tergite H dorsally and the aggenital plate ventrally, and bearing 2 pairs of small setae and a non-protuberant ventrocaudal opening, the metapodosomal venter with a pair of sporothecae within coxisternal plates IV and with apodemes 4 and 5 well developed but apodemes 3 reduced, the aggenital plate with only 1 pair of setae, the unguinal setae  $u'-u''$  setiform but the subunguinal seta  $s$  enlarged and spinelike on tarsus I, and tarsi II and III each with 8 setae, including  $p'$  and  $pl'''$ , and with the tectal setae  $tc'-tc''$  not elongated.

Athyreacarid females resemble those of Caraboacaridae Mahunka (1970) in having a fusiform body, a tripartite tergite C, the setae of tergite EF longitudinally aligned, apodemes 3 and 4 well developed but apodemes 5 reduced, leg I with 5 segments, leg IV with subquadrangular trochanter, dorsal seta  $d$  elongated on femora I to IV, and tarsus IV retaining proral seta  $p'$ . Caraboacarid females differ from athyreacarids in having the gnathosomal capsule greatly widened and the palpi vestigial, the prodorsum with bothridia and capi-

tate bothridial setae  $sc_1$ , the pseudanal tergite PS small, largely overlapped by tergite H dorsally and the aggenital plate ventrally, and bearing 1 pair of small setae and non-protuberant ventrocaudal opening, coxisternal plates I and II each with 2 pairs of setigenous structures of which  $1a$  modified into adhesive discs and  $2b$  sometimes spinelike, the metapodosomal venter with coxisternal plates III and IV fully consolidated medially, with a median poststernal apodeme and lacking a separate midventral plate, the aggenital plate lacking setae (alveolar vestiges of 1 pair sometimes evident), leg I not enlarged and without a claw, leg IV with a fused tibiotarsus and vestigial claws, femur and genu I each with 4 setae, lacking  $v'$  and  $d$ , respectively, tarsus I with 10 setae, lacking subunguinal seta  $s$  and apparently unguinal setae  $u'-u''$  (rather than the fastigials as indicated in LINDQUIST 1986, though further evidence needed to confirm this), with fastigial setae setiform rather than eupathidial, tarsus II with 8 setae including  $p'$ ,  $tc'-tc''$ ,  $pl'''$ , tarsus III with 7 setae including  $p'$ ,  $tc'-tc''$  but lacking  $pl'''$ , tibiotarsus IV with 6 tarsal setae (not 7 as stated in LINDQUIST, 1986) including  $p'$ ,  $tc'$  but lacking  $tc''$ ,  $pl'''$ , and with  $u''$  elongate-flagelliform.

In other respects, athyreacarid females resemble those of Heterocheylidae Trägårdh (see LINDQUIST and KETHLEY 1975) in having relatively prominent palpi, a fusiform body, the prodorsum lacking bothridial setae  $sc_1$ , dorsal seta  $d$  elongated on tibiae I to IV, and particularly in segment PS forming a caudal conical capsule bearing prominent pseudanal setae. However, heterocheylid females differ in many major respects from athyreacarids, in that the former have an exposed primary genital opening flanked by genital valves bearing 2 pairs of genital setae, a large, elongate-rectangular midsternal plate between coxisternal plates III and IV, the prodorsum with setae  $sc_2$  modified into "ampulliform organs", partial consolidation of tergites C and D, leg I not enlarged and lacking an ambulacrum, legs II to IV lacking claws, each with tarsal unguinal seta  $u''$  modified into a large spine and with the genual segment shortened and devoid of setae, and a neotenous suppression of a variety of setae on the leg segments and coxisternal plates, as

well as only 1 pair of aggenital setae and 2 pairs of pseudanal setae. The similarities between athyreacarid and heterocheylid females are hypothesized to be convergences : heterocheylid mites are thought to represent a much more early derivative lineage of Heterostigmata, as discussed by LINDQUIST (1986).

The phylogenetic relationships of Athyreacaridae with other families of heterostigmatic mites are problematical at present. The family is tentatively placed with Trochometridiidae in the superfamily Trochometridioidea, based on the synapomorphic setal pattern of tarsus IV (lacking *tc'* though retaining *tc''*, *pl''*, *p'*) and the elongation of seta *d* on the femur and tibia of each of legs I to IV ; other similarities between the 2 families noted in the remarks above are symplesiomorphies. Synapomorphies tentatively hypothesized for adult females of Athyreacaridae include the losses of prodorsal bothridia *sc*<sub>1</sub> and their setae, the loss of dorsal gnathosomal setae *ch*<sub>2</sub>, and the development of the pseudanal somite into a caudal capsule bearing 3 pairs of elongated *ps* setae and a protruding bivalved opening. Hypotheses on the relationships of Athyreacaridae will be developed further, in light of comparisons with other new family-group taxa of Heterostigmata, to be considered in a subsequent paper, at which time this family-group may require recognition as a subfamily or tribe instead of a family.

The family Athyreacaridae is currently known only from adult females that are phoretic on the ventral body surfaces of geotrupine scarab beetles of the genus *Neoathyreus*, tribe Athyreini. *Neoathyreus* is primarily neotropical in distribution, with about 45 species known from South America (HOWDEN 1985), 13 from Central America and Mexico (HOWDEN 1964, HOWDEN and GILL 1984), 2 from Hispaniola and 1 from Cuba (HOWDEN 1978). The tribe Athyreini sensu HOWDEN and MARTINEZ (1963) includes 3 other genera of which *Athyreus* and *Parathyreus* are South American and *Pseudoathyreus* is African-Oriental. Athyreacarid mites have not been found on beetles of these genera examined to date. The feeding habits and type of symbiotic association that these mites may have with their beetle hosts are unknown. The extensive areas of greatly plicated soft cuticle

between the dorsal and ventral plates of the body indicate that adult females are capable of very expansive physogastry, probably much like that observed in trochometridiid females (CROSS and BOHART 1979). The mites almost certainly undergo their life cycle in the subterranean galleries dug by their adult beetle hosts, but whether they are parasitoids or fungivores there is problematical. Very little is known about the habits of athyreine beetles. Observations on 2 species of *Neoathyreus* in South America indicate that an adult beetle digs a gallery 10 to 20 cm vertically into the soil and provisions the bottom of the burrow with a cut and compacted accumulation of graminaceous plant fragments (MARTÍNEZ 1987). Such provisioning would appear to form an ideal substrate for fungal growth, in the absence of beetle brood.

Description of the family is lengthy, and of type genus brief, because adult females of the only 2 known groups of species, both associated with beetles of the same genus, are so similar to each other morphologically. If mites representing other genera of this family are discovered as associates of other taxa of insects, the family description will perforce be shortened and broadened, with various of the characteristics described for the family becoming generic-level characteristics.

The name of the family and genus is a compound of tribal name of their beetle associates and "acarus", the common name latinized from Greek for mites generally. It is comparable in construction with "Caraboacaridae", a family of heterostigmatic mites associated with carabid beetles.

#### **Athyreacarus** new genus

Figs. 1-12

*Type species* : *Athyreacarus pleiotretus* new species. Genus based on adult females representing a cluster of apparently 4 species (3 undescribed), in distinction to another, undescribed cluster of 5 species (all undescribed).

*Diagnosis*. Adult females are readily distinguished from those of another cluster of undescribed species

in this family by lacking either setae  $v_2$  on the prodorsum or setae  $c_1$  on middorsal plate C or both, by usually having a paired field, or cluster, of porelike structures either laterad of scapular setae  $sc_2$  on the prodorsum or laterally on middorsal plate C, or in both areas, by having caudal setae  $ps_{1,2}$  the longest or subequally the longest setae of the idiosoma, and by their moderately large size (idiosomal length 470 to 650  $\mu\text{m}$ ).

*Description of Adult Female.* With the character states of the family Athyreacaridae as described above, but restricted and augmented as follows :

*Idiosomal dorsum.* Idiosomal length 470-650  $\mu\text{m}$ . Prodorsum with setae  $v_2$  present and short, or reduced to alveolar vestiges, these located closely anteriorad of alveolar vestiges of  $sc_1$ . Prodorsum sometimes with a paired cluster of 2-6 porelike structures laterad of setae  $sc_2$ . Tergite C usually lacking setae  $c_1$  on middorsal plate, but these setae may be present when setae  $v_2$  absent on prodorsum ; this middorsal plate sometimes with a paired cluster of 3-9 porelike structures laterally. Setae of prodorsum and tergites C, D, EF, H moderately short to ultralong, shorter than or subequally as long as ultralong setae  $ps_{1,2}$  caudally.

*Idiosomal venter.* Aggenital plate with 2 or 3 pairs of setae, usually lacking  $ag_3$ .

*Legs.* Tarsus I with tectal eupathidia  $tc'-tc''$  subequal to, or slightly (up to 5  $\mu\text{m}$ ) shorter than, fastigial eupathidia  $ft'-ft''$ .

**Remarks.** Adult females of *Athyreacarus* resemble those of the other cluster of undescribed species of Athyreacaridae at hand in the diversity of character states described for the family. Those of the latter cluster differ from *Athyreacarus* by retaining both  $c_1$  as well developed setae on the middorsal plate of tergite C and  $v_2$  as small setae on the prodorsal shield, by lacking paired cluster of porelike structures on the prodorsum and middorsal plate C, by having the caudal pseudanal setae well developed yet clearly exceeded in length by prodorsal setae  $sc_2$  and opisthosomal dorsal setae  $c_2, d, f$  and sometimes also  $c_1, e, h_{1,2}$ , by having the tectal eupathidia slightly to clearly longer than the fastigial eupathi-

dia on tarsus I, and by their moderately small size (idiosomal length 250 to 350, rarely to 425  $\mu\text{m}$ ).

Synapomorphies tentatively hypothesized for adult females of *Athyreacarus* include the loss of setae  $v_2$  or  $c_1$  or both, and the presence of at least faintly developed paired fields of porelike structures on the prodorsum or middorsal plate C or both. A synapomorphy hypothesized for those of the other cluster of species of Athyreacaridae is the enlargement of at least  $sc_2, c_2, d$  and  $f$  into ultralong setae that exceed the pseudanal setae in length.

#### ***Athyreacarus pleiotretus* n. sp.**

Figs. 1-12

*Diagnosis.* Adult females of this species are closely similar to those of an undescribed species found on *Neoathyreus excavatus* (Laporte) (= *N. quadridentatus* Howden) from El Salvador and of another found on *N. corinthius* (Klug) from Argentina in lacking setae  $c_1$  on middorsal plate C, in having caudal setae  $ps_{1,2}$  clearly longer than other setae of the body dorsum, and in having only 2 pairs of aggenital setae. They differ from both, however, in having a better defined subsurface reticulation on some areas of the idiosomal dorsum (particularly tergite D) and aggenital shield of maturely sclerotized specimens, in having the distance between the setal alveoli of  $sc_1$  and  $sc_2$  only 2 to 4 times (instead of 5 to 8 times) the alveolar diameter of  $sc_1$  on the prodorsum, and in having setae  $h_2$  shorter than  $h_1$  (instead of subequal to them). Those from Salvadorean *N. excavatus* further differ in usually lacking the paired fields of porelike structures on the prodorsum and in having these structures more weakly evident on middorsal plate C, in effacement of cupules  $ia, im, ip$ , in having a greater interval between the alveoli of setae  $e$  and  $f$ , and setae  $e$  similarly attenuated and at least three-fourths as long as  $f$ . Those from Argentinian *N. corinthius* further differ in retaining  $v_2$  as short setae on the prodorsum, in lacking the paired fields of porelike structures on middorsal plate C though having them on the prodorsum, and in having setae  $e$  shorter (about 1.5 times as long as interval between bases of  $e$  and  $f$ , compared with

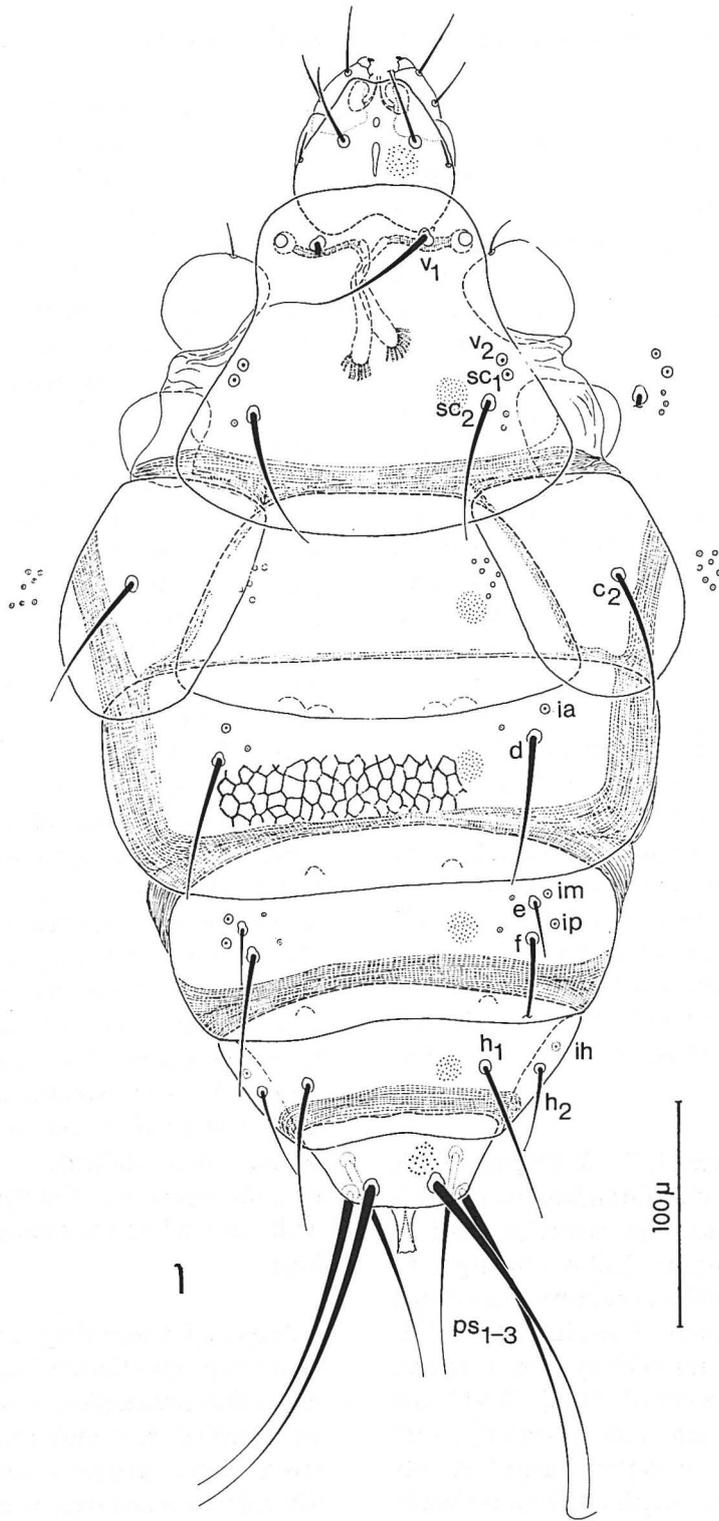


FIG. 1 : *Athyreacarus pleiotretus* n. gen. et sp., adult female, dorsal view of body ; variation in pattern of porelike structures on prodorsum and middorsal plate C shown peripherally. Density of surface punctation shown in circular areas on gnathosoma, prodorsum, and opisthosomal plates.

3 to 5 times as long as this interval in *A. pleiotretus*).

*Description of Adult Female. Gnathosoma* (Figs. 1, 2, 9). Gnathosomal capsule, excluding palpi, subquadrangular in ventral aspect, its width (80-85  $\mu\text{m}$ ) 1.1-1.2X greater than middorsal length (70-77  $\mu\text{m}$ ); anterior half of stylophore subtrapezoidal, its anterior margin slightly indented medially. Dorsal face of stylophore with setae  $ch_1$  slightly barbed, usually blunt-tipped, 37-58  $\mu\text{m}$  long, separated by interval of 30-36  $\mu\text{m}$ ; dorsomedian apodeme evident internally, interrupted near base and at level of bases of setae  $ch_1$ ; palpcoxal setae 12-14  $\mu\text{m}$  long. Ventral face of subcapitulum with 2 pairs of setae inserted on its anterior half, the medial pair barbed, separated by interval of 21-27  $\mu\text{m}$ , 51-72  $\mu\text{m}$  long and about 4-5X longer than the inconspicuous lateral pair; a pair of internal struts converging from posterolateral condyles of subcapitulum to level of bases of medial pair of ventral setae where interval separating struts is half of that basally (fig. 2). Cheliceral stylets 18-22  $\mu\text{m}$  long, attached to conspicuous levers that are each about 13-14  $\mu\text{m}$  wide and separated by only 3-4  $\mu\text{m}$ . Pharyngeal region outlined by thinly sclerotized walls, with weakly defined musculature. Palpi projected freely about 3-14  $\mu\text{m}$  anterior of apex of stylophore; palpal femorogenu with femoral seta blunter and shorter (27-32  $\mu\text{m}$ ) than genual seta (34-41  $\mu\text{m}$ ), both setae slightly barbed; length of palpal tibiotarsal solenidion 10-12  $\mu\text{m}$ .

*Idiosomal dorsum* (Figs. 1, 7, 8). Dorsal shields finely punctate, and with subsurface reticulation evident to variable extent on posterior third of prodorsal shield, on posterior half of midtergite C, on most of surface of tergite D between setae  $d$ , and on middle third of surfaces of tergites EF and H, between setae  $f$  and  $h_1$ , respectively (Fig. 1, shown on tergite D only). Prodorsal shield 159-171  $\mu\text{m}$  long medially, 183-207  $\mu\text{m}$  wide posteriorly, with vertical setae  $v_1$  smooth or slightly barbed, usually less tapered than, and its length (78-98  $\mu\text{m}$ ) slightly longer or shorter than, scapular setae  $sc_2$  (64-88  $\mu\text{m}$ );  $v_1$  transversely aligned with stigmata,  $sc_2$  inserted about 44-52  $\mu\text{m}$  from posterior margin of

shield; transverse interval between  $v_1$  47-58  $\mu\text{m}$ , between  $sc_2$  100-115  $\mu\text{m}$ . Alveolar vestiges of setae  $v_2$  and  $sc_1$  positioned 5-7  $\mu\text{m}$  apart on either side, lateral of oblique alignment with setae  $v_1$  and  $sc_2$ ; vestiges of  $sc_1$  located 9-19  $\mu\text{m}$  ( $\bar{x} = 14$ ,  $n = 20$ ) anterolaterad of bases of setae  $sc_2$  (this distance equivalent to 2-4 times alveolar diameter of  $sc_1$ ). A field or cluster of 2-6 porelike structures, more evident on some specimens than others, located closely laterad of bases of  $sc_2$  on either side. Opisthosomal dorsal setae slender, smooth, attenuate:  $d$  and  $h_1$  (61-83  $\mu\text{m}$ ,  $\bar{x} = 73$ ,  $n = 14$ ) nearly as long as  $c_2$  (76-97  $\mu\text{m}$ ),  $f$  (51-75  $\mu\text{m}$ ) about twice as long as  $e$  (24-47  $\mu\text{m}$ ); caudal setae  $ps_{1,2}$  ultralong (160-190  $\mu\text{m}$ ),  $ps_3$  shorter (100-130  $\mu\text{m}$ ),  $ps$  setae almost imperceptibly sparsely barbed. Middorsal plate C lacking setae  $c_1$  but with a cluster of 3-7 porelike structures on either side, like those on prodorsum. Tergite D with cupules  $ia$  7-15  $\mu\text{m}$  anterior or anterolaterad of bases of setae  $d$ , and a porelike structure 10-12  $\mu\text{m}$  anteromedial of  $d$ . Tergite EF with setae  $e$  and  $f$  nearly longitudinally aligned, cupules  $im$  3-7  $\mu\text{m}$  anterolaterad of  $e$ ,  $ip$  6-12  $\mu\text{m}$  anterolaterad of  $f$  and with a porelike structure 7-10  $\mu\text{m}$  anteromedial of each of setae  $e$  and  $f$ ; alveolus of  $e$  separated from that of  $f$  by interval of 5-10  $\mu\text{m}$  (equivalent to 1.0-1.6 times an alveolar diameter). Tergite D with pair of subsurface scleronodules anteromedial of setae  $d$ ; a more weakly formed pair of these structures also present in similar position on each of tergites EF and H. Tergite H with cupules  $ih$  12-17  $\mu\text{m}$  laterad or anterolaterad of  $h_2$  on ventrolateral curvature of tergite (often difficult to discern), and lacking porelike structures. Caudal pseudanal capsule PS with terminal valves strongly projecting, 23-27  $\mu\text{m}$  long.

*Idiosomal venter* (Fig. 2). Ventral shields finely punctate as on idiosomal dorsum, and with similar subsurface reticulation sometimes evident but only on aggenital and midsternal plates; all setae of ventral shields smooth, attenuated. Apodemes 1 heavily sclerotized and pigmented, about 4 times broader than apodemes 2. Apodemes 2 recurved posteromedially where they unite with prosternal apodeme. Prosternal apodeme continuous along entire length,

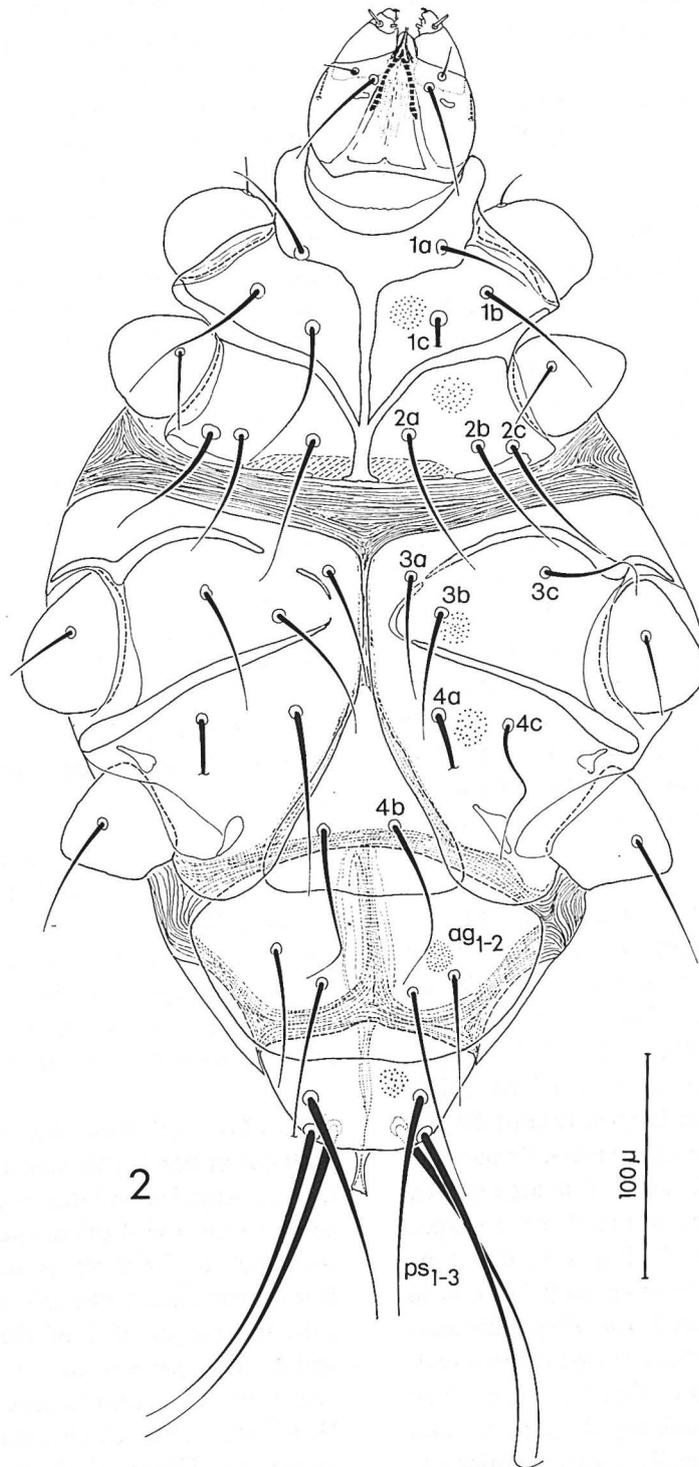


FIG. 2 : *Athyreacarus pleiotretus* n. gen. et sp., adult female, ventral view of body. Density of surface punctation shown in circular areas on coxisternal, aggenital, and caudal plates.

extending to posterior margin of coxisternal plates II, which is desclerotized to variable extent. Coxisternal plates I and II with setae subequal in length (64-80  $\mu\text{m}$ ) except *1a* shorter (49-66  $\mu\text{m}$ ) and *2a* sometimes 10-12  $\mu\text{m}$  longer. Setae *1a* inserted on apodemes 1, *1b* and *1c* nearly transversely aligned, and *2a*, *2b*, *2c* transversely aligned. Sejugal apodeme reduced, with short lateral remnant on either side, and sometimes with short or interrupted extensions from its midline union with prosternal apodeme. Coxisternal setae on plates III-IV similarly long, though *3b* and *4a* (73-90  $\mu\text{m}$ ) tend to be slightly longer than *3a*, *3c*, *4c* (58-77  $\mu\text{m}$ ), and *4b* slightly longer again (80-95  $\mu\text{m}$ ); rarely, *4c* absent on one side. Apodemes 3 gently arched laterally but interrupted or effaced medially near setae *3a*. Apodemes 4 oblique and nearly straight, continuous to level of variable effacement medially where they would otherwise unite with apodemes 3 near setae *3a*. Apodemes 5 reduced, extending for short distance anteromedially from posterior condyle of trochanters IV. Aggenital plate with usually 2 pairs of setae, *ag*<sub>1</sub> (80-100  $\mu\text{m}$ ) slightly longer than *ag*<sub>2</sub> (60-80  $\mu\text{m}$ ); rarely, *ag*<sub>2</sub> absent on one side, or another unpaired seta *ag*<sub>3</sub> present on one side, anterior of *ag*<sub>1</sub>; soft valves of genital opening 70-85  $\mu\text{m}$  long beneath aggenital plate.

*Legs* (Figs. 3-6). Legs I shorter than legs II to IV, with genual, tibial, tarsal segments about half again thicker than on other legs. Legs progressively longer from I to IV, their lengths, including trochanters but excluding apoteles: I, 170-195  $\mu\text{m}$ ; II, 195-215  $\mu\text{m}$ ; III, 240-270  $\mu\text{m}$ ; IV, 300-330  $\mu\text{m}$ . Leg I with tibia the thickest (60-65  $\mu\text{m}$ ) and longest (about 60  $\mu\text{m}$ ) segment, about 1.5X longer than tarsus, its paraxial face convexly arched; single claw of tarsus I greatly enlarged, tightly incurved, apposed to enlarged spinelike unguinal setae *u'*-*u''* (Fig. 11); *u'* simply spinelike but *u''* somewhat bifid apically. Tarsi II to IV with apices desclerotized for short distance (about 5  $\mu\text{m}$ ) before pretarsus; paired claws asymmetrical, with posterolateral element larger than anterolateral element on each leg (Fig. 10); claws with ventral thickenings basally, more prominently so on tarsi II and III; claws of tarsi IV smaller, less tightly curved basally than on tarsi II and III.

Number of setae on each of leg segments as stated for family; setal homologies denoted in Figs. 3-6. Femoral setae all setiform, with *d* greatly elongated on all legs (180-220  $\mu\text{m}$  on I and III, 160-185  $\mu\text{m}$  on II, 200-240  $\mu\text{m}$  on IV). Tibial seta *d* similarly elongated on all legs (120-155  $\mu\text{m}$  on I to III, 170-190  $\mu\text{m}$  on IV). Setae *pl'*-*pl''* on tarsus I elongate (75-85  $\mu\text{m}$ ), with almost imperceptibly, narrowly spatulate apices. Setae *tc'*-*tc''* on tarsi II and III and *tc''* on tarsus IV elongate (60-85  $\mu\text{m}$ ), with curved, narrowly spatulate apices; seta *p'* absent on tarsi II and III but present as short (24-28  $\mu\text{m}$ ,  $\bar{x}$  = 26.5, n = 11), stiff, poorly tapered and almost imperceptibly barbed seta dorsodistally on tarsus IV.

Length of idiosoma 470-540 ( $\bar{x}$  = 500)  $\mu\text{m}$ ; width between setae *c*<sub>2</sub> 210-250 ( $\bar{x}$  = 223)  $\mu\text{m}$  (15 specimens).

*Adult Male and Larva.* Unknown.

*Types.* Holotype, adult female, Honduras, Siguatepeque, 18 June 1979, removed by E. E. LINDQUIST from mesosternum of *Neoathyreus mexicanus* collected by J. A. CHEMSAK & A. E. MICHELbacher; type No. 20,348 in the Canadian National Collection.

*Paratypes*: 15 adult females, with data given below; paratypes deposited in the British Museum (Natural History), London, the Canadian National Collection, Ottawa, the United States National Museum of Natural History, Washington, D. C., the Zoologisches Museum, Universität Hamburg, and the collection of M. KALISZEWSKI.

*Locality and Host Records.* Based on limited material at hand, this species has a wider distribution in association with a greater variety of host species than the 8 other species of Athyreacaridae for which we have representatives. Records extend from Costa Rica north to central Mexico, coinciding with the ranges of 2 of the species of hosts with which it is known to be commonly associated, based on authoritative host determinations by Dr. H. F. HOWDEN. Confirmed hosts: *Neoathyreus mexicanus* (Klug), *N. interruptus* Howden, *N. tridentatus* (Macleay); unconfirmed host: *N. excavatus* (Laporte).

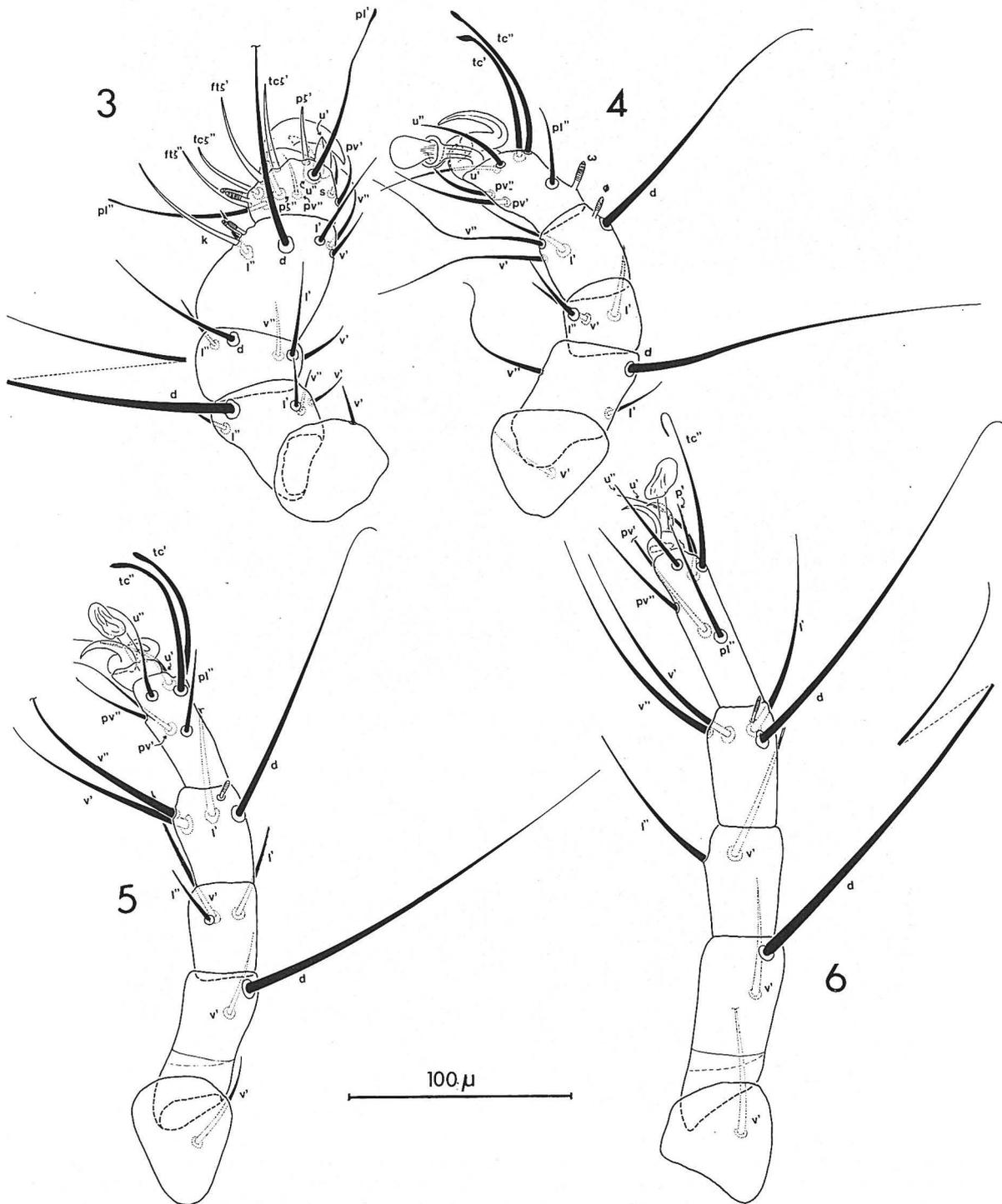


FIG. 3-6 : *Athyreacarus pleiotretus* n. gen. et sp., adult female, legs I to IV in anterolateral aspect : 3, leg I ; 4, leg II ; 5, leg III ; 6, leg IV.

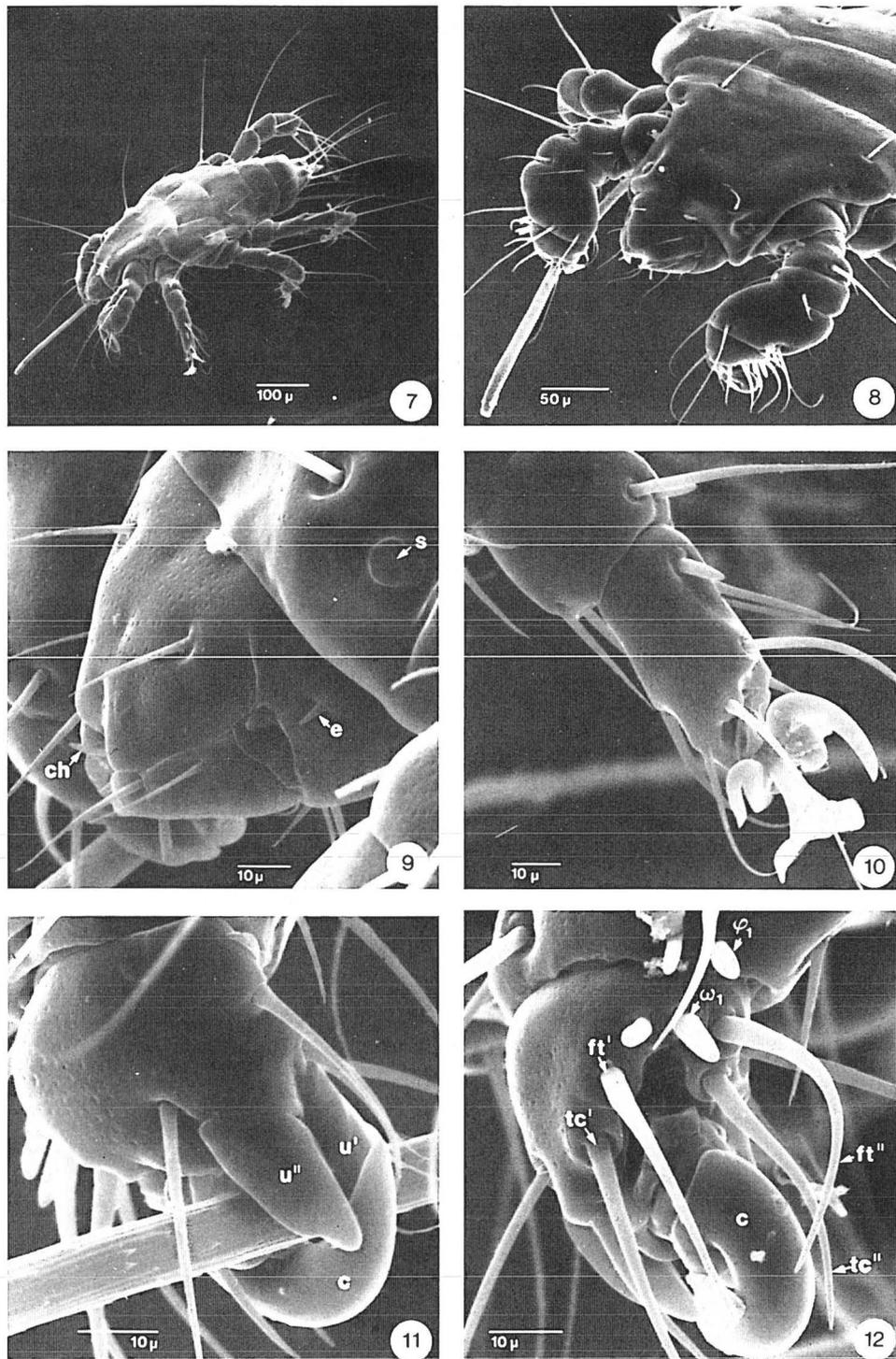


FIG. 7-12 : *Athyreacarus pleiotretus* n. gen. et sp., scanning electron micrographs of adult female : 7, habitus, dorsolateral aspect, with a host beetle hair grasped by right leg I ; 8, anterior half of body and legs I, anterodorsal aspect, with a host beetle hair grasped by right leg I ; 9, gnathosoma and prodorsal stigma, dorsolateral aspect ; 10, tibia and tarsus of leg II, dorsal aspect, showing asymmetry of claws and soft, expanded apex of stalked empodium ; 11, tarsus of leg I, ventral aspect, showing host beetle hair held by enlarged tarsal claw in apposition to the two enlarged, spinelike, unguinal setae ; 12, tarsus of leg I, dorsal aspect, showing the proximity of the two tarsal and the two tibial solenidia, the subequally sized fastigial and tectal eupathidia, and the dorsoapical depression accomodating the soft cuticle of the pretarsus and levation of its claw. Abbreviations : c, claw ; ch, cheliceral stylet ; e, palpcoxal seta ; s, stigma ; u'-u'', unguinal setae ; notation in Fig. 12 explained in text.

COSTA RICA. Puntarenas : 1, Monteverde Reserve, 1 500 m, 17 Aug. 1987, ex. forefemur of *N. tridentus* collected by H. & A. HOWDEN.

EL SALVADOR. San Salvador : 3, San Salvador, 2 June 1958, ex. mid-trochanteral hairs of *N. mexicanus* collected by O. L. CARTWRIGHT ; 1, same data except 23 May 1958, ex. ventral pronotal hairs of *N. mexicanus*.

HONDURAS. Francisco Morazan : 4, Zamorano, 7 July 1948, ex. *N. excavatus* (?) collected by T. H. HUBBELL ; 1, see holotype data.

GUATEMALA. Escuintla : 2, El Salto, 28 June 1934, between trochanters of forelegs of *N. interruptus* collected by F. X. WILLIAMS. Suchitepéquez : 1, Rio Olimpo, Finca San Rafael, Cuyotenango, 1 Nov. 1965, ex. prosternum of *N. mexicanus* collected by J. M. CAMPBELL.

MEXICO. Veracruz : 2, Lago Catemaco, 8-16 Aug. 1960, ex intercoxal region of *N. interruptus* collected by H. F. HOWDEN.

*Etymology.* The specific epithet, *pleiotretus* is a latinized combination of the Greek words *pleio* meaning more, and *tretos*, meaning porous, and is intended to indicate the paired fields of porelike structures on the prodorsum and tergite C of adult females of this species.

*Remarks.* In addition to the material above, we have studied 11 females closely similar to this species removed from beetles of *Neoathyreus granulicollis* Howden from several localities in Mexico, as follows :

Guanajuato : 5, 11 mi. SW Acombaro, 17 Aug. 1954, ex. forefemur and mesosternum of *N. granulicollis* collected by E. G. LINSLEY, J. W. MACSWAIN, R. F. SMITH. Jalisco : 3, 15 km. S. Mazamitla, 5500ft., 29 July 1952, ex. abdominal venter of *N. granulicollis* collected by F. W. WERNER ; 2, Guadalajara, 19 Aug. 1970, ex. mesosternum of *N. granulicollis* collected by G. ECHO. Nayarit : 1, Jalisco, 23 Aug. 1954, ex. thoracic venter of *N. granulicollis* collected by J. KEEF. These specimens differ from typical *Athyreacarus pleiotretus* by their larger size (idiosomal length 555-635  $\mu\text{m}$ ,  $\bar{x}$  = 590), by the greater distance between the alveolar vestiges

of setae  $sc_1$  and  $sc_2$  (17-29  $\mu\text{m}$ ,  $\bar{x}$  = 21), by the greater length of setae  $h_1$  (80-150  $\mu\text{m}$ ,  $\bar{x}$  = 111) which in some individuals approach the length of setae  $ps_{1,2}$  (170-190  $\mu\text{m}$ ), and by the greater length of proral seta  $p'$  on tarsus IV (27-37  $\mu\text{m}$ ,  $\bar{x}$  = 32). The latter four differences may be correlated with larger body size. These specimens are excluded from the type series but tentatively regarded as variants of *A. pleiotretus* until additional material from other localities becomes available to assess variability better between populations of the same species.

The paired fields of porelike structures on the prodorsal shield and middorsal plate C in adult females of *Athyreacarus pleiotretus*, and developed to a lesser extent in those of other species of this genus, are unique among the described taxa of Heterostigmata. The origin and function of these structures are unknown. On middorsal plate C, 1 pair of the porelike structures may represent the vestiges of setae  $c_1$ , as a rudimentary nub of a seta sometimes appears to be present, much like those in the alveoli of  $v_2$  and  $sc_1$  on the prodorsum. However, the other porelike structures are probably not of setal origin : they are usually asymmetrical in number and position in the paired fields ; clusters of several setae are not found in small paired fields in these or other areas in any of the known acariform mites ; and on middorsal plate C, they are present in one undescribed species of *Athyreacarus* that retains  $c_1$  as strongly developed setae on the same plate.

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