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COLLOHMANNIA JOHNSTONI N. SP. (ACARI, ORIBATIDA) FROM WEST VIRGINIA (U.S.A.), INCLUDING DESCRIPTION OF ONTOGENY, SETAL VARIATION, NOTES ON BIOLOGY AND SYSTEMATICS OF COLLOHMANNIIDAE

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ABSTRACT — *Collohmannia* (Collohmanniidae) is a genus of physically large oribatid mites with low extant diversity and high endemism. It includes the only species outside Brachypylina known to exhibit strong sexual dimorphism and courtship behavior, including nuptial feeding, and it has phylogenetic importance as a possible close outgroup of the diverse mixonomatan taxon Ptyctima. Herein, we describe all instars of the first member of the genus known outside of Eurasia: *Collohmannia johnstoni* **n. sp.** from forest litter in the mountains of northern West Virginia, USA. Males are distinguishable by the apparatus on genu IV used to hold the nuptial fluid: a hypertrophied seta with flattened, asymmetrical diamond shape and an absence of small cuticular tubercles. We also redescribe the genus *Collohmannia* using characters of both adults and juveniles, and give a new diagnosis of Collohmanniidae; noted for the first time is an extensive association of setae with dermal glands. Field samples suggest that *C. johnstoni* is highly aggregated, with a mean density of 100 per m^2. Sample data are consistent with a 1:1 sex ratio and with the continual presence of all instars in the population, probably even during winter. Females are ovoviviparous, retaining eggs in their oviducts until the development of the larva, and larvae were found within females on all sampling dates. The prelarva (within eggs removed from females) is moderately regressed, retaining distinct leg remnants. Based on laboratory observations and gut contents of field-collected specimens, all active instars appear to feed directly on decomposing leaves of deciduous trees. Insemination was not directly observed, but courtship is generally similar to that previously described for *C. gigantea*. Morphological and molecular data concerning relationships between Collohmanniidae and Ptyctima are summarized but the issue remains unresolved. Ptyctima Oudemans, 1906 is considered equivalent to Euptyctima Grandjean, 1967.

KEYWORDS — Appalachian soil fauna; oribatid mite; vertitions; sexual dimorphism; nuptial feeding

INTRODUCTION

Species of the oribatid mite family Collohmanniidae are of interest for several reasons. First, they are among the largest of oribatid mites, with total length of adults exceeding 1 mm and in some cases 2 mm. Second, they are among the few oribatid mite taxa, and the only one outside Brachypylina, known to have courtship behavior and strong sexual dimorphism (Schuster 1962, Grandjean 1966, Behan-Pelletier and Eamer 2010). Third, they are rather isolated and apparently relictual in both morphological and biogeographic senses. Their morphological distinctness has resulted in the recognition of Collohmannioidea, one of several monofamilial superfamilies in the middle-derivative and para-

phyletic infraorder Mixonomata (Grandjean 1969; Schatz *et al.* 2011). As indicated below, the few known species have rather restricted distributions in forested temperate regions of Eurasia and North America. Fourth, they potentially occupy an important phylogenetic position as the sister-taxon of Ptyctima, a diverse group of middle-derivative oribatid mites with a characteristic defensive form and behavior (Grandjean 1969; Sanders and Norton 2004). Lastly, they are among the best known oribatid mites in terms of exocrine glands and chemical ecology (Raspotnig 2006 and cited references).

This high level of interest contrasts with their very low diversity. When proposed by Grandjean (1958a), Collohmanniidae was monobasic and the family currently comprises only four nominal species, in two genera. *Collohmannia* Sellnick, 1922 includes three named species, of which the best known is the type-species *C. gigantea* Sellnick, 1922 (= *C. nova* Sellnick, 1932) from southeastern Europe. Weigmann (2006) indicated that it has a Holarctic distribution, but this was an error (G. Weigmann, pers. comm., 2012). Also incorrect is the record of this species from the Soviet Far East (Krivolutsky *et al.* 1995; Ryabinin and Pan'kov 2002); there is no primary record of any *Collohmannia* species from this region (N. A. Ryabinin, pers. comm., 2011). Further, the records of *C. gigantea* from the Caucasus (Krivolutsky *et al.* 1995; Murvanidze and Darejanashvili 2000; Shtanchaeva and Subías 2010) are incorrect; they are based on specimens of an undescribed *Collohmannia* species (see below). The other two species are relatively poorly known and represented only by the original collections: *C. asiatica* Krivolutsky and Christov, 1970 (in Christov 1970) from the Republic of Tadjikistan and the fossil species *C. schusteri* Norton, 2006 from Baltic amber. Sellnick (1918) proposed the monotypic second genus, *Embolacarus* and its type-species *E. pergratus* based on a Baltic amber fossil that no longer exists. This mite has not been rediscovered, but based on the original description, Norton (2006) included *Embolacarus* in Collohmanniidae and noted its possible synonymy with *Collohmannia*.

The family is somewhat more diverse than would be suggested by its two extant and two fossil species. An undescribed species of *Collohmannia* from West Virginia, USA, has been mentioned in several publications (e.g. Marshall *et al.* 1987; Norton and Behan-Pelletier 2009) and sequence data for its 18S rRNA gene is present in GenBank (AF022029, as *Collohmannia* sp.; Pachl *et al.* 2012). We have seen specimens of two other undescribed extant *Collohmannia* species: one is from the Caucasus (Sukhum, Abkhazia), the other is from Turkey (mites kindly provided by Drs. Andrei Tolstikov and Umucusum Shtanchaeva, and by Prof. Dr. Reinhart Schuster, respectively). Also, we have briefly studied a specimen of yet another new species from Baltic amber, courtesy of Carsten Gröhn. The emerging picture is that, while having very modest diversity, extant collohmanniid species have a high degree of endemism, and probably there are more species to discover. Since the three known Baltic amber collections each represents a different species, past diversity may have been significantly greater.

Our main purpose is to formally describe the species from West Virginia, as *Collohmannia johnstoni* **n. sp.** The development and variability of leg setation are complicated subjects and therefore treated separately, except for some generalities included in the formal description. Like the European species *C. gigantea*, juveniles are collected along with adults, and it is easily maintained alive in the laboratory, at least for short periods of time. This allowed us to study all developmental instars and to obtain some limited information about feeding and reproductive biology; like *C. gigantea*, *C. johnstoni* feeds directly on decaying leaves, and the two species have a similar courtship behavior. Secondary goals are to use recent or new data about adults and juveniles to reformulate the generic description and familial diagnosis, and to summarize ideas about phylogenetic relationships of the family.

MATERIALS AND METHODS

Specimens — Adult and juvenile specimens of *Collohmannia johnstoni* **n. sp.** were extracted from samples of litter and humus layers with Berlese-Tullgren funnels; locations are described below.

Collecting vessels contained either 70-95 % ethanol (for preserved specimens) or a 9:1 plaster-of-Paris and charcoal mixture (for living mites). Additional larvae were reared from eggs laid by females in small (ca. 30 ml) glass culture jars with plaster bottoms (as above); these were kept at room temperature with food (discussed below) supplied as needed. Preserved specimens of *C. gigantea* – about three dozen adults, two deutonymphs and one tritonymph – used for direct comparisons, were collected from Krottendorf, Austria by Dr. Manfred Walzl and donated for our study.

Observations of living mites — *Collohmannia johnstoni* **n. sp.** was observed at various times in the laboratory since its original discovery in 1980, using several types of small dishes with a plaster-charcoal substrate. We also used parallel glass microscope slides held in a slotted wooden block, with plaster-charcoal partially filling the 2-3 mm space between them, which allowed observations in lateral aspect using a horizontally oriented stereomicroscope.

Specimen preparation and documentation — Cuticular features were observed on whole or dissected specimens in cavity slides with lactic acid medium (Grandjean 1949b). For observations with oil-immersion lenses, dissected parts were permanently mounted in Hoyer's medium. To help understand certain structures, thick sections were cut with a razor blade through cleared (by lactic acid or Nesbitt's fluid) or uncleared specimens, then studied in cavity slides or mounted in Hoyer's medium. Most observations were made with Nikon E800 or Jenaval compound microscopes, under bright-field or Nomarski (DIC) illumination; living mites were studied with a Nikon SMZU stereomicroscope. Light micrographs were obtained with Nikon CoolPix 995, AmScope MU800 or Scope Tec DCM 500 digital cameras mounted on the various microscopes. When appropriate, image stacks were combined using the Helicon Focus Pro (v. 5.0) suite; these are indicated below as 'layered.' Most of the images were color-corrected with GIMP (v. 2.6.8) for levels, color balance and sharpness (unsharp mask filter). Drawings were made with a Wacom Intuos 4M pen tablet using a live capture from the camera transferred through a VLC media player (v. 0.9.9) as a background in the InkScape graphic suite (Sidorchuk and Vorontsov 2014). Specimens for scanning electron microscopy (SEM) were critical-point dried and sputter-coated with gold (prepared by Dr. V. M. Behan-Pelletier).

Terminology and measurements — Morphological terminology is mostly that of F. Grandjean (see Travé and Vachon 1975 for references and Travé *et al.* 1996 or Norton and Behan-Pelletier 2009 for overview); terms are translated from French (van der Hammen 1980) but in most instances Grandjean's original abbreviations are retained. Body length was measured in lateral aspect, from the tip of the rostrum to the posterior edge of the notogaster. Unless otherwise noted, width refers to the maximum width in dorsal aspect (found on the notogaster). The degree of hysterosomal distension was not considered during measurements but it can affect length and width by several percent, due to telescoping of the rather wide dorsal part of the sejugal articulation. Measurements of specific structures or distances are only representative, taken from roughly average-sized individuals and usually with no range given. If males and females differ significantly, both measurements are given, preceded by M and F, respectively. Setal formulas are given as number per segment for appendages (from femur to tarsus) and as number per podosomal segment (I-IV) for epimeres. Paired structures are described in the singular unless noted. Unless otherwise indicated, parentheses around leg setal notations denote the two members of a pseudosymmetrical pair on a given leg segment, rather than a true bilateral pair.

RESULTS

Collohmannia johnstoni n. sp. (Figs. 1-19)

Diagnosis — With characters of *Collohmannia* (see Sellnick 1960 and below).

Adult. Total length 1435-1945 μm. Hysterosoma slightly to significantly compressed dorsoventrally, 1.2-1.5 times broader than high. Bothridial seta filiform, gradually tapered in distal third; with minute, rather sparse barbs; dorsolaterally directed

with gentle sigmoid curve in middle third. Notogaster with five pairs of subflagellate setae (e_1, e_2, h_1, h_2, p_1), noticeably longer than others. Leg tarsus I with four solenidia; neotrichy limited to several (lateral) setae; tarsus of both sexes similar, not noticeably swollen relative to other tarsi, male without ribbon-like setae. Tarsus II with setal pair (*pl*). Seta *v"* of male genu IV hypertrophied, in form of large, flattened, asymmetrical diamond, with low crest across widest part and distally tapered to point that extends well beyond end of segment; tibia IV not modified.

Ontogeny. Setal formula of protonymphal leg IV 0-0-0-0-7; tectal pair forms in deutonymph. Iteral setae form in tritonymph on tarsi I-III, absent from IV; accessory pair (v_3) forms in tritonymph on tarsus IV.

Adult

Dimensions, color and general form (Figs. 1-4) — Adults are large, dichoid mites having a sejugal articulation that is broad dorsally but narrow ventrally; relative movement of proterosoma and hysterosoma therefore is restricted mostly to modest dorsoventral flexing, with the base of the prodorsum capable of slight telescoping under the notogaster, particularly in males. The total length of females (n = 49) ranges from 1542-1950 μm (mean 1767) and that of males (n = 35) 1435-1688 μm (mean 1555). Maximum width is respectively 970-1333 μm (mean 1148) and 800-1058 μm (mean 946), slightly less than 2/3 the total length. In both sexes the hysterosoma is usually about 1.4 times wider than high at the level of the genital plates (mean 1.36; range 1.23-1.55), and is sub-elliptical in cross-section (Figs. 1D, 10B); the under-turned part of the notogaster can occupy ¾ of the width in ventral aspect. Non-gravid, contracted females can have a rather flattened venter. In dorsoventral aspect, outlines are well-rounded (Figs. 1A, B; 2A, B): that of the prodorsum is somewhat pear-shaped in both sexes and the notogaster is usually elliptical or (in females) sometimes slightly ovate, wider anteriorly (see below).

In reflected light, living mature adults are opaque and nearly black (Fig. 19D). In living teneral adults and in adults long-preserved in alcohol there is more heterogeneity of color, as follows. The notogaster is medium to dark reddish-brown (Fig. 2), with a darker, narrow collar along the anterior border. The mid-region usually appears somewhat darker, due at least in part to internal objects that show vaguely through the slightly translucent cuticle; these can include food and fecal boli, but most noticeably the region around the pair of large opisthonotal glands usually darkens in alcohol ('autocoloration' of Raspotnig *et al.* 2001). One anomalous male had a variegated pattern (Fig. 2D). In females, eggs nearest the surface can be discerned through the cuticle. Ventral sclerites and legs are medium brown, mostly lacking the reddish tint. The prodorsum is the lightest major sclerite, mostly yellowish brown. It appears darker anteriorly due to the doubled cuticle of the rostrum and to the underlying mouthparts showing through the slightly translucent cuticle; the posterolateral edges are also darker, as described below. Articulating cuticle is cream-colored and setae are hyaline and shine in reflected light, contrasting strongly with the pigmented sclerites (Figs. 2, 9A, 10).

The genders tend to differ in several body measurements and proportions, but these overlap and therefore are not definitive. For example, adults longer than 1700 μm are invariably female, and those shorter than 1500 μm are invariably male. Females usually have a proportionally larger hysterosoma, sometimes much larger: measured in dorsal view, the projected surface area of the notogaster is 8-17 times larger than that of the prodorsum, while in males it is less variable and usually smaller, 6-9 times. In ventral view, the prosoma (measured along the midline from tip of rostrum to posterior end of coxisternum) usually occupies a slightly greater proportion of the body length in males (0.36-0.44) than in females (0.33-0.39). Another difference is that usually the notogaster of females is proportionally broader anteriorly; as a result, in the humeral region a line drawn from the intersection of prodorsal and notogastral outlines to the insertion of seta *cp* on the same side forms an angle with the body axis that is 36-48° in males (Fig. 2D) but 48-57° in females.

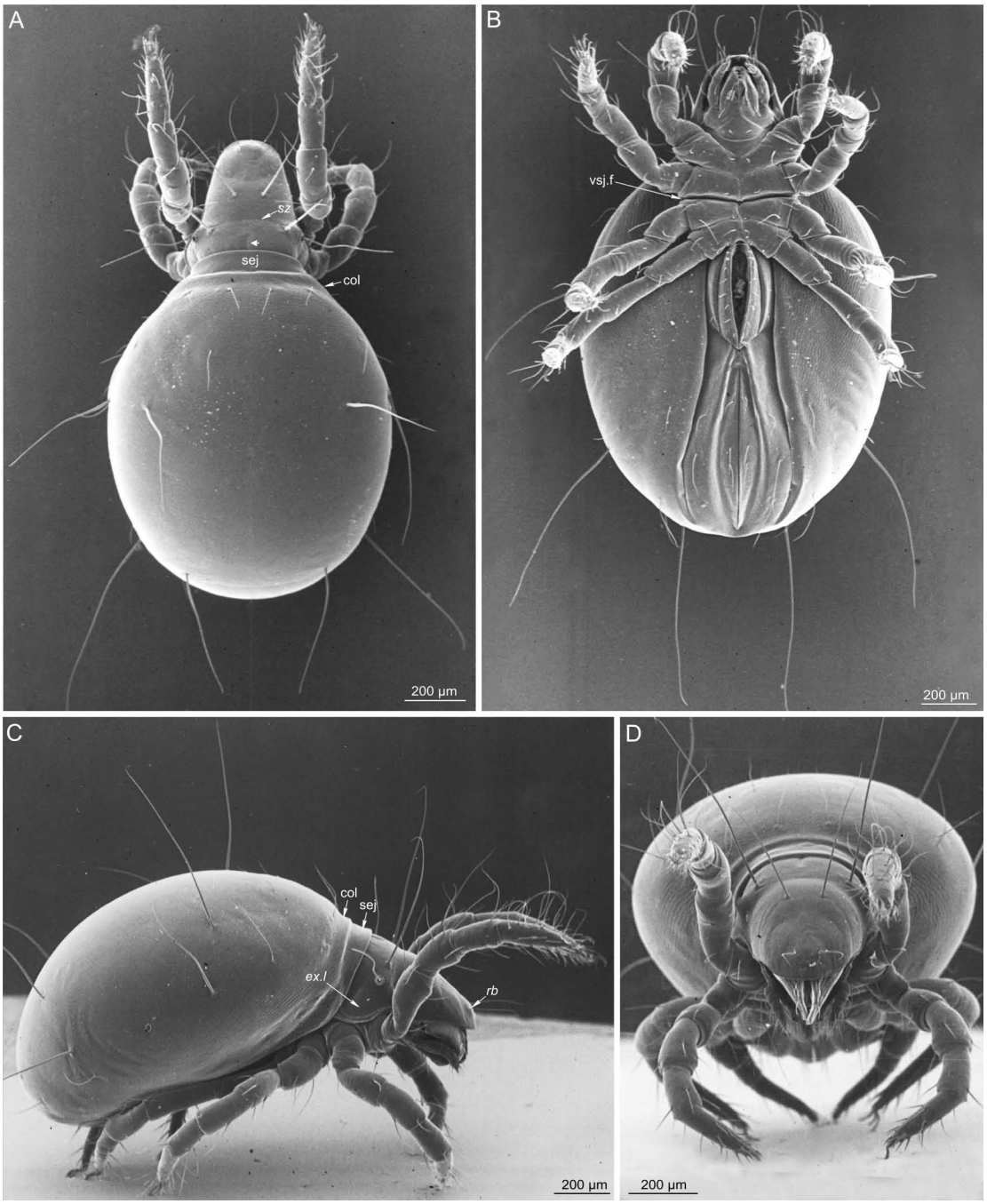


FIGURE 1: *Collohmannia johnstoni* **n. sp.** adults, scanning electron micrographs: A – male, dorsal view; B – female, ventral view; C – male, lateral view; D – male, frontal view. Abbreviations: *col* – notogastral collar, *ex.l* – exobothridial lobe; *rb* – rostral bulge, *sej* – sejugal articulation, *sz* – linear groove, *vsj.f* – ventrosejugal furrow.

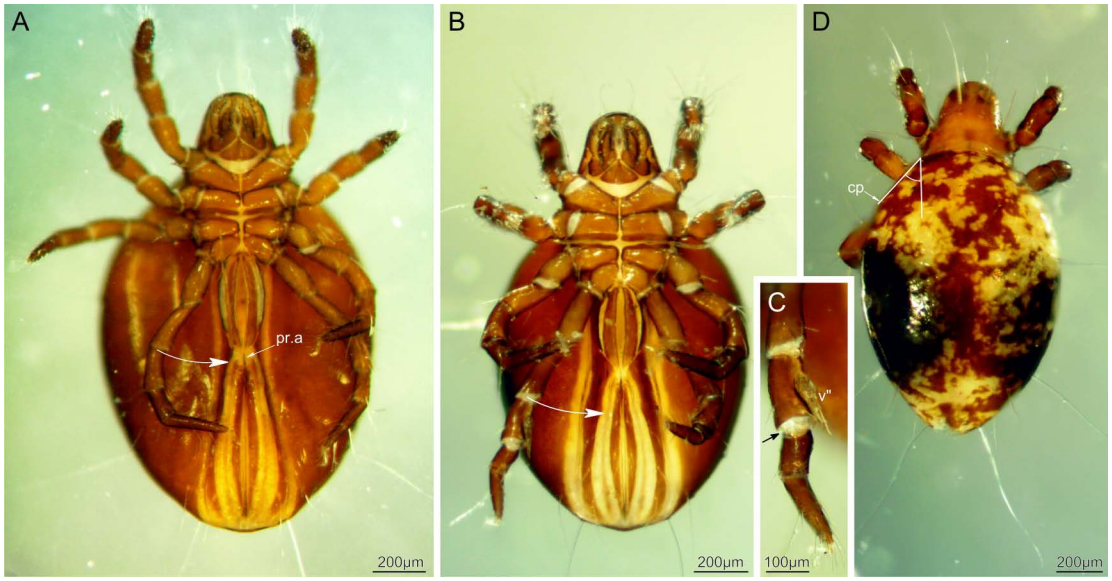


FIGURE 2: *Collohmannia johnstoni* **n. sp.** adults, light micrographs, incident illumination: A, B – female and male (respectively) in ventral view; arrows indicate the reach of femur IV. C – male leg IV, note seta *v"* and the broad articulation (arrow) allowing dorsal flexing of tibia. D – male with aberrant cuticle coloration, dorsal view; superimposed angle is indicative of gender (see explanation in text). Abbreviations: *pr.a* – preanal apodeme, *cp* – position of notogastral seta. Each image layered and color- and sharpness-enhanced (see Material and Methods).

Other than the highly modified genu IV seta *v"* of males (see below), two traits easily distinguish sexes (Fig. 2A, B). Measured along the sagittal plane, the genital plates of females are slightly longer than the coxisternum, while in males they are slightly shorter than the coxisternum. Second, males have proportionally larger legs. Specifically, when leg IV is directed posteriorly, in females the femur reaches only to the posterior end of the genital plate, whereas in males it reaches further, to a level about one-fifth of the distance along the anal plate.

Integument (Figs. 5, 7, 9) — Sclerotized cuticle is shiny in reflected light, and lacks apparent cerotegument or adherent debris. The notogaster and plates of the anogenital region – but not the prodorsum or coxisternum – have imbricate surface sculpture, giving a 'shagreened' appearance that is discernible in transmitted light (Fig. 5A-C, G), but most apparent in reflected light and under SEM (Fig. 6C). Articulating cuticle is simple and cream-colored in preserved specimens, but some broad articulations are bordered with cuticle having both the color of articulations and the imbricate surface sculpture of sclerites (*t.cu*, Fig. 5A, G). This type of cuticle is referred to below as transitional; its appearance and location is consistent with having elasticity that is intermediate between that of the harder sclerite and the soft articulating cuticle, but this is supposition. Seen in transmitted light, nearly all sclerotized cuticle has dense, fine porosity, but small circumscribed areas of more luminous and slightly larger pores (porose areas) exist and are conspicuous in transmitted light (Figs. 3-5). The alveolus of most body setae is surrounded by a small area or single ring of such broader pores (Fig. 5D-G), and often a larger porose area (*po* in the figures) is adjacent to the seta or a short distance away. These porose areas have different forms and sizes, as described below, but each seems to be underlain by a cluster of gland-like cells (*gl*, Fig. 5B; see Remark 1).

Certain regions of several structures, including the labrum, spermatopositor and chelicera, have special cuticle in which sclerotized, pigmented layers are overlain by sharply contrasting layers that are hyaline and flexible. We refer to these as 'embedded' sclerites.

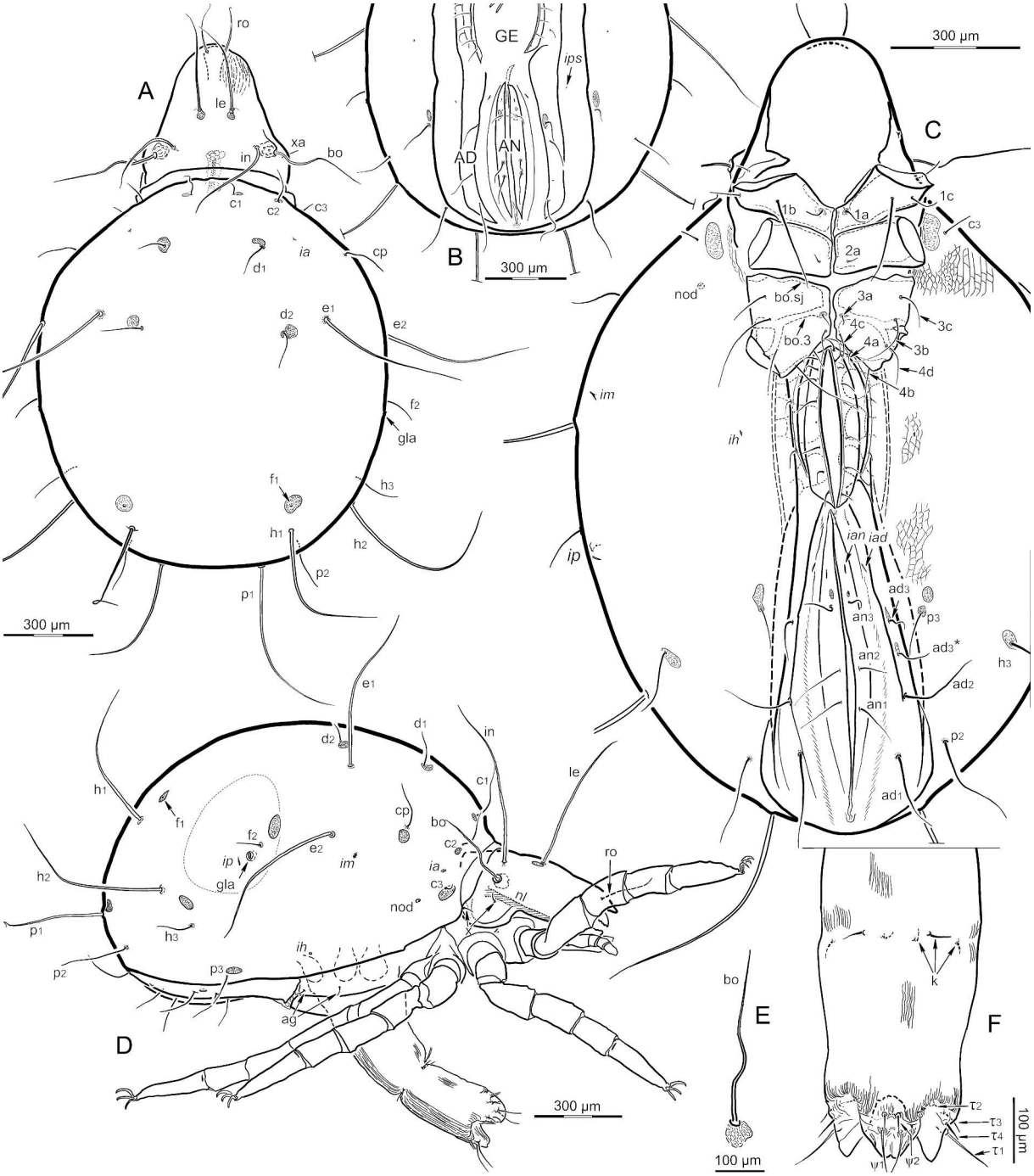


FIGURE 3: *Collohmannia johnstoni* **n. sp.** female: A – dorsal view, legs omitted; B – partial ventral view of strongly distended specimen; C – ventral view of contracted specimen, legs and gnathosoma omitted; D – lateral view, ovipositor extended, leg details omitted; E – bothridial seta; F – distal part of ovipositor, posterior view (artificially distended slightly to better show setae *k*). See text for abbreviations.

Prodorsum (Figs. 1, 3, 4, 7-9) — The sclerotized cuticle of this region forms an isolated aspis, *i.e.* it is separated laterally from epimeres by soft cuticle (Figs. 7A, 9A). Its outline in dorsal aspect is broadest near the level of the bothridia, abruptly narrowing anterior to setae *in*, then narrowing slightly and gradually to the broadly rounded, smooth-edged rostrum. In lateral aspect it curves only slightly from its base to the rostral setae, then slightly more strongly to the smoothly rounded rostral margin. The length, comprising about 25-35 % of the total body length, is about equal to the maximum prodorsal width in dorsal aspect. The cuticle of the aspis is uniform in having dense fine pores, which are absent only from the pale, thin edge of the rostrum. Prodorsal setae generally have no conspicuous basal ring of larger pores, and only one (paired) porose area exists, usually positioned posterior and adjacent to the lamellar seta (*po*, Fig. 7A); rarely the seta inserts eccentrically within the area. This round area (ca. 30-50 μm diameter) shows as a sharply defined macula in transmitted light, made pale due to the thinness of its internally excavated cuticle (Fig. 7E); it looks superficially similar to a muscle sigillum, but is underlain by gland-like cells, not muscles (*gl*, Fig. 7F).

With minor exceptions, the aspis surface is smooth and without imbricate sculpturing or obvious relief features. The exceptions include a slight medial bulge on the rostrum (*rb*, Figs. 1C, 7A-D) and two indistinct transverse grooves – one linear, just anterior to the interlamellar setae (*sz*, Fig. 1A) and a second, broader groove anterior to the lamellar setae. There is also a small longitudinal groove posteromedially, above the sagittal apodeme (Fig. 1A, arrow).

Seen in sagittal section, the rostral tectum occupies the distal 40 % of the aspis (Fig. 7B) and has distinct regions. The distal edge comprises a very narrow, uncolored tectal limb (*tl*), ca. 20-30 μm wide. Throughout the rest of the tectum the dorsal and ventral (rostrophragma, *rp*) cuticles are clearly distinguishable. These cuticles are well separated in the region of the rostral bulge (Fig. 7B, D), then come together at mid-length, and then separate in the posterior region of the tectum where the sclerotized rostrophragma diverges from the surface cuticle. At its posterior end the rostrophragma attaches (at *) to the soft cheliceral frame (*c.fr*, Fig. 7C). A pair of paler regions lie posterolateral to the rostral bulge; here the two cuticular layers nearly touch (large black arrow in Fig. 7A, D), and the internal surface is excavated to form irregular striae, seen in transmitted light (Figs. 3A, 4C, 7A)

Two regions of the aspis margin are distinguishable in lateral view, with the inward-facing prodorsal condyle (*pK*) marking their boundary (Figs. 4A, 9D). The simple, thin edge of the rostral tectum occupies the anterior half, with a weakly concave outline. Running proximally from *pK*, the aspal margin appears doubled by a distinct submarginal carina (*car*, Fig. 9D); it runs almost straight above leg I, but turns ventrally in the exobothridial region to form the border of a large exobothridial lobe (*ex.l*; Fig. 1C). This lobe is a simple extension of the prodorsal aspis, not an overhanging 'prodorsal tectum' (see Grandjean 1970). Condyle *pK* (Figs. 4A, 9D; see also Fig. 17A), which articulates with the posterodorsal corner of the subcapitulum, is the enlarged anterior end of an oblique, straight rib-like thickening ('nervure latérale') on the inner face of the sclerite (*nl*, Figs. 3D, 4A, 7E, F, 9D). Posteriorly from the condyle, the rib follows the straight margin above leg I, then continues to traverse the base of the exobothridial lobe between the bothridium and seta *xa*, before curving ventrally and effacing in the middle of the lobe (Fig. 9D). No muscles were seen attaching at the rib; its function seems to be lateral stabilization and support of the distal condyle.

The posterior margin of the aspis projects ventrally at a right-angle from its attachment (*) with the soft sejugal cuticle; it forms a thick, vertical occipital phragma (*op*, Fig. 7B, H), an apodematal wall that connects laterally to the exobothridial lobes. A portion of the large extrinsic muscles of the chelicera (*mu*, Fig. 7F-H) originate on the anterior face of the phragma; others originate from the thin, shallow sagittal apodeme (*sa*, Fig. 7A, G), ca. 65-85 μm long, and from sigilla on either side and immediately anterior to it; yet other cheliceral muscles originate from patches of sigilla on the exobothridial lobe and anterior to the bothridium (*sg*, Fig.

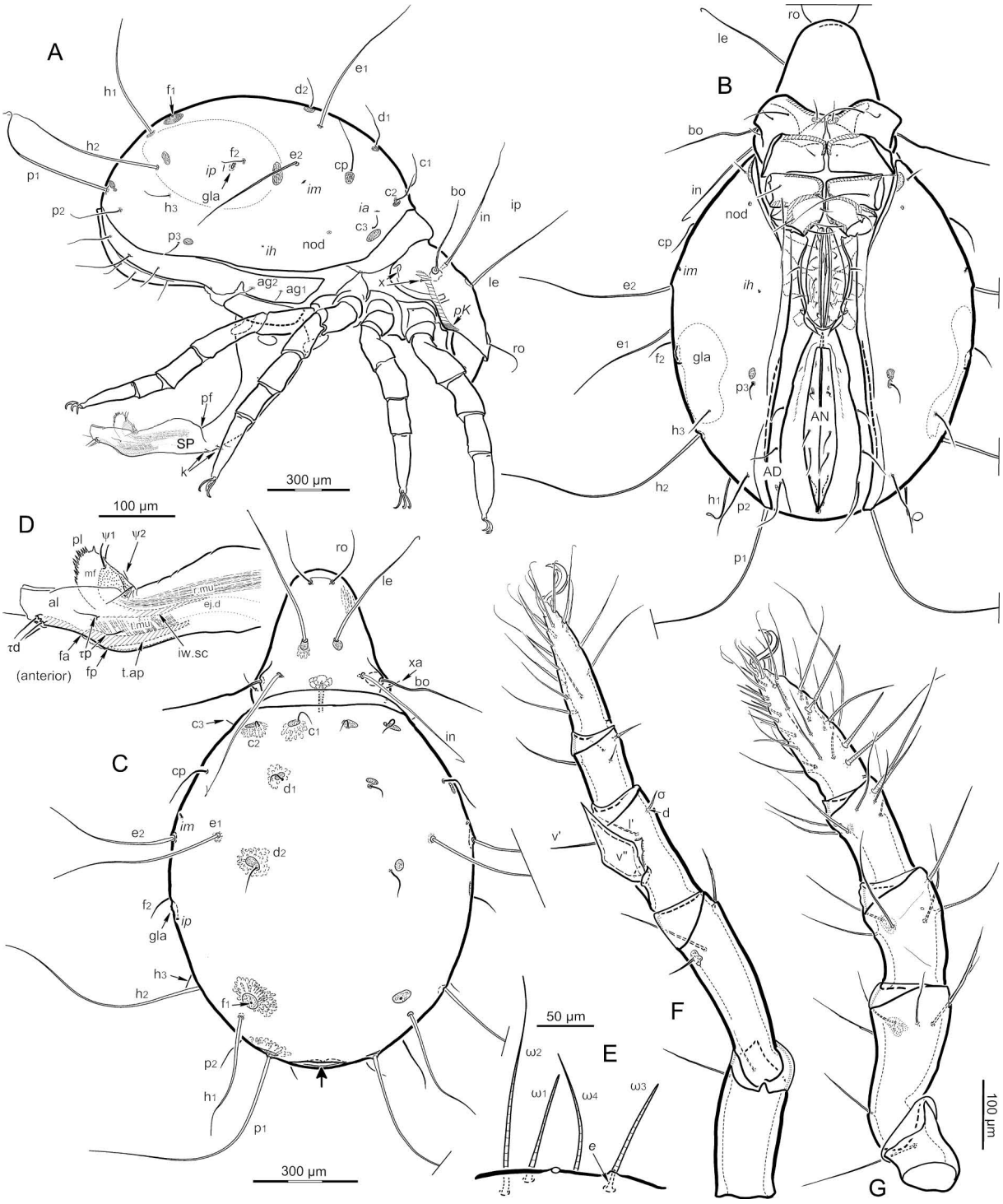


FIGURE 4: *Collohmannia johnstoni* **n. sp.** male: A – lateral view, spermatopositor extended, leg details omitted; B – ventral view of contracted specimen, legs omitted; C – dorsal view of contracted specimen, legs omitted; heavy arrow points to soft terminus of body; D – distal part of spermatopositor; E – solenidia and famulus of tarsus I, proximal to left, setae omitted; F – left leg IV, adaxial view; G – right leg I, abaxial view. See text for abbreviations.

7A). On the posterior (hysterosomal) side of the occipital phragma, prodorsum-retractor muscles that originate in the hysterosoma insert via numerous tendons (*te*, Fig. 7H). The insertions are immediately below the attachment of the sejugal cuticle (not shown, see Fig. 7B, *sj.c*), side-by-side in a row behind each bothridial region. Several other tendons from probable retractor or adjustor muscles insert together at a small sigillum on the posterior edge of the exobothridial lobe (one muscle, *mu*, is visible on Fig. 7H).

Prodorsal setation is normal (Figs. 3, 4). Interlamellar (*in*) and lamellar (*le*) setae are smooth, erect, subflagellate, ca. 550 and 450 μm long, respectively; *in* inserts medial to the bothridia (mutual distance of pair ca. 280 μm); seta *le* inserts at about mid-length of the aspis (mutual distance of pair ca. 90 μm). The finely attenuated rostral seta (*ro*) is directed anteriorly and distally curved (ca. 160 μm long); the pair is inserted on the rostral bulge (mutual distance ca. 60 μm). Both exobothridial setae insert on the exobothridial lobe and are short, simple; *xa* (ca. 50 μm) is transversely aligned with seta *in*, whereas *xp* (ca. 25 μm) inserts near the posterior margin of sclerotization.

The bothridium (Fig. 8) opens on a slight bulge, about equidistant between setae *in* and *xa*. It has a small, inconspicuous circular opening (arrows, Fig. 8A, D), less than three times the width of the bothridial seta, with a narrowly reinforced rim and a complex internal structure that surrounds the tight sigmoid bend at the base of the seta. Moving inward from the opening, three distinct regions can be recognized by the form of their cuticular wall. The first (*br.1*, Fig. 8A, B, D) is a cup-like chamber, lined with dense spicules and twice as wide as the opening, through which the bothridial seta first descends. The next (*br.2*, Fig. 8B-D), surrounding the U-shaped bottom curvature of the seta, comprises several dozen contiguous locules (*lo*, Fig. 8C) – sausage-shaped outpockets from the central tube that collectively appear like the drupelets of a raspberry; the locules are thin-walled but not porose, and none is extended as a trachea or brachytrachea. The third region (*br.3*, Fig. 8A, B, D) lies at the top of the sigmoid bend; its broad outpockets form irregular lobes with very thick walls having an intricate pattern of narrow slits, somewhat resembling a brain-surface when viewed flat. The slits resemble broad pore canals when viewed in optical section (Fig. 8A, D), but they open into the chamber, rather than into the body as pore canals do. This innermost region constricts abruptly to form a narrow collar that surrounds the short, descending terminal bend just prior to the actual setal insertion (*, Fig. 8D). External to the bothridium, the bothridial seta (*bo*, Fig. 3E; M370, F440 μm long) is filiform, with rather sparse, inconspicuous barbs; it is directed dorsolaterally with a gentle sigmoid curve in its middle third. It is isodiametric for most of its length (basal two-thirds to more than nine-tenths), then tapers to a narrow but stiff tip. A hyaline, isotropic external layer covers the entire seta and includes the isotropic barbs, but the layer is most easily distinguished from the birefringent core at the setal tip (*iso*, Fig. 8E).

Notogaster (Figs. 1-6, 10) — The notogaster comprises about 65-75 % of the total length, generally a higher percentage in females than in males (see above). Seen in dorsal aspect, it is 1.1-1.5 times as long as wide: while there is great overlap, males have the largest ratios and gravid females the smallest. The cuticle is imbricate dorsally and lateroventrally, but the pattern is weak or absent in the pygidial region and in a wide pleural band that reaches anteriorly to the level of lyrifissure *im*. The 'cells' of the imbrication vary in shape (from diamond to rhomboid, Figs. 5A, G, 6C), but are similar in height, mostly between 10-15 μm. The cell length varies greatly, from about 10 to more than 100 μm; cells are aligned end-to-end, in a pattern that generally parallels the notogastral margin (*i.e.*, transverse in the sejugal region, longitudinal in the lateroventral region). The anterior margin of the notogaster is slightly constricted, forming a collar (*col*, Figs. 1A, C, 5A) that appears darker than the rest of the notogaster in preserved specimens. The juncture of this collar with the broad sejugal articulation (*sej*) is distinct, but it comprises one of the transitional articulations noted above; *i.e.* the dark, well-sclerotized imbricate collar is bordered by more flexible, pale, imbricate transitional cuticle (*t.cu*, Fig. 5A), which

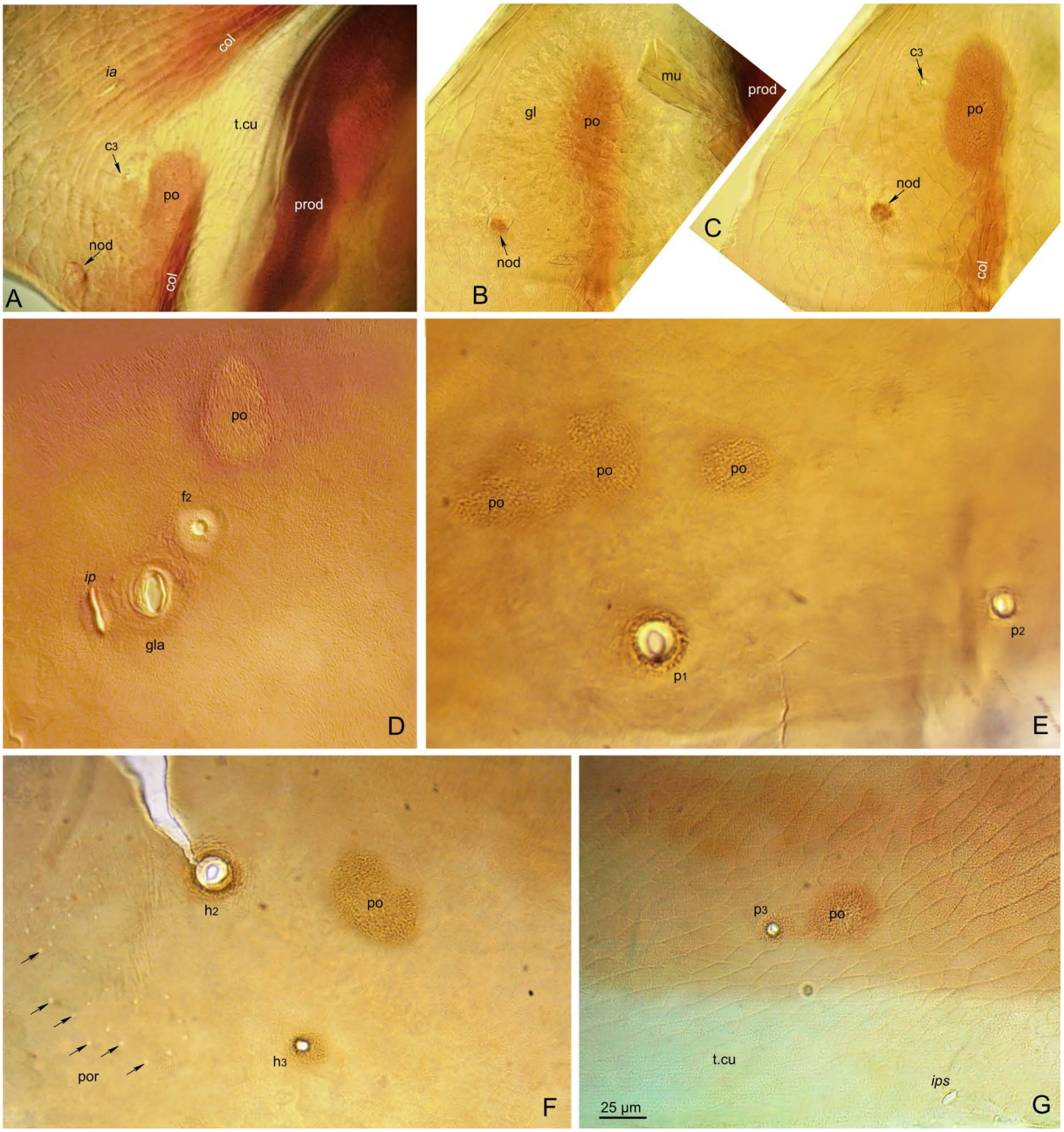


FIGURE 5: *Collohmannia johnstoni* **n. sp.** adults, brightfield transmitted light micrographs of notogastral fragments from dissected specimens: A-C – humeral region. A – anterolateral view, showing posterior extension of transitional cuticle; B – internal view showing gland-like cells of porose area near seta c_3; C – external view of same cuticle; D – vicinity of opisthonotal gland opening; E – region of setae p_1 and p_2 showing fragmented porose area; note ring of pores around alveolus p_1 and shape of setal insertion in alveolar membrane; F – vicinity of setae h_2 and h_3 with porose area and group of larger pores (see note to E); G – vicinity of seta p_3 with lyrifissure *ips* in transitional cuticle along ventral margin of notogaster. Abbreviations: *col* – notogastral 'collar', *gl* – gland associated with porose area; *mu* – muscle, *nod* – nodule, *po* – porose area, *por* – separate pore, *prod* – prodorsum, *t.cu* – transitional cuticle. Each image layered and color- and sharpness-enhanced (see Material and Methods).

then blends into soft, pale cuticle that lacks surface pattern. In lateral aspect the three types of progressively more flexible cuticle often appear tiered, but when the prodorsum is retracted most of the soft cuticle can be hidden (Fig. 5A). Usually there is a slight incursion of paler imbricate cuticle into a crease or undulation in the collar, above seta c_3 (Fig. 5A).

The body form is considered dichoid, since a sejugal articulation runs completely around the mite, but the width of the articulation is not uniform. The broad dorsal part continues around the notogaster as a circumgastric band (in the fashion of holoid taxa), such that the articulation of the notogaster with ventral plates has a similar structure and range of flexibility. In the anogenital region the articulation forms a plicature zone (*pz.1*, Fig. 10A, D), folded or exposed according to degree of body distension. Posterior to the anal region the paired zones flatten and merge to form a terminal sinus, a permanently exposed pale region of transitional cuticle; in posterior view the sinus appears rounded or triangular (arrow, Fig. 10B), and it is visible even in dorsal view as a pale terminus of the body (arrow, Fig. 4C). Just lateral to the top of the plicature angle, a thin intercalary sclerite (*is.1*, Fig. 10A, B, D) supports the insertions of the transverse compressor muscle band originating on the notogaster.

Notogastral setae comprise 15 pairs, plus a distinct alveolar vestige of seta f_1. All setae are smooth, simple, but they vary greatly in size. Five pairs are long, flagellate and conspicuous: e_1 (M580, F660 μm); e_2 (M580, F550 μm); h_1 (M490, F440 μm); h_2 (M640, F590 μm); and p_1 (M490, F540 μm). These large setae insert on low tubercles and are slightly flattened at their base, which is also expressed in the shape of their insertion in the alveolar membrane (p_1, Fig. 5E). Other setae are shorter and finely attenuate; in approximately decreasing order of size, they include: p_2 (M220, F230 μm); *cp* (M150, F230); c_1 (M170, F200 μm); d_1 (M170, F200 μm); c_2 (M170, F170); h_3 (M150, F 100); p_3 (M120, F120 μm); d_2 (M110, F100 μm); f_2 (M90, F110 μm); and c_3 (M55, F65 μm). Most notogastral setae have at least a small ring of porosity at their base that stands out from the general cuticular porosity by having pores that appear slightly larger and more luminous in transmitted light (Fig. 5E, F). This ring is similar in diameter for all notogastral setae (except vestige f_1), such that it is narrower around the five flagellate setae, which have a relatively large alveolus. The porose rings around medium to small setae are each closely adjacent to, or merged with, a larger porose area that contrasts with the background porosity also by having cuticle of darker color (Fig. 5D-G). Most of these larger areas are slightly oblong, 20-90 μm at their widest dimension. If they merge with the porose ring around a seta, the appearance is similar to that of the excentrosclerites of juvenile oripodoid mites (e.g. Grandjean 1959b); alveolar vestige f_1 differs in being always well within a relatively large and often circular porose area (50-90 μm). The position of the large porose areas varies considerably among and within individuals: not only can they be attached or slightly removed from the ring (with a few exceptions noted below), but the diameter of a given area can vary by 100 %. Porose areas in the anterior half of the notogaster – those associated with *c*-row setae, d_1 and e_1 – are generally lateral or anterolateral to the seta. The area near f_2 is usually removed anterodorsally from the seta, evenly spaced and aligned with *ip* and *gla* (Figs. 3D, 5D), or is shifted further anteriorly (Fig. 4A); it is often the largest individual porose area (75-95 μm). Another porose area (40-60 μm) is either dorsal to seta h_3 (Fig. 3D) or slightly anterior to h_2 (Fig. 4A). An elongated porose area dorsal to large seta p_1 can be 100-130 μm long, but it may be broken into smaller sections (Fig. 5E); a small porose area is closely anterodorsal to p_3, but no separate area was seen near seta p_2.

These porose areas appear to be dermal glands (see Remark 1). On lightly cleared specimens with soft tissues somewhat preserved, each area (including that near prodorsal seta *le*) is underlain by an umbrella-shaped cluster of drop-like, sometimes elongated cells. While similar in color to surrounding tissue, the cells are clearly defined under bright-field illumination, and the cluster is always centered on the porose area (Figs. 4C, 5B). Seen perpendicular to the surface, the diameter of each cluster is about three times that of the respective porose

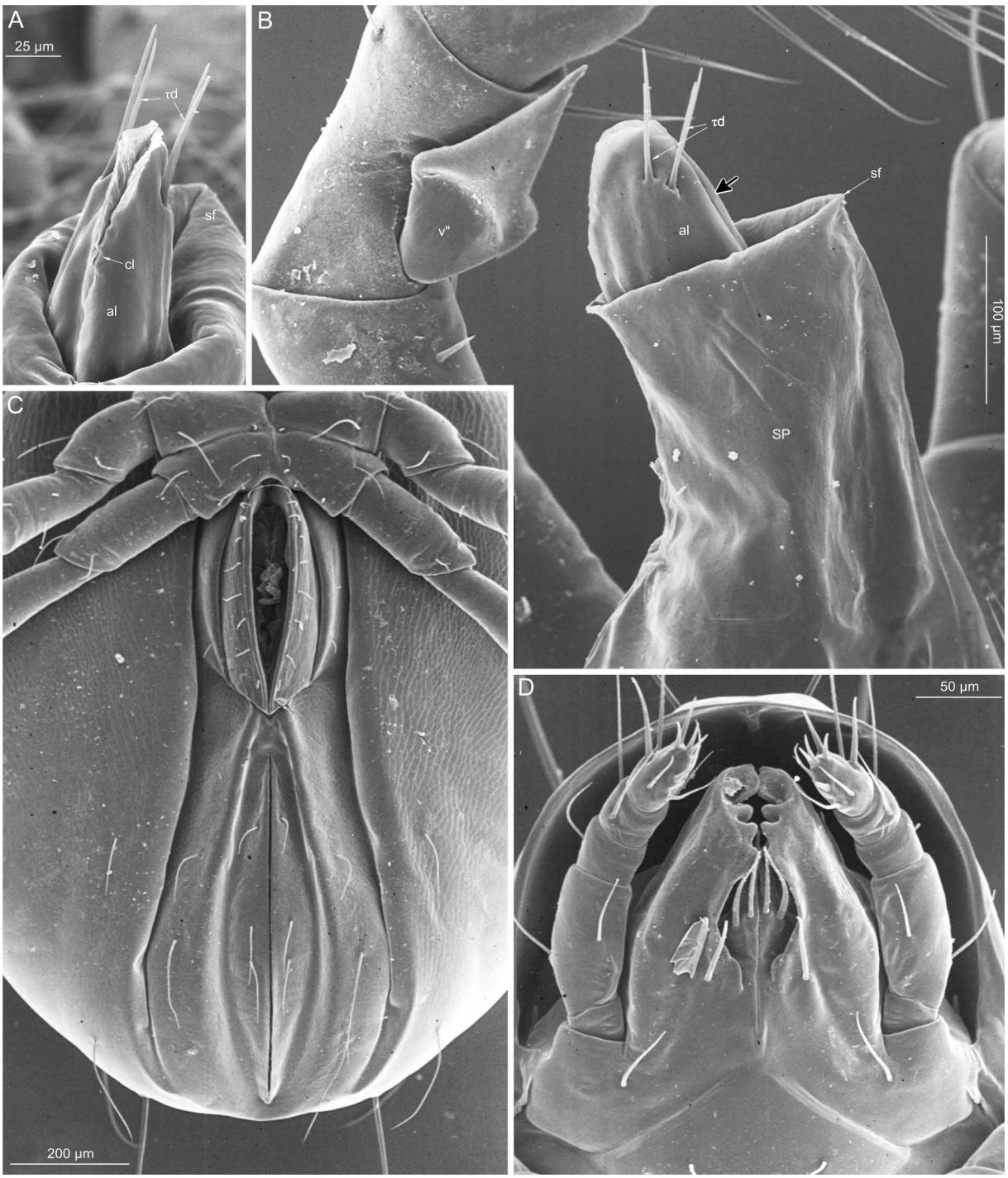


FIGURE 6: *Collohmannia johnstoni* **n. sp.** adults, scanning electron micrographs: A, B – male; C, D – female. A – partly extended spermatopositor, posteroventral view; B – genital region, sagittal view, venter to top, anterior to right, showing partly extended spermatopositor and part of leg IV showing modified genual seta *v"* (heavy black arrow indicates meeting of anterior lobe pair); C – hysterosoma, ventral view; D – subcapitulum and rostrum, ventral view. Abbreviations: *cl* – posterior cleft, *sf* – secondary fold; *SP* – spermatopositor, *τd* – distal eupathidia.

area, and its depth is about the diameter of the area. Isolated, individual large pores are present in the region posterior to setae h_2 and h_3 (*por*, Fig. 5F), but we could not determine their nature.

The typical five pairs of lyrifissures are present, but not uniform: *ia*, *im* and *ip* are ca. 20-25 μm long and slit-like, *i.e.* formed as typical lyrifissures (Fig. 5A, D); *ia* is located between setae c_2 and c_3, *im* is anteroventral to seta e_2, and *ip* is closely posterior to the opisthonotal gland opening (*gla*). By contrast, lyrifissure *ih* is small (ca. 10 μm) and almost pore-like, inconspicuous among the imbricate pattern near the ventral margin of the notogaster, at about mid-length (Figs. 3C, 4B). Lyrifissure *ips* is similar, but is on the transitional cuticle (pale but imbricate) of the plicature fold, at a level just anterior to seta p_3 (Figs. 3B, 5G), and is difficult to see without dissection. In transmitted light, a small, dark internal nodule is visible approximately aligned between *ih* and seta c_3 (*nod*, Figs. 3C, D, 4A, B, 5B, C); tendons from the dorsum attach here. The opisthonotal gland is flat, lens-like, with a diameter of ca. 450 μm.

Coxisternum (Figs. 1B, 2A, B, 3C, 4B, 9) — The four epimeres are progressively narrower, such that the coxisternum tapers significantly from anterior to posterior; epimere I is 1.4-1.5 times wider than IV. The coxisternum is divided into four parts by a cross of soft cuticle, of which the central intersection is relatively large (Fig. 9B). The soft ventrosejugal furrow (or scissure) is narrow but deeply indented (*vsj.f*, Fig. 1B, 9B), providing a transverse axis for dorsoventral flexing. The shallow sagittal (or sternal) scissure (*st.s*, Fig. 9B) separates the epimeral plate pairs, except for a very narrow connection at the anterior margin of epimere I (often broken during preparation). Each plate of epimere II has a transverse band of weakness (*w*, Fig. 9B) at the level of seta *2a*, vaguely indicated by lighter color in transmitted light. The medial edges of the paired plates are not uniform: those of epimere I merge in a simple fashion with the sagittal scissure for most of their length; in epimere II the anterior half of each medial edge (stopping at *w*) turns inward along the sagittal scissure, forming a thick, dark margin in transmitted light (*sm.2*, Fig. 9B); in epimere III a similar margin reaches posteriorly past seta *3a*; and in epimere IV a much weaker inturned margin (*sm.4*) reaches posteriorly to seta *4c*. The sagittal scissure widens posteriorly to form a triangular patch of cuticle behind the plates of epimere IV. While it appears soft relative to the epimeres, the central region of this triangle is lightly sclerotized and porose, and its posterior edge is slightly concave, forming a saddle (*sd*, Fig. 9B) that accommodates the anterior margin of the genital plates. The unsclerotized lateral parts of the triangle merge with the soft postpedal furrow that isolates epimere IV from the plates of the genital region. By contrast, the broadly triangular region of cuticle between epimere I and the subcapitulum is entirely soft.

On each side of the sagittal scissure, the fusion between plates of epimeres I and II is complete, as is that between III and IV. However, the lines of fusion are well marked externally by shallow grooves (Fig. 1B) and in transmitted or reflected light by dark, slightly oblique epimeral borders (Fig. 2A, B). Border III (*bo.3*, Fig. 9B) appears to fork near the medial margin to encompass seta *3a*. The epimeral plates are strongly and evenly porose, and generally lack circumscribed areas of larger pores (*i.e.* porose areas), but there are two locations that might represent the porose area of dermal glands. One surrounds seta *3a*, filling the forked medial part of *bo.3*; the pores within this small circular area are more luminous, and the cuticle is thinner. A similar small area underlies seta *1a*. On each side of epimere IV, a strong internal ridge (*r*) runs posteriorly from *bo.3* to the insertion of seta *4d*, and may extend further to merge with the small marginal condyle (*con*) that articulates with trochanter IV. In some specimens, a vague analogous internal ridge runs obliquely across the lateral half of epimere III from *bo.sj* to the respective marginal condyle, passing near seta *3c*.

Apodemes I and II, extending internally from the anterior margin of their respective epimeral plate, are roughly triangular in form, reaching a peak near mid-width of their plate; apodeme I (*ap.1*, Fig. 9B) has its medial limit near seta *1a*, while apodeme II starts closer to the midline and rises more steeply. The sejugal apodeme is smaller and

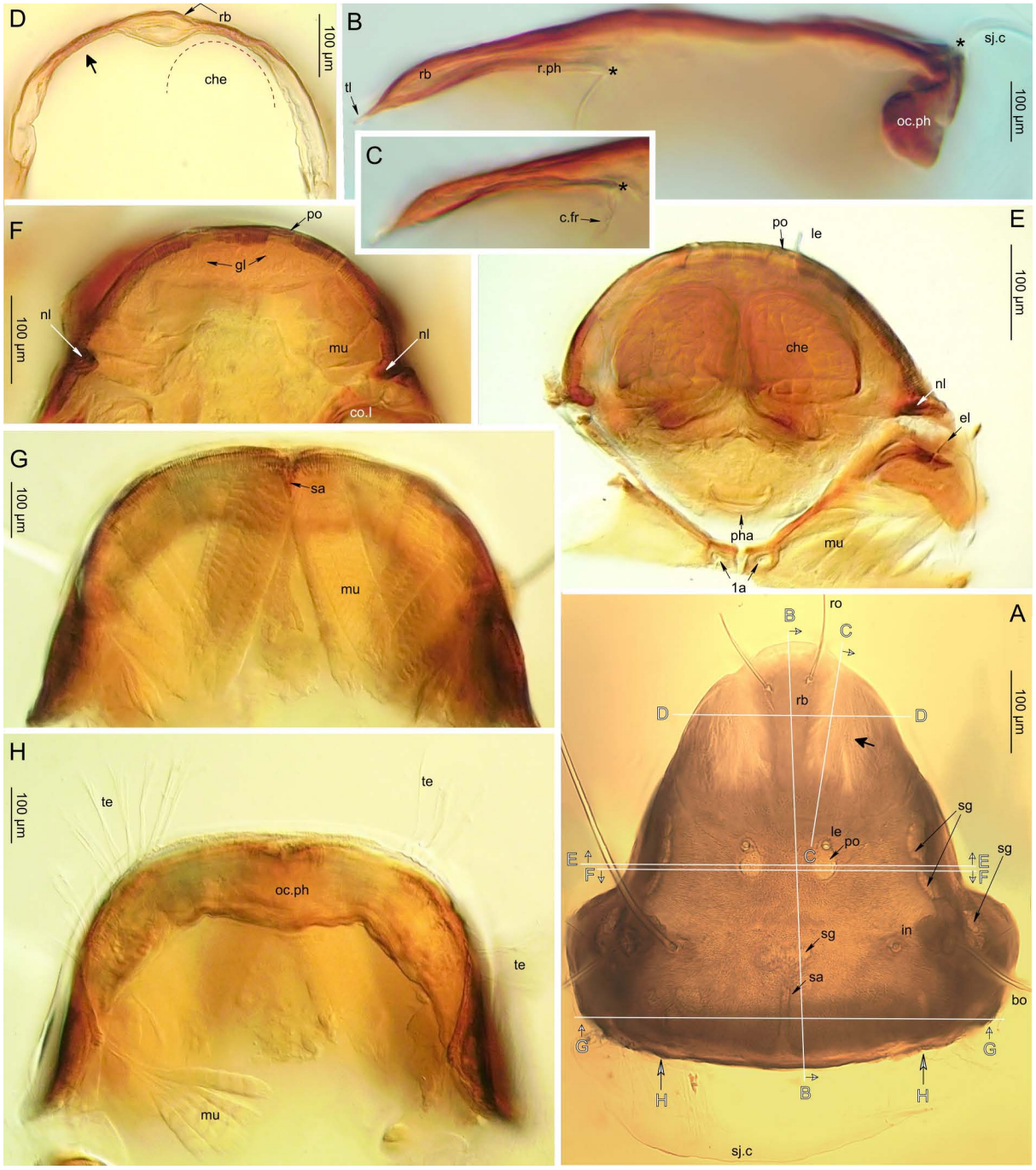


FIGURE 7: *Collohmannia johnstoni* **n. sp.** adults, dissections of prodorsum, light micrographs with brightfield (A-D) or DIC (E-H) transmitted illumination: A – prodorsal shield: lines labeled with letters show positions of respective cross-sections and associated arrows show observational view; B – near-sagittal section; C – oblique section of striated area above chelicera; D – rostral tectum at level of rostral bulge (dashed outline of chelicera); E – full transverse section at level of setae *le*; F – section near E showing unstained glandular cells of porose areas *le* (chelicerae displaced); G – transverse section of prodorsum at level of sagittal apodeme; H – posterior view of dissected prodorsum showing occipital phragma. Abbreviations: *c.fr* – cheliceral frame (line *bt* of Grandjean 1966), *che* – chelicera, *co.I* – cotyloid wall I, *gl* – gland, *mu* – muscle, *nl* – lateral rib (nervure), *oc.ph* – occipital phragma, *pha* – pharynx, *po* – porose area, *rb* – rostral bulge, *r.ph* – rostrophragma, *sa* – sagittal apodeme, *sg* – muscle sigillae, *sj.c* – sejugal cuticle, *te* – tendons of prodorsum-retractor muscles, *tl* – tectal limb, * – junction of sclerotized and soft cuticle; large black arrow in A and D points to striated area above chelicera. Each image layered and color- and sharpness-enhanced (see Material and Methods).

less conspicuous; it rises from the sejugal border of epimere III, starting near the medial margin, rising to a peak at about the middle of the border, then dropping quickly away to disappear well medial to the leg insertion. Apodeme III is highest near the leg insertion, then gradually diminishes to end medially at the fork in *bo.3*. There is no apodeme IV.

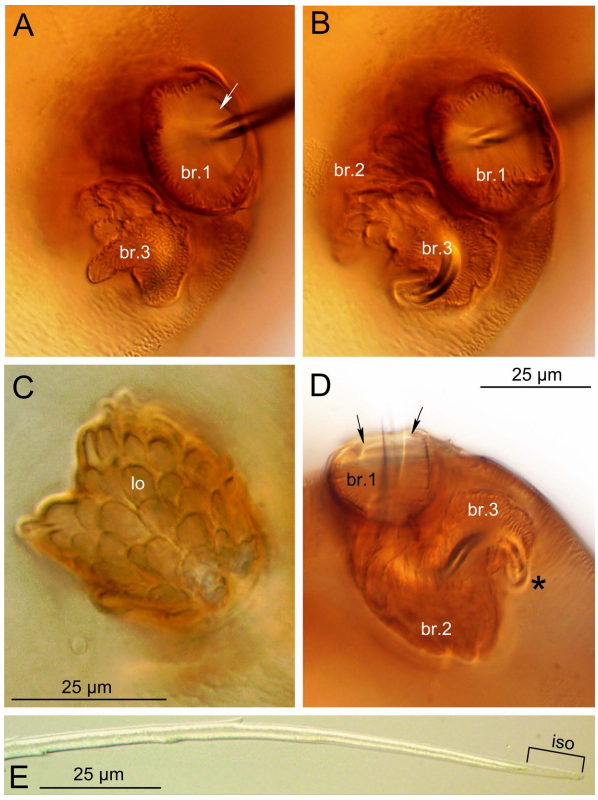


FIGURE 8: *Collohmannia johnstoni* **n. sp.** adult, bothridium and bothridial seta, transmitted light micrographs, DIC: A – shallow optical section from external view (arrow points to bothridial opening); B – same, slightly deeper; C – internal view, showing locules of region 3; D – optical section, showing all regions in cross-section; E – distal region of bothridial seta. Abbreviations: *iso* – isotropic tip of seta *bo*, *lo* – locules, *br.1-br.3* – bothridial regions (see text), * – insertion of seta *bo*. Each image color- and sharpness-enhanced; C, D layered (see Material and Methods).

The small supracoxal region of each epimere, above the leg insertions (Fig. 9A), serves as the origin for muscles; most of these appear to insert on the endosternum as suspensors, though they were not studied thoroughly. On epimeres II and IV the supracoxal region is simply constructed – it is the dorsal part of a short, subcylindrical extension of the epimere to which the trochanter articulates – but on I and III there are other features. Above leg I the small supracoxal seta (*eI*) inserts just proximal to the articulation with the trochanter; it is ca. 12 µm long, spiniform but with a rounded tip (Fig. 9D, E). The sclerotized supracoxal cuticle expands anteriorly, rising dorsally from its general curvature, to form a broad flange along which the epimere meets the soft pleural cuticle; the flange ends in a short beak-like extension (Fig. 9D) that is isolated by a narrow but distinct notch or groove. At the posterior end of this flange is the typical gland opening (*g*), from which products of coxal and lateral accessory glands presumably emerge (see Woodring 1973 for a detailed description of the glands of C. *gigantea*). The gland opening and ducts are well visible, but no clearly defined podocephalic canal was observed in this region, even though it is distinct where it crosses to the subcapitulum (see below). The supracoxal region of epimere III rises in a large triangular extension (*tr.e*, Fig. 9A-C) from which large muscles run to the endosternum. The extension ends in an internal apophysis on which insert thin tendons or fasciae of several groups of muscles that appear to originate on the notogaster. Near the base of the triangle two long tendons insert at a small, but clearly marked sigillum (*sg*, Fig. 9C).

The epimeral setation (I to IV) is 3-1-3-4. Coxisternal setae all are smooth and finely attenuate, but they differ widely in size: *3a* is shortest (ca. 40 µm); *1b* and *3b* are conspicuously long (240, 270 µm), about twice the length of the next longest seta, *4b* (130 µm); setae of epimere I are about 60-70 µm; others are about 90-100 µm long.

Anogenital region (Figs. 1B, 2A, B, 3B-D, 4A, B, 6C, 10) — The venter comprises three pairs of rather narrow plates – genital, anal and fused aggenito-adanal plates – that collectively occupy the area behind the coxisternum. In highly distended specimens (Fig. 3B) their collective width does not vary much longitudinally, but in more laterally contracted specimens (Fig. 3C) the venter assumes a rather elongated pear-shaped outline. All sclerotized plates are porose and have imbricate cuticular

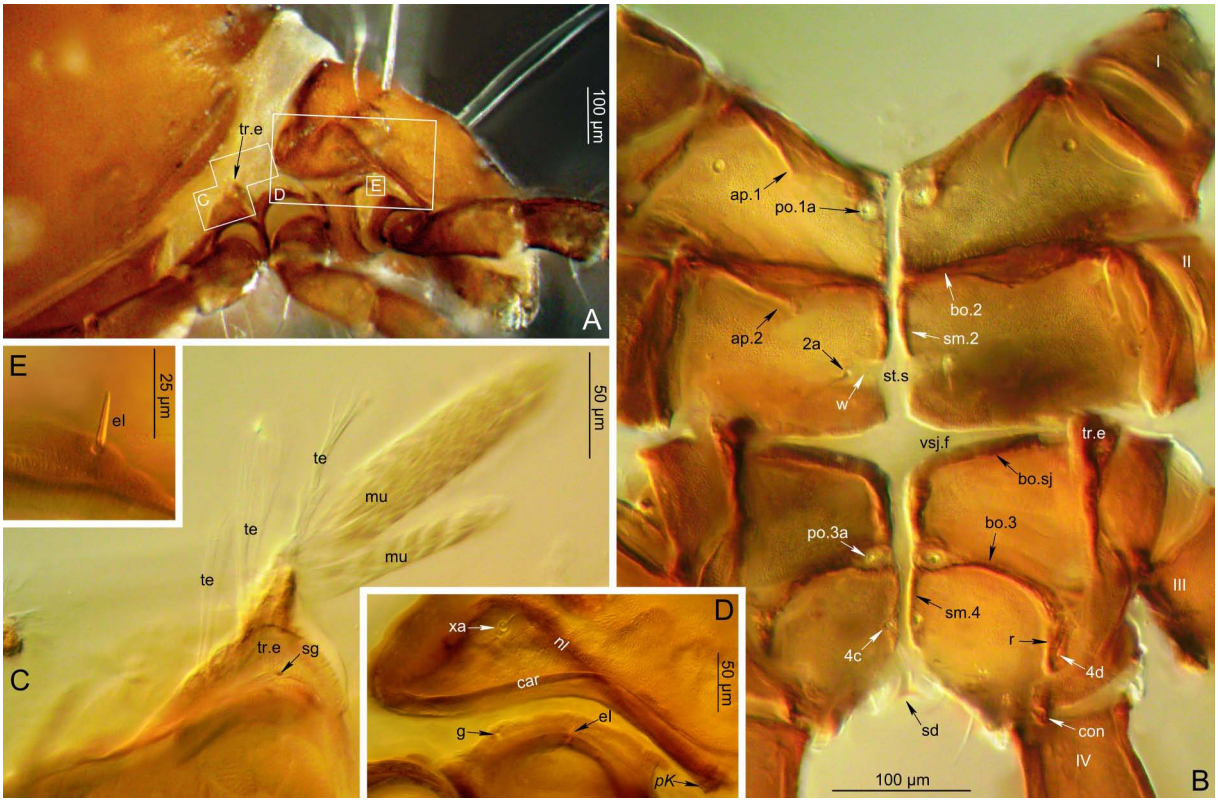


FIGURE 9: *Collohmannia johnstoni* **n. sp.** adult, details of coxisternum, light micrographs: incident (A), or transmitted light with DIC (B, C, E) or brightfield (D) illumination: A – lateral overview, showing positions of C-E; B – separated coxisternum, dorsal view; C – separated epimere III, triangular extension of supracoxal region, lateral view; D – detail of supracoxal area of intact epimere I and part of prodorsum, lateral view; E – same view, detail of supracoxal seta. Abbreviations: *ap.1*, *ap.2* – apodemes 1, 2, respectively; *bo.2*-*bo.4*, – borders of epimeres 2-4, respectively; *bo.sj* – sejugal border; *car* – submarginal carina; *pK* – prodorsal condyle; *po.1a*, *po.3a* – porose areas around respective setae; *r* – ridge of epimere IV; *st.s* – sternal scissure; *vsj.f* – ventrosejugal furrow; *te* – tendon; *w* – area of weakness; *tr.e* – triangular extension of epimere III. Each image layered and color- and sharpness-enhanced (see Material and Methods).

sculpturing, although the latter can be quite faint on the anal plates. In cross section all plates are oblique and connected to adjacent plates by softer cuticle that is angled in the opposite direction; thus, each pair forms a 'V' that becomes flatter with greater hysterosomal distension (Fig. 10). Including the notogaster, the folded effect gives the cross section a flattened W form on each side (Fig. 10D).

The genital plates comprise ca. 1/3 the length of the anogenital region in both sexes. Together, they occupy a narrow elliptical space in ventral aspect that is usually more elongated in females: ca. 2.5-3.5 times longer than broad (F) vs. ca. 2.0-2.5 (M), though proportions vary with plate orientation and degree of hysterosomal distension. Seen flat, each genital plate is at least twice as broad at the oblique posterior margin as at the tapered, rounded anterior end. In lateral view, the outline is distinctly convex, bulging more strongly outward in the anterior half, and the anterior margin projects internally as a small apophysis for muscle attachment. In the anterior half, a narrow strip of the medial margin of each genital plate is delineated by a low carina from the row of genital setae (see below); in the posterior half a separate low carina parallels the margin but this is medial to the setal row. The actual edge of the valve comprises a narrow band of pale cuticle; this is the limit of the unsclerotized cuticle that forms the wall of the genital vestibule (pregenital chamber). Genital setae are aligned in a single row near the me-

dial margin, and they spread along almost the entire length of the plate with spacing that is slightly closer anteriorly (Figs. 3C, 6C); rarely, a posterior seta may be inserted away from the margin. Genital setae are simple, finely attenuate, with lengths that decrease gradually from anterior (usually 60-80 μm) to posterior (30-40 μm). Usually, there is no noticeable ring of larger, more luminous pores around the alveolus, and no separate porose areas were seen. There are 7, 8 or 9 setae on each plate; respectively, these numbers were on 2, 7 and 15 of 24 plates examined, and 5 of the 12 studied individuals were asymmetrical in setal count.

Together, the anal valves have an outline in ventral view that is lens-like: narrowly elliptical, broadest near the middle and tapered at each end (Figs. 1B, 3C). They are convex in lateral view, particularly in the middle of their length (Figs. 3D, 4A). The plates themselves are strap-like, ca. 35-50 μm wide in the middle, tapering at both ends (Fig. 10A). Along most of their length, the medial edge attaches to soft, pale cuticle lining the anal vestibule (rectal chamber), but anteriorly the plate edges invaginate and fuse to form the linear preanal apodeme, with much of its approximately 120 μm length extending forward from the plates. This apodeme, which is visible through the cuticle in intact mites as a dark line (*pr.a*, Figs. 2A, 10A), serves as the origin for part of the long series of transverse ventral compressor muscles that insert at the lateral margin of the adanal plate, as well as oblique muscles leading anteriorly to the genital plates. At the posterior end of the anal vestibule, an unpaired, conical cluster of suspensor muscles from the notogaster tapers to insert on an indistinct postanal apodeme (*pa.a*, Fig. 10A-C). Lyrifissure *ian* is consistently present near the anterior end of each anal plate, longitudinally aligned, and ca. 15-30 μm long; it can have a typical, slit-like form or be slightly oval. The three pairs of anal setae are longitudinally aligned at midwidth; an_1 (100-190 μm) is well anterior to the others, such that *ian* is about midway between the seta and the anterior end of the plate; an_2 (100-110 μm) is at mid-length, and an_3 (60-100 μm) is less than a setal-length behind it. The setae are simple, finely attenuate, and usually have a narrow ring of luminous pores around the alveolus, A small, inconspicuous, separate porose area is usually present immediately anterior to ad_1.

The two components of the long aggenital-adanal plate are distinguishable by a deep notch of unsclerotized cuticle that separates them along the medial margin, opposite the posterior part of the genital plate; depending on orientation, it can appear linear (large arrow, Fig. 10A) or V-shaped (Fig. 4A). Seen flat, the aggenital portion is subrhomboid, about 100-110 μm wide. It bears two simple, attenuate aggenital setae (ca. 30-45 μm) that are longitudinally aligned in the posterior half of the plate (ag_1, ag_2; Fig. 4A). These insert eccentrically in small porose areas that are several times as wide as the setal alveolus; no separate porose areas were noticed. Anteriorly, the adanal portion of the compound plate has the same width and direction as the aggenital portion, but it twists toward the side and narrows posteriorly to less than half its anterior width, ending at the same level as the anal plate and intercalary sclerite. The posteriorly-decreasing adanal plate width is complemented by an increasing width of transitional cuticle (pale but porose and imbricate) along its medial side, such that the entire width of the adanal cuticle is similar throughout. The transitional cuticle forms a second plicature zone (*pz.2*; Fig. 10A, D) that leads dorsomedially from the medial edge of each adanal plate to form a plicature angle with the anal valve. All along the line of juncture, just lateral to the top of the plicature angle, lies a second intercalary sclerite (*is.2*, Fig. 10A, D); this thin, brown band of sclerotization probably helps maintain the form of the fold and serves for insertion of a band of transverse compressor muscles that originate on the lateral edge of the adanal plate. Lyrifissure *iad* lies anteriorly in the plicature zone, which indicates that *pz.2* is part of the adanal segment. Lyrifissure *iad* is similar to *ian* in size and form and aligned at the same transverse level, but is slightly oblique in orientation. The three pairs of adanal setae are almost evenly spaced in the posterior half of the adanal portion of the plate, and insert on its margin, just lateral to the beginning of the pale transitional cuticle (Fig. 3C, 4B). The setae are simple and finely

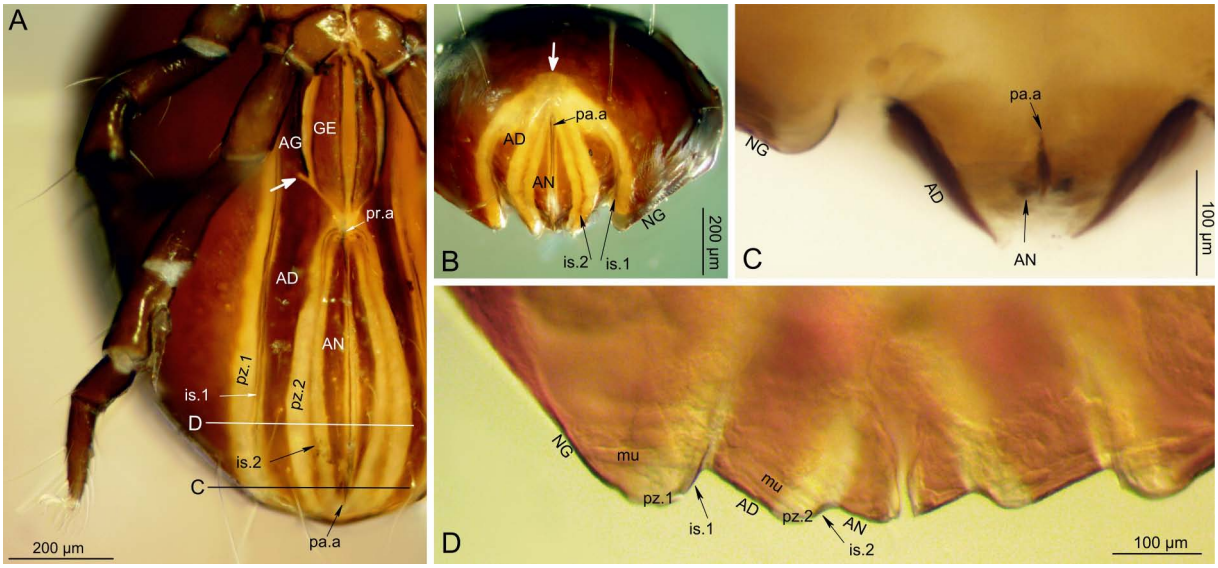


FIGURE 10: *Collohmannia johnstoni* **n. sp.** adult, ano-genital region: A, B – male, incident light; C, D – female, transmitted brightfield (C) or DIC (D) illumination. A – ventral overview, showing positions of cross-sections; large white arrow points to notch of unsclerotized cuticle between adanal and aggenital plates; B – posterior view of hysterosoma, white arrow points to soft terminus of body; C - cross section at level of postanal apodeme; D – cross-section showing composition and musculature of the mid-anal region. Abbreviations: *AG, AN, AD, GE* – aggenital, anal, adanal, genital plates, *gl* – gland, *is.1*, *is.2* – intercalary sclerites, *mu* – muscle, *NG* – notogaster, *pa.a* – postanal apodeme, *pr.a* – preanal apodeme. Each image layered and color- and sharpness-enhanced (see Material and Methods).

attenuate; an_2 and an_3 are similar (ca. 200-230 µm), while an_1 is shorter (ca. 100-125 µm); each has a narrow ring of luminous pores around its base. A small porose area lies just anterior to an_3 or may merge with the porose area at its base. Rarely, a fourth adanal seta exists unilaterally, aligned with the others, which may represent a duplication of an_3. When four are present, each of the two most anterior setae can have a separate porose area near its base, and in typical specimens only an_3 has such an area.

Genital vestibule and genitalia — The genital papillae are large, the posterior papilla (ca. 95 µm) being slightly shorter than the other two (ca. 110-120 µm). All have similar form, with a single discrete basal annulus and a larger, slightly flattened ovate distal portion that respectively comprise about ¼ and ¾ of the total length.

The female ovipositor is a thick, densely plicate double-walled tube, typical of oribatid mites in its general form and setation (Figs. 3D, F, 13 A; cf. Grandjean 1956; Ermilov 2010, 2011a). When fully extended it is directed anteroventrally (in the descriptions below, one should imagine it projects straight ventrally) and is slightly shorter than the height of the hysterosoma. There are three pairs of short (ca. 30 µm), simple, acuminate coronal setae (*k*) around the mid-length constriction. The three distal lobes – unpaired posterior (or ventral) and paired anterior (or dorsal) lobes – are relatively short, comprising about one-third the total length of the distal section (i.e. distal to setae *k*); each is broadly rounded, about as wide as long. The outer face of each lobe is smooth in its distal half, but without evidence of a sclerite (neither pigmented nor porose). The inner faces, which meet when the ovipositor is retracted, seem less deformable than outer faces. That of the posterior lobe (*pl*, Fig. 13A, insert) is convex and darkly pigmented, possibly sclerotized. In contrast, the inner face of each anterior lobe (*al*) is colorless and concave, accommodating the convex posterior lobe when the ovipositor is retracted. Each lobe has the usual complement of four setae. Seta τ_1 (ca. 90 µm) on each ventral lobe, and pair ψ_1 (ca. 80 µm) on the dorsal lobe are longest and are finely attenuate; they insert on distinct, sclerotized tubercles in the smooth distal half

of the respective lobe, well proximal to its tip. Other setae are shorter (τ_2, ψ_2 ca. 30; $\tau_{3\text{-}4}$ ca. 40 μm), tapered but blunt-ended; they insert on smaller tubercles and more proximally, at the limit of the plicate cuticle. All setae are eupathidial.

By contrast, the male spermatopositor ('penis') is highly atypical of oribatid mites (cf. Woodring 1970). As Grandjean (1966) noted for *C. gigantea*, the length and direction of the spermatopositor are consistent with mating behavior (see below, and Remark 2). When fully extended (SP, Fig. 4A) it is longer than the ovipositor and has the same general facies, but lacks the dense plication and bends postero- rather than anteroventrally (discussed below as if ventrally directed). Like the ovipositor, it is a double-walled tube; when retracted, the distal part is pulled inside the proximal part (Fig. 6A, B), and the doubly-folded structure is pulled into the genital vestibule. The softest, most deformable region is where the primary, most distal fold occurs (*pf*, Fig. 4A) but there is no distinct constriction, as exists in the ovipositor. The cuticle of the proximal (dorsal) part is smooth and featureless, except for two pairs of eupathidial coronal setae (*k*; Fig. 4A). These insert dorsal to the primary fold, therefore are between primary and secondary (*sf*, Fig. 6A, B) folds when the spermatopositor is fully retracted. They are not arranged in a ring, as in the ovipositor, but rather are all on the anterior face, with one pair proximal to the other.

The part distal to the primary fold is ca. 250 μm long, of which the terminal lobes comprise slightly less than half. The paired anterior lobes (*al*, Fig. 4D) are large, laterally-flattened, and mostly immovable with respect to each other and to the main tube. They form the distal region of a tongue-shaped terminal structure (Figs. 4D, 6A, B), with a distinct bulge in its anterior outline. Externally, the anterior half of each lobe is noticeably sclerotized and porose. Where the lobe joins the main tube, about in the middle of the bulge, the sclerotized cuticle abruptly thins, and then changes to soft cuticle proximal to the bulge. The posterior half of each lobe has flexible, unpigmented cuticle. The lobes are separate distally, but they cannot spread far apart because they fuse basally in the anterior midline (point marked *fa* in Fig. 4D); here the sclerites turn internally as a single, laterally-flattened medial apodeme, which Woodring (1970) called the tongue (*t.ap*). The attached portion of the tongue (from *fa* to *fp*) is rather short, and for this distance the sclerite is covered externally with a hyaline cuticular layer. Proximal to *fp* the apodeme leaves the surface cuticle and extends freely as a narrow blade-like arm, almost three times the length of the attached portion. This long, freely projecting apodeme is unlike the antero-posteriorly flattened apodeme of *C. gigantea*, and more typical of that of other oribatid mites (Woodring 1970). Posteriorly, the mostly-soft inner surfaces of the opposing anterior lobes form a deep cleft (*cl*; Fig. 6A) into which the posterior lobe is pulled during retraction (see below).

Each anterior lobe bears two large, distal eupathidial setae (τd, Figs. 4D, 6A, B; ca. 50 μm). They are tapered, but distally rounded, and insert close together near the distal limit of sclerotization. Two similar, but shorter proximal setae (τp, ca. 20 μm) insert near the dorsal limit of each sclerite, one more proximal than the other. This complement is homologous with the four setae ($\tau_{1\text{-}4}$) of the paired ovipositor lobes, but specific notations are uncertain.

The unpaired posterior lobe (*pl*, Fig. 4D) is also highly compressed laterally, but is much differently structured. It is movable, swinging outward when the spermatopositor is fully extended. But when the spermatopositor is retracted (Fig. 6A, B), the lobe is rotated inward and fully enveloped in the cleft formed between the supple, free posterior halves of the anterior lobes (this creates the 'central pleat' of Woodring 1970; see Remark 2). Basally, the surface of the lobe comprises a thick, embedded (hyaline-covered) sclerite, ca. 50 μm long. The sclerite has a very narrowly U-shaped cross-section, like a hairpin, such that most of it is parallel with the walls of the anterior lobes. The sclerite is well pigmented and conspicuously, but irregularly porose. On each side, the lobe is extended distally beyond the sclerite, about an equal length, by a broad flap of very thin, membranous cuticle (*mf*, Fig. 4D); the flaps are rounded and the pair meet medially at the distal edge of the sclerite. They bear some minute cilia scattered on their proximal surface (not shown)

and terminate in a fringe of much longer (ca. 15 μm) setules. These membranous flaps are easily overlooked, making the posterior lobe appear much shorter than the anterior lobes. Proximal to the sclerite, a region of transversely striate soft cuticle attaches the lobe to the main tube. Two pairs of eupathidial setae insert on the posterior lobe: pair ψ_1 (ca. 35 μm) insert close to the midline at the distal edge of the sclerite, and pair ψ_2 (ca. 15 μm) insert at its base, directly aligned with ψ_1 (Fig. 4D).

In addition to the sclerites of the three lobes, which are on the outer wall of the spermatopositor, the inner wall ('inner cup' of Woodring 1970) has a pair of elongated sclerites (*iw.sc*, Fig. 4D) that are conspicuous in transmitted light. They are broad and weakly porose on the inner face of each anterior lobe (in the region lateral to the posterior lobe sclerite), where they may add structural support to the cleft; then they narrow abruptly and gradually taper to end at a level slightly proximal to the end of the tongue-apodeme.

Our observations of musculature are superficial and require confirmation by histology, but the descriptions of Woodring (1970) seem to apply also to *C. johnstoni*. The largest muscles seem to be retractors that insert at various locations, including around the primary fold. A thick, seemingly unpaired and strongly banded muscle (*r.mu*, Fig. 4D) inserts at the base of the posterior lobe, running between the inner-wall sclerites. An oblique band of muscles runs laterodistally from each side of the tongue; the more proximal members attach directly on the outer wall and the more distal members are directed toward the broad part of sclerite *iw.sc*, but we are uncertain if they attach there.

Gnathosoma (Figs. 6D, 11, 12) — Many traits of the mouthparts are typical of middle-derivative oribatid mites, and shared by most members of Nothrina (cf. Grandjean, 1957a, van der Hammen 1968). The subcapitulum is stenarthric and approximately as wide as long. All sclerotized ventral cuticle is strongly porose, like most of the body cuticle, but there are no circumscribed areas of larger, more luminous pores, not even around the base of setae. The mentum (*men*, Fig. 11D) is triangular, about twice as wide as long. A coarse, dark sclerotized region on the ventral surface of the pharynx (*ph.s*, Figs. 11D, 12G) shows by transparency; it is narrow at the mid-ventral commissure, then broadens posteriorly. The pattern is reticulate, but edges are strongest, giving its outline a 'wish-bone' appearance. At its narrow anterior end, the structure appears to attach the pharynx to the subcapitulum, but it stays with the pharynx during dissection. The robust gena (*gen*) blends smoothly into a porose manubrial zone (between dorsolateral fissure *f* and line *l.br* on Fig. 11D), beyond which is the strong, colorless, birefringent rutellum (*rut*). The single hypostomal (*h*) and two genal (*a*, *m*, Fig. 11D) setae are finely acuminate, inconspicuously barbed, and similar in size, usually 70-80 μm.

The dorsal surface has the usual paired cheliceral groove ('mandibular fossa'), with relatively widely spaced pore canals (not illustrated). The posterior region is dominated by a large capitular apodeme that has a broadly curved margin in dorsal aspect and an inverted-V shape in cross-section (*c.ap*; Fig. 12H, I); the two halves are fully connected, articulating at a weak scissure along the sagittal peak (*). At its projecting posterolateral corner, each gena has a deep vertical groove where the prodorsal condyle (*pK*) articulates; the podocephalic canal (*cp*; Fig. 12H, J) passes across the soft articulating cuticle attached to this groove, on its way to the cervical region. The post-palpal (laterocoxal) seta (*ep*, Figs. 11D, 12H, J) inserts in a small, strongly bulging, tubercle-like patch of soft cuticle on the dorsal margin of the gena, just anterior to the groove; it is a short (usually 11-13 μm) thick, hollow spine, varying from acute to nearly truncate, and minutely roughened distally.

The rutellum (*rut*, Fig. 11D) has the common mixonomatan form: it is directed obliquely, exposing the lateral lips medially (i.e. it is atelobasic), and of similar width throughout. The distal edge is truncated, with four obvious teeth that increase in size from ventral to dorsal; a fifth, most dorsal tooth is seen in ventral view mostly by transparency. The dorsal surface (Fig. 12K) is concave, but has two sharply defined carinae (*car*), an oblique one, directed anteroventrally from the rutellar base to the middle tooth, and a smaller carina that extends

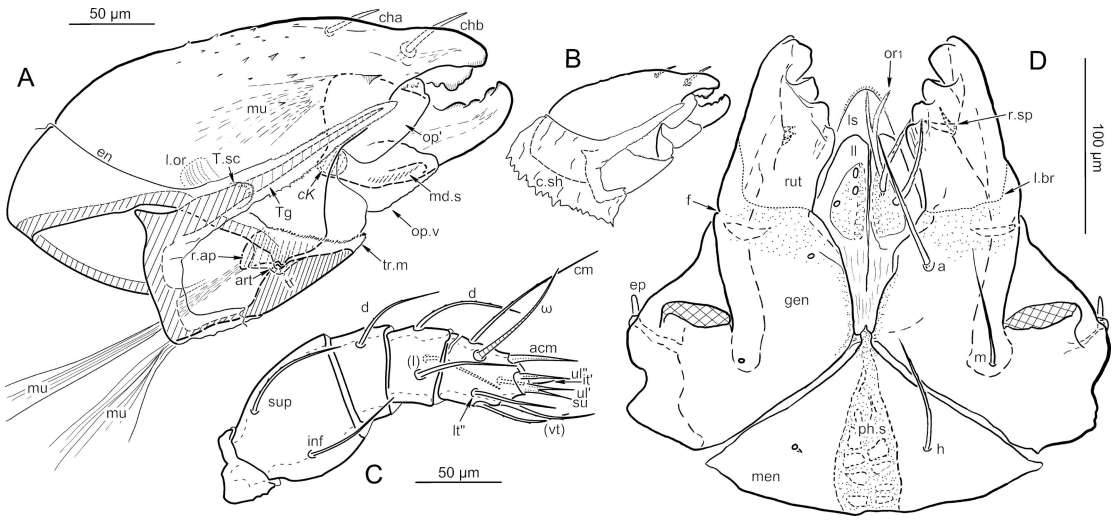


FIGURE 11: *Collohmannia johnstoni* **n. sp.** adult, details of gnathosoma: A – left chelicera, adaxial view, with sheath removed except to show attachment line; B – same, but cheliceral sheath shown; C – right palp, posterior (abaxial) view, slightly flattened in preparation; D – subcapitulum, ventral view, palps omitted, setae on left side of image represented only by alveoli. Abbreviations: *a, m* – genal setae, *art* – part of articulation with trochanter, *cha*, *chb* – cheliceral setae, *cK* – cheliceral condyle, *c.sh* – cheliceral sheath, *en* – line of attachment of cheliceral sheath, *ep* – post-palpal seta, *f* – dorsolateral fissure at the base of rutellum, *l.br* – proximal limit of birefringence, *l.or* – lamellated organ, *ls* – labrum, *md.s* – abaxial scale of movable digit, *men* – mentum, *mu* – muscle, *op', op.v* – adaxial and ventral oncophyses, *ph.s* – pharyngeal sclerite, *r.ap* – retractor apophysis, *r.sp* – rutellar spine, *Tg* – Trägårdh's organ, *T.sc* – scale at base of Trägårdh's organ, *tr* – thickest part of ventral cuticle of trochanter. *tr.m* – fringed distal margin of trochanteral tectum, *gen* - gena, *h* – hypostomal seta, *rut* – rutellum.

from the middle of the oblique carina to the base of the most dorsal tooth. The position and direction of these carinae resembles those of the rutellar brush of many Nothrina and Brachypylina, but they have no cilia. However, immediately ventral to the position where these carinae meet are 1-3 spines. The spines are smooth, hyaline, tapered and rounded distally, and commonly broken near midlength; they are isotropic in polarized light, contrasting strongly with the highly birefringent rutellum. Usually there are two such spines, similar in size and slightly diverging but with adjacent bases (*r.sp*, Figs. 11D right side, 12L), but of 14 rutella examined, three (Fig. 12K) had a single spine, and one (Fig. 11D left side) had three small spines.

The mouth lacks a ventral lip. The paired, adjacent lateral lips (*ll*, Fig. 11D) each has a distinct, porose, distally tapering sclerite, covering about half the ventral surface; the medial edge of each sclerite is aligned along the medial edge of the lip, and is distinctly thickened. The sclerite bears the usual three adoral setae, all with minute barbs: or_1 (ca. 40 µm), inserted at the narrow tip of the sclerite, has a smooth base but a distal, dorsally curving fork with dense small barbs; the slightly longer or_2 and or_3 (ca. 60-70 µm), aligned transversely or obliquely across the middle of the sclerite, are simple, and barbed for most of their length. The distal parts of adoral setae are frequently broken. Dorsally, each lip has a row of posteriorly curved cilia along the lateral edge only. The long labrum (*ls*) is transverse at its base and tapers to a rounded tip that is similar in shape to the lateral lips, and extends slightly beyond them. A weak embedded sclerite occupies much of the dorsal surface, starting at the base of the labrum and narrowing gradually to efface in the distal quarter; the hyaline coating strongly bulges up, ridge-like, along most of the midline. The lateral margins of the sclerite are thickened to form narrow supporting ribs (*sr*, Fig. 12H); proximally, each rib turns medially a short distance to form an attachment point for the pair of typical levator muscles. Three parallel U-shaped rows of distally-directed cilia encircle the soft tip (Fig. 11D); the dorsal row is short, reaching proximally on each side to

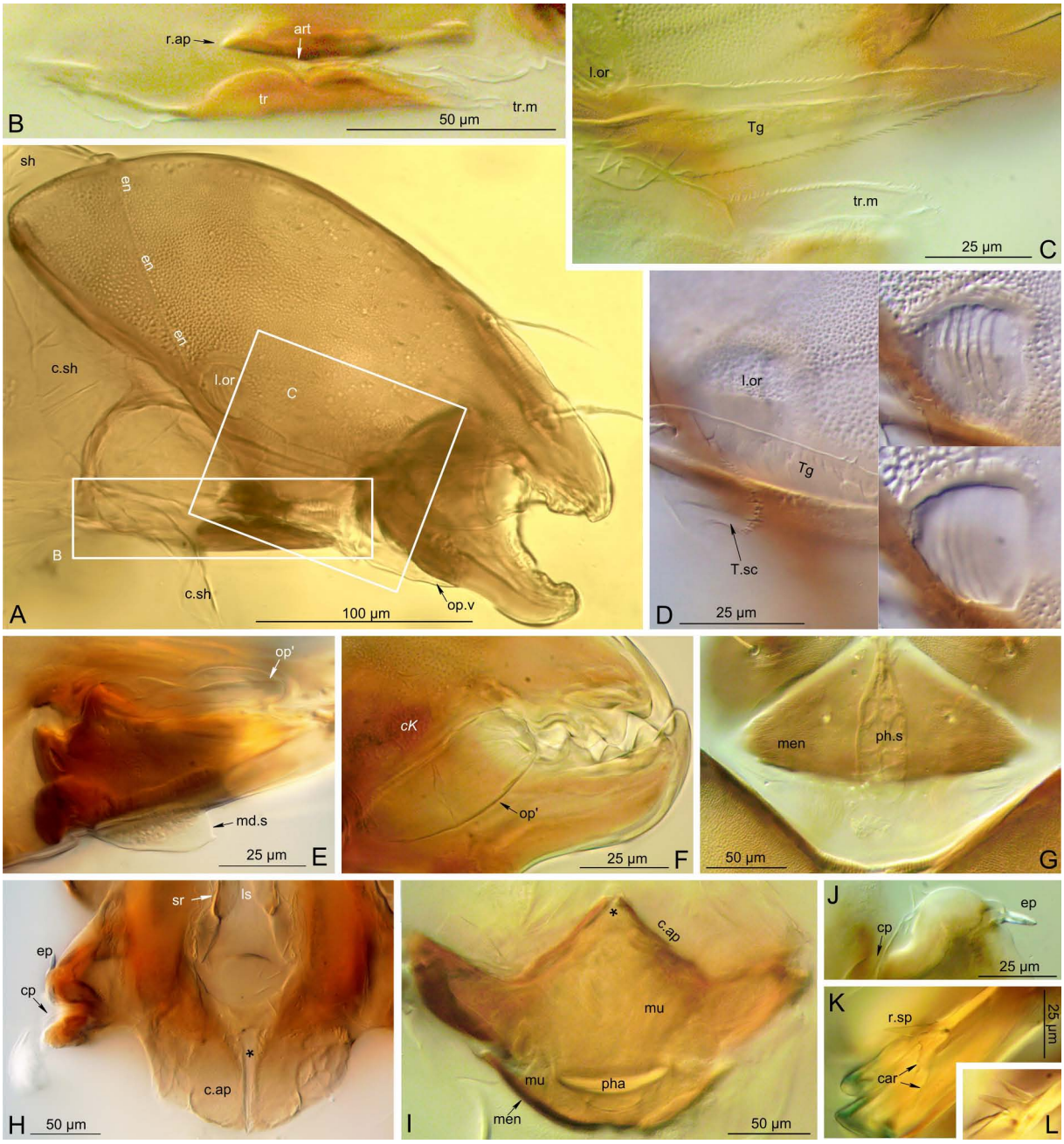


FIGURE 12: *Collohmannia johnstoni* **n. sp.** adult, details of gnathosoma, separated structures. Transmitted light micrographs, with bright-field (A), DIC (B-I) or polarized (J-L) illumination: A – chelicera overview, showing positions of B-D; B – optical section of cheliceral trochanter and vicinity; C – Trägårdh's organ and hyaline margin of trochanteral tectum; D – detail of surface around lamellated organ (left), with successive optical sections (right, deepest at bottom); E – movable digit of chelicera, ventral view, distal to right; F – cheliceral chela; G – posterior region of subcapitulum, ventral view; H – posterior half of subcapitulum, dorsal view; I – cross-section of subcapitulum at level of (*) in H, posterior view; J – posterolateral corner of subcapitulum, lateral view; K – dorsal face of rutellum, distal to lower left, with rare single spine; L – same view of rutellum with typical two spines. Abbreviations: *c.ap* – capitular apodema, *car* – carinae, *cp* – podocephalic canal, *pha* – pharynx, *sr* – supporting rib of labrum, *te* – tendons of muscles; others given in Fig. 11. Each image layered and color- and sharpness-enhanced (see Material and Methods).

only about the end of the sclerite, while the middle and ventral rows reach about one-third the distance to the labral base. No separate transverse rows of cilia were noticed on the dorsal surface. The ventral surface has about a dozen transverse grooves distributed along its whole length; overhanging each groove is a row of minute, proximally-directed cilia.

The palp (Fig. 11C) is five-segmented, about 150-200 μm long; measured along the lateral midline, segments of a 200 μm palp (trochanter to tarsus) were 14-73-25-33-55 μm. The respective setal counts (solenidion in parentheses) are 0-2-1-3-9(1). Four distal tarsal setae are eupathidial: setae *ul″*, *ul′* and *su* insert in a distal pad of soft cuticle, with the latter two being fused in their basal third (but counted separately); *acm* inserts just proximodorsal to them in a separate large alveolus. Solenidion ω inserts high on the abaxial face, at a level slightly distal to seta *cm* and well proximal to *acm*; it is about 1.5 times the length of the tarsus, tapers evenly to a thin, rounded tip (ceratiform), and curves gently laterad. The tarsal lyrifissure is well formed.

The chelicera has a typical chelate-dentate form (Figs. 11A, B, 12A). The soft cuticle of the cheliceral sheath (*c.sh*) attaches to the dorsal half of the principal segment along a strongly oblique line (*en*) positioned so that the principal cheliceral segment is 'inserted' into the flexible cheliceral sheaths, *i.e.*, about the basal fifth of it is internalized. The cuticle of the internal portion retains the same porosity as that external to the sheath (see Remark 3). Near the ventral midline of the principal segment, a thick apophysis projects internally (*r.ap*, Fig. 11A), and serves as the insertion for one of the large retractor muscles (*mu*). The chelicera is emarginated proximally on the adaxial (anterior) face, where the principal segment meets the trochanter at nearly a right angle. On its abaxial face, the principal cheliceral segment is essentially smooth, but the adaxial face has numerous hard spicules of various sizes (Fig. 11A); most of these are in the middle third of the external portion, but usually a more distal one is largest. The two abaxial setae of the principal segment are acute to acuminate and relatively short: *cha* is near the dorsal midline, ca. 40 μm long, and is weakly barbed in the distal half; *chb* is on the abaxial face, near the base of the fixed digit, only slightly longer (ca. 50 μm) than *cha* but noticeably thicker and almost smooth. On each digit, the distal extent of porosity is sharply defined, beyond which is dense birefringent cuticle bearing the teeth: on the principal digit porosity stops just distal to seta *chb*, while on the fixed digit it occupies the basal third adaxially and the basal half abaxially. The fixed digit has four well-aligned teeth, plus a fifth small tooth that is subterminal on the adaxial side; the movable digit has four teeth, the distal two are offset to receive the terminal and subterminal teeth of the fixed digit (Fig. 12F).

In approximately the middle of the adaxial face are Trägårdh's organ (*Tg*, Figs. 11A, 12C, D) and the lamellated organ (*l.or*). Trägårdh's organ – essentially an elongated oncophysis (Alberti *et al.* 2011) – extends distally from the soft cuticle at the juncture of the trochanter, principal segment and cheliceral sheath. It is well developed, tapering gradually and extending distally to just beyond the base of the movable digit. A thin, lightly sclerotized central area (an embedded sclerite) is surrounded by membranous cuticle with a fine fringe of cilia; near its base a small scale-like flap (*T.sc*, Figs. 11A, 12D) also is fringed with cilia. The organ is delicate: the fringed cuticle is often torn away or even the entire organ is lost when chelicerae are dissected from the gnathosoma. The lamellated organ ('fenestrate area' fe_1 of van der Hammen 1968) lies just dorsal to the base of Trägårdh's organ, near line *en*. It is a proprioceptor associated with a portion of the large levator muscle of the movable digit (Alberti *et al.* 2011) and is covered with thin, but porose cuticle (Fig. 12D, left).

The cheliceral trochanter has the general form of a deeply convex scale that underlies the principal segment, most noticeably on the adaxial face; it is subtriangular in adaxial view, and the ventral half of the cheliceral sheath attaches along its vertical proximal edge. Its cuticle is sclerotized but mostly rather thin in the proximal 2/3, where it is excavated by large regions of muscle insertions; narrow places where no muscles attach (*i.e.* cuticle of normal thickness) show in transparency as darker lines, analogous to the dark epimeral borders of the cox-

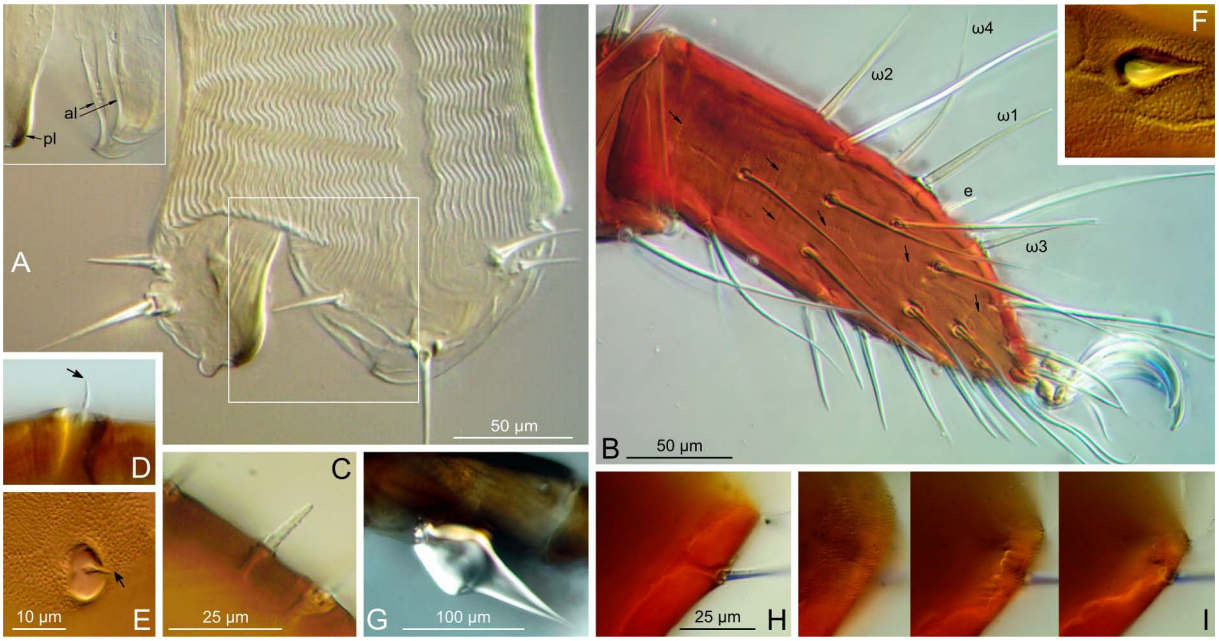


FIGURE 13: *Collohmannia johnstoni* **n. sp.** adult, detail of ovipositor and legs. Light micrographs, polarized (G) or DIC (all others) illumination: A – distal end of ovipositor, surface view (lateral view, anterior to right), with insert showing anterior lobes (*al*) and unpaired posterior lobe (*pl*) by optical section through the sagittal plane; B – female left tarsus I, anterior (abaxial) view, small black arrows point to lines of larger pores that are present on all leg segments; C – female tarsus I, close-up of famulus; D – optical section through common alveolus of genual seta *d* (arrow) and solenidion (removed), male; E – same, dorsal view; F – alveolus of seta *pv′*, male tarsus IV, distal to right; G – male genu IV, posterior (abaxial) view, showing enlarged seta *v″*. H – section of cuticle of genu II in the vicinity of seta *v″* (normal cuticle); I – same, in the vicinity of seta *v′* (excavated porose area). D-F to same scale. Each image layered and color- and sharpness-enhanced (see Material and Methods).

isternum. The ventral cuticle is thin proximally but abruptly thickens in the mid-region (*tr*, Figs. 11A, 12B), then gradually becomes thinner distally. The articulation between trochanter and the principal cheliceral segment is inconspicuous and we did not study its full path; it is most noticeable by transparency in the ventral midline (*art*, Figs. 11A, 12B), at the thickest point of the trochanteral cuticle. The part of the trochanter that extends distal to this articulation is a tectum, a large protective scale. The tectum gradually thins distally and near its margin it is hyaline and membranous, fringed with distally directed, inconspicuous cilia (*tr.m*, Figs. 11A, 12B, C). This U-shaped, hyaline region of the tectum-called the 'ventral process' by Grandjean (1947a; *pr.v*)-covers the broad arthrodial membrane of the movable digit from below.

The complement of oncophyses associated with the articulation of the movable digit is similar to that described by van der Hammen (1968) and Alberti *et al.* (2011) for the nothrine genera *Hermannia* and *Archegozetes*, respectively. Oncophysis *op′* is a soft, hyaline lobe projecting over the base of the movable digit on the adaxial face (Figs. 11A, 12E, F). Oncophysis *op.v* (Figs. 11A, 12A) does not project as a lobe, but extends from the articulation onto the ventral region of the fixed digit where it attaches; its distal extent coincides exactly with the end of porosity and the beginning of birefringence in the digit cuticle. Under the hyaline coating, pore canals are clearly visible in the underlying sclerotized layers of the fixed digit, but they are noticeably less dense than in most other porose cuticle, as with the embedded sclerite on the posterior lobe of the spermatopositor (see above).

Both oncophyses give the impression of being deformable and fluid-filled, consistent with observations of *Hermannia* by Bäumler (1970) that they inflate under pressure. The membranous distal margin of the trochanteral tectum (*tr.m*) has been con-

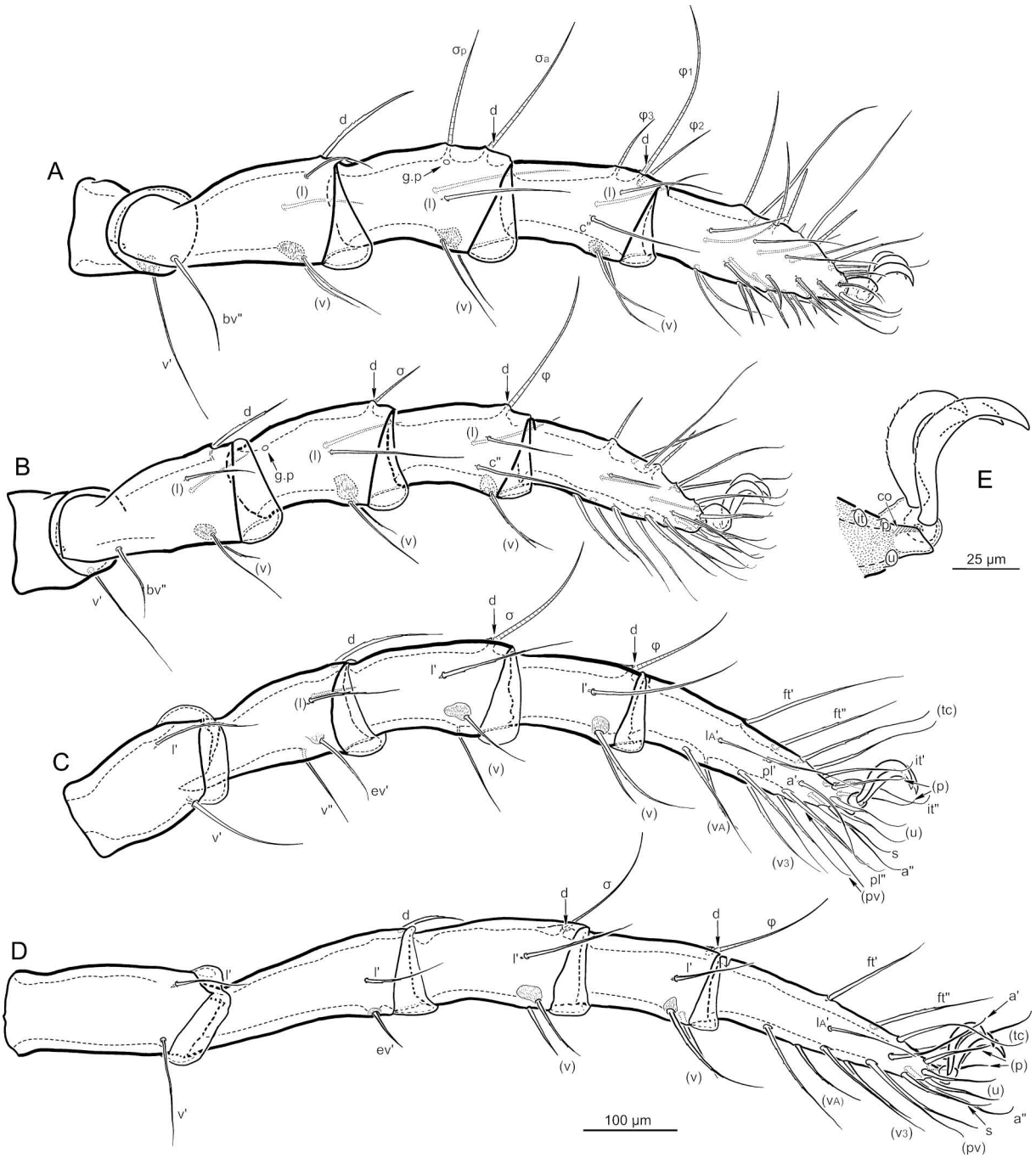


FIGURE 14: *Collohmannia johnstoni* **n. sp.** female, legs, all abaxial view (right legs I, II, posterior; left legs III, IV, anterior): A – leg I; B – leg II; C – leg III; D – leg IV; E – detail of ambulacral region of leg II, showing condylar rib (*co*).

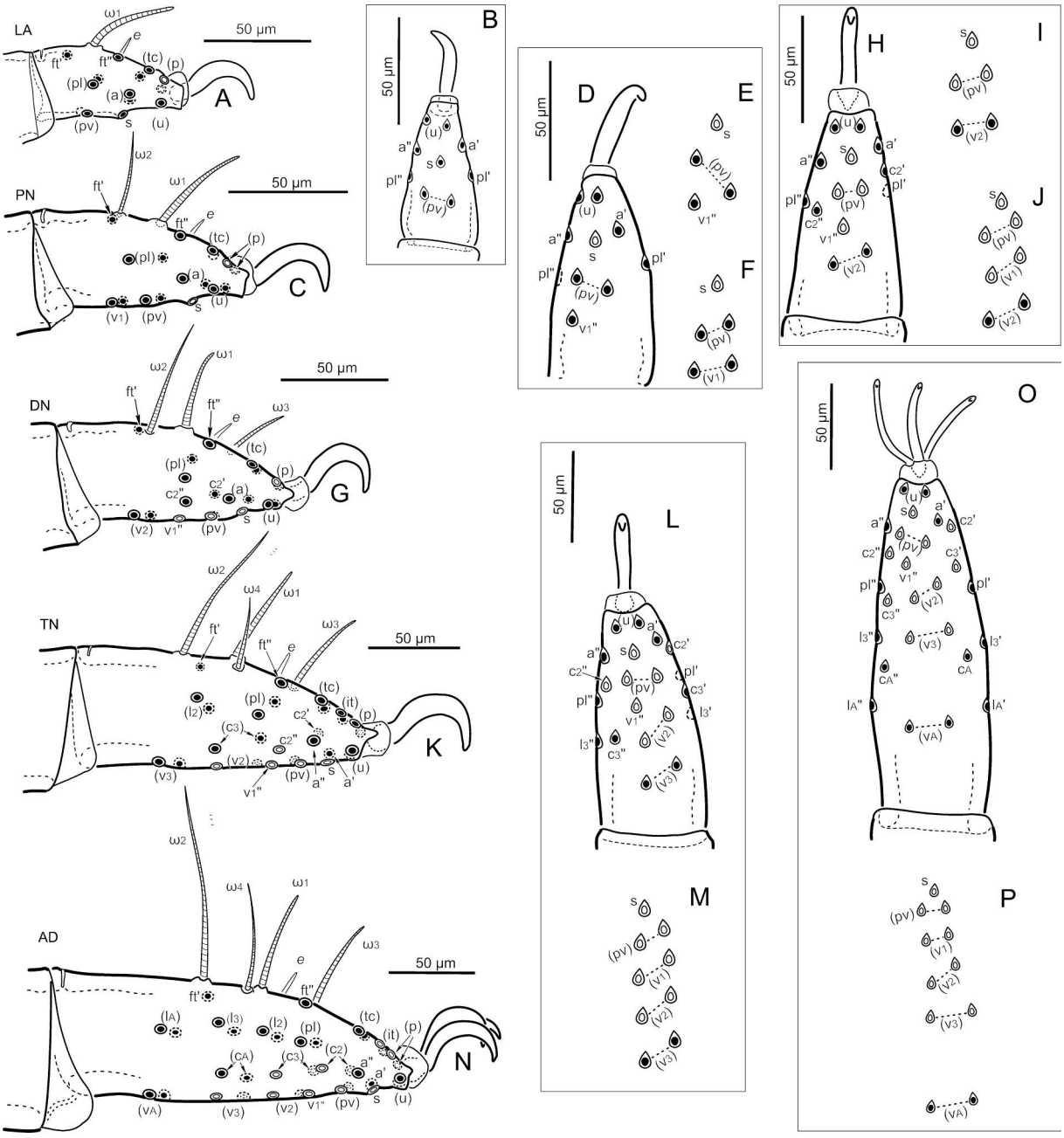


FIGURE 15: *Collohmannia johnstoni* **n. sp.**, setal development of right tarsus I (semi-schematic): A – larva, posterior (abaxial) view; B – same, ventral view; C – protonymph, posterior view, fullest setation observed; D – same, ventral view, most common case; E, F – same, but variations of ventral setation ; G – deutonymph, posterior view, fullest setation observed; H – same, ventral view (note disjunctions, and gap left by absence of v_1'); I, J – same, but variations of ventral setation; K – tritonymph, posterior view, fullest setation observed; L – same, ventral view (note as in H); M – same, but variation of ventral setation; N – adult female, posterior view, fullest setation observed; O – same, ventral view (note as in H); P – same, but variation of ventral setation. Circles and drop-shapes with full outlines indicate alveoli of posterior setae, those with dotted lines indicate anterior setae; solid internal circles indicate normal setae, open internal circles indicate eupathidia; labeled dashed lines connect respective pseudosymmetrical setal pairs.

sidered an oncophysis in the three studies mentioned above, the so-called 'coxal oncophysis' (their *op.x*), but the term is probably inappropriate, since it derives from a sclerite, not soft arthrodial cuticle.

Abaxially, just dorsal to *op.v*, a thin, stiff scale projects horizontally from the movable digit (*md.s*, Fig. 12E). Most of the scale is hyaline, but its base has porose, sclerotized cuticle, such that in lateral aspect the movable digit seems to have a short ridge along its ventral adaxial edge (Fig. 11A).

Legs (Figs. 4F, G, 13-16) — Overall, legs are rather simple, tubular in form (Fig. 14). Leg IV is longest, ca. 0.6 times as long as the body in both sexes. Relative to leg IV, other legs have approximately the following proportional length (males tend toward the higher fractions): I (0.80-0.83), II (0.74-0.76), III (0.83-0.92). Width of most segments is slightly greater on I-II than on III-IV. At its base, tarsus I is ca. 1.3 times thicker than tarsus IV, but all tarsi have similar thickness distally; tarsi I and II taper mostly in their distal third, but tarsi III and IV taper gradually, throughout their length.

Sclerotized leg cuticle is generally porose, like that of the body, but there are isolated lines of more luminous pores that form no discernible larger pattern (Fig. 13B, F); these are most abundant and conspicuous on tibiae and tarsi. There are no differentiated areas of larger pores that could be compared to the discrete adaxial respiratory areas on femora and trochanters III and IV of most Brachypylina. However, on femora, genua and tibiae, setae of the anterior ventral rows (*v'*, *ev'*) insert eccentrically in a small, rounded, luminous porose area similar to those of the notogaster (Fig. 13, cf. H, I); these were not seen associated with any other leg seta. Several types of cuticle are present distally on the tarsus. The normal, porose sclerotized cuticle (Fig, 13B, F) stops at the level of proral and unguinal setae insertions (Fig. 14E). The tarsus continues laterally and ventrally as a U-shaped extension that is mostly pale but seems stiff, not deformable; only along the upper edge is sclerotization retained, where it forms a rigid, elongated condylar rib that supports the ambulacrum (*co*, Fig. 14E). Superficially this pigmented rib resembles the condylophores of most desmonomatan taxa, but unlike them it is not

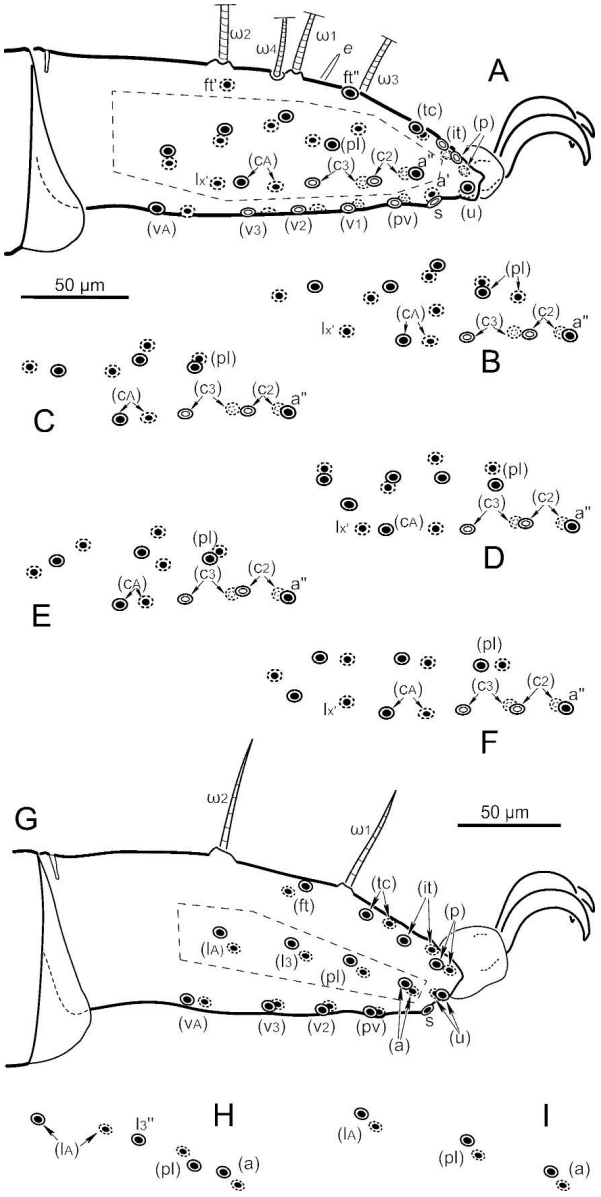


FIGURE 16: *Collohmannia johnstoni* **n. sp.** adult, tarsi I and II (all posterior, abaxial view) showing variation of lateral setae, which are all those setae without labels: A-F – right tarsus I. A – most common case (region of variation circumscribed with dashed line); B-F – variations; G-I – right tarsus II. G – most common case (dashed line as in A); H, I – variations. Circles with full outlines indicate alveoli of posterior setae, those with dotted lines indicate anterior setae; solid internal circles indicate normal setae, open internal circles indicate eupathidia.

an isolated, cylindrical structure. Most distally is the soft, deformable ambulacral pad from which the claws emerge. The pad extends proximally in the dorsal region to the level of the proral setae, thereby 'capping' the U-shaped extension and allowing the ambulacrum to flex backward.

The pretarsal ambulacrum of each leg is tridactylous, with the empodial claw being similar to laterals, except very slightly shorter. Each claw has minute, inconspicuous barbs along its dorsal curvature, except near the base and tip. The globular basilar piece – generally similar to that described by Grandjean (1941) for *Camisia* – is isotropic and slightly pigmented, with a pair of small cotyloid cavities that articulate with the end of the respective condylar rib. There is no clear channel in the ventral tarsal cuticle to guide the tendon of the ambulacral depressor muscle, but a vague proximal groove accommodates the distal part of the muscle entering from the tibia.

Except for the rare absence of tibia II seta *v″*, the setation of adult legs varies only on tarsi (Table 2). Numerical formulas (counts on legs I-IV) of the proximal segments are as follows: trochanters (1-1-2-2); femora (6-6-5-3); genua (5*-5*-4*-4*); tibiae (6*-6*-4*-4*). An asterix indicates that this count includes minute seta *d* (see below), which is easily missed so that the count appears to be one fewer. The tarsal setation is rich in accessory setae of the *l* and *v* rows, as well as an intermediate *c* row on tarsus I only. The total count of tarsal setae varies considerably, both within and among individuals, and this is due almost entirely to variation in the *l* and *v* rows (Tables 1, 2; see below, Development and variation of leg setation). The following represents the most common count for tarsi I-IV (famulus not included on I), preceded in parentheses by the minimum observed and followed by the maximum observed: (35)37(39)-(23)25(26)-(21)22(23)-(17)18(19). The relative size, position and identity of setae are shown in Figs. 14, 15. Except for *d*, setae of the basal four segments are thin, finely attenuate, and have inconspicuous, minute barbs (mostly not illustrated) in approximately the middle third. Seta *d* of the femora is similar, but slightly thicker and distally acicular. Seta *d* of all genua and tibiae is minute and coupled to a solenidion on the respective segment; for leg I, this is σ_a on the genu and φ_1 on the tibia. The seta is appressed to the anterior (') side of the solenidion and inserted with it in the same alveolus; it is seen best when the solenidion is detached, as often happens after long treatment in a clearing agent (Fig. 13D, E). The seta lacks barbs and ranges in length from about 3-15 μm, with longer setae (*i.e.* that of genu I) being attenuate and shorter ones spiniform; on a given leg the genual seta *d* is usually longer than that of the tibia.

Tarsal setae have a variety of forms. On tarsi II-IV the more proximal setae are similar to those of basal segments, *i.e.*, finely attenuate and minutely barbed. More distal setae – tectals (*tc*), iterals (*it*), prorals (*p*), unguinals (*u*), antelaterals (*a*), primiventrals (*pv*) and the unpaired subunginal, *s* – are somewhat flattened, ribbon-like, in their distal third and usually curl strongly dorsad near the tip. Alveoli of most setae in lateral and ventral regions are tear-shaped (Fig. 13F), rather than circular, with the point directed distally. On tarsus I, setae (*it*), (*p*), *s*, (*pv*), (c_1), (c_2), (v_1, if present), (v_2), and (v_3) are eupathidial, i.e. hollow, shorter than other setae, lacking barbs and slightly curving ventrally near the tip. The famulus (*e*, ca. 15 μm) is erect, bluntly spiniform and roughened by numerous microtubercles or callosities (Fig. 13C); it lies approximately in the dorsal midline, usually closest to seta *ft″* and solenidion ω_3, but the three do not form a tight tarsal-cluster.

Solenidial counts (legs I-IV) are as follows: genua (2-1-1-1); tibiae (3-1-1-1); tarsi (4-2-0-0). Relative sizes and positions are shown in Figs. 14, 15. Most are finely attenuate (piliform in the terminology of Grandjean 1935) to sub-flagellate, but ω_1 and ω_3 of tarsus I, and ω_1 and ω_2 of tarsus II taper only to a thick, rounded tip (ceratiform).

Two other cuticular features are present on legs. Each tarsus has a relatively large transverse lyrifissure (ca. 25-30 μm long) immediately distal to its base, almost centered in the dorsal midline. On genua I-III (but not IV), a so-called genual pore (*po*) is present high on the posterior (") side; each comprises a simple canal through the procuticle that is covered with thin, hyaline cuticle. On genu I it is in

TABLE 1: Development of leg setae and solenidia in *Collohmannia johnstoni* **n. sp.** [1, 2].

	Trochanter	*Femur*	*Genu*	*Tibia*	*Tarsus*
Leg I					
Larva	-	d, bv"	d*σ_a, σ_p (l)	d*φ_1, l', v', c"	(ft), (pl), (tc), (p), (u), s, (a), (pv) e, ω_1
Pn	v'	-	-	-	$\underline{v}_1'$, $\underline{v}_1''$, ω_2
Dn	-	l', l"↓, v', v"↓	(v)	φ_2	$\underline{l}_2'$, $\underline{l}_2''$, (v_2), (c_2), ω_3
Tn	-	-	-	v"↑	it', it"↑, (v_3), (l_3), (c_3), ω_4
Adult	-	-	-	l"↑, ϕ_3	(c_A), (v_A), 3–6 l' setae, 2–4 l" setae (see text)
Leg II					
Larva	-	d, bv"	d*σ, (l)	d*φ, l', v', c"	(ft), (pl), (tc), (p), (u), s, (a), (pv), ω_1
Pn	v'	-	-	-	-
Dn	-	l'↓, l"↓	v', v"↓	-	$\underline{v}_2'$, $\underline{v}_2''$, ω_2
Tn	-	(v)	-	-	$\underline{l}_3'$, $\underline{l}_3''$, (v_3), (it)
Adult	-	-	-	l", v"↑	(l_A), (v_A)
Leg III					
Larva	-	d, ev'	d*σ, l'	d*φ, l', v'	(ft), pl' (tc), (p), (u), s, (a), (pv)
Pn	v'	-	-	-	-
Dn	l'	l'↓	(v)	-	$\underline{v}_2'$, $\underline{v}_2''$
Tn	-	-	-	-	(v_3) (it)
Adult	-	l", v"	-	v"↑	l_A', (v_A)
Leg IV					
Pn	-	-	-	-	ft" (p), (u), (pv)
Dn	v'	d, ev'	d*σ	d*φ, v'	ft' (tc), (a), s
Tn	l'	l'	l'↓, (v)	-	$\underline{l}_3'$, $\underline{v}_3'$, v_3"
Adult	-	-	-	l'↑, v"↑	l'_A, (v_A)

[1]For *amphistasic* setae (iteral pair on tarsi and all setae of other segments) the cell indicates the instar of first appearance or, if it is vertitional (variable), the instar of most common first appearance; if vertitional, a following arrow points to the less common, alternative cell (frequency indicated in Table 2). For *eustasic* 'accessory' setae of tarsi (rows *l*, *c* and *v*), the seta is indicated in its appropriate cell; underlined italics indicates variable presence, with observed frequencies indicated in Table 2; if absent, the seta is also absent from subsequent instars of the same individual.

[2]Parentheses indicate that both setae of the pseudosymmetrical pair (', ") appear together; a dash (-) indicates there is no addition in that instar; an asterisk (*) indicates that seta *d* is present only as a minute vestige and coupled with the respective solenidion, usually in the same alveolus. Abbreviations: Pn (protonymph; Dn (deutonymph); Tn (tritonymph). Subscripts of eustasic tarsal setae of rows (*l*), (*v*) and (*c*) denote the instar in which they form (1, 2, 3, A = Pn, Dn, Tn, adult, respectively). Studied adults were female.

TABLE 2: Vertitional variation in the ontogeny of leg setae in *Collohmannia johnstoni* **n. sp.** [1]

Leg	Segment	Instar	Seta	Frequency of presence based on 20 observations	Amphistasic (a) or eustasic (e)
I	femur	Dn	v"	17	a
		Dn	l"	18	a
	tibia	Dn	v"	6	a
		Tn	l"	6	a
	tarsus	Pn	v_1'	5	e
		Pn	v_1"	20[2]	e
		Dn	v_1'	4	e
		Dn	v_1"	19	e
		Dn	l_2'	4	e
		Dn	l_2"	4	e
		Dn	it"	1	a
		Tn	v_1'	2	e
		Tn	v_1"	19	e
		Tn	l_2'	5	e
		Tn	l_2"	4	e
		adult	v_1'	5	e
		adult	v_1"	20[2]	e
		adult	lateral setae - see text		e
II	femur	Dn	l'	14	a
		Dn	l"	19	a
	genu	Dn	v"	17	a
	tibia	Tn	v"	3	a
		adult	v"	17	a
	tarsus	Dn	v_2'	13	e
		Dn	v_2"	10	e
		Tn	v_2'	5	e
		Tn	v_2"	12	e
		Tn	l_3'	1	e
		Tn	l_3"	4	e
		adult	l_3'	8	e
		adult	l_3"	4	e
		adult	v_2'	13	e
		adult	v_2"	15	e
III	femur	Dn	l'	10	a
	tibia	Tn	v"	4	a
	tarsus	Dn	v_2'	5	e
		Dn	v_2"	17	e
		Tn	v_2'	1	e
		Tn	v_2"	10	e
		adult	v_2'	4	e
		adult	v_2"	15	e
IV	genu	Tn	l'	16	a
	tibia	Tn	v"	2	a
		Tn	l'	1	a
	tarsus	Tn	v_3'	19	e
		Tn	l_3'	5	e
		adult	l_3'	4	e

[1]Abbreviations: Pn (protonymph; Dn (deutonymph); Tn (tritonymph). Studied adults were female.

[2]Eustasic seta v_1" of tarsus I existed on all studied legs of Pn and adult, but this is probably sampling error: the data are included for comparison with its frequency in other instars.

mid-segment, approximately aligned between seta *l"* and solenidion σ_p (Fig. 14A); on one leg examined, two tandem pores were present on genu I (as observed by Grandjean 1958a in *Perlohmannia*). On genua II and III the pore is far proximal, close to the articulation with the femur (Figs. 14B).

The legs of males are similar to those of females, with the following exceptions. The solenidia on tarsus I are more evenly spaced and each is more proximally positioned (cf. Fig. 4E, G with Figs. 14A, 15N). More striking are the modifications of leg IV relating to the transfer of materials that are interpreted as nuptial food (See below: Courtship behavior). The expanse of articulating cuticle between genu and tibia seems larger than in the female, such that the tibia can flex dorsally to an unusual extent (Fig. 2C, arrow); presumably this prevents interference between distal segments when legs IV come together during courtship. The genu is thicker than that of females, with a strong adaxial depression accommodating a strikingly hypertrophied seta *v"* (Figs. 2C, 4F, 6B). This seta is inserted unusually high on the posterior face, and has the form of an asymmetrical diamond. Its thick base is separated from the flattened distal region by a well-defined, curved drop-off across its broadest part; the distal region is tapered and elongated to extend well beyond the end of the segment. The entire seta is strongly birefringent in polarized light (Fig. 13G). Solenidion σ is smaller than that of females but has the same piliform shape and coupled minute seta *d*. The tibia is unmodified, except for being slightly shorter than in females, and having a smaller solenidion φ.

Active juvenile instars (Figs. 17-19)

Dimensions, facies, integument — The total length range (mean in parentheses) for 10 specimens of each juvenile instar is as follows: larva 382-607 (473); protonymph (Pn) 723-843 (760); deutonymph (Dn) 856-1021 (952); tritonymph (Tn) 1100-1478 (1286). Body proportions are similar among the instars, with maximum width being about half the length (0.40-0.56). Larvae are most variable in length: expressed as a percentage of the mean, the range is 48 % (225/473). We attribute this to the fact that each individual larva expands significantly from the time it ecloses from the egg to when it attains its final length after the commencement of feeding. This aspect of variation, which is not applicable to studied nymphs, was not controlled in sampling of larvae, so individual differences in time-since-eclosion probably magnified the observed range. Among nymphs, the percentage is much lower, *viz*.: Pn (16 %), Dn (17 %); Tn (29 %). The near doubling of the range between Dn and Tn, with the latter approaching the figure for adults (31 %), suggests that the size difference between males and females is attained largely in the Tn.

Nymphs are strikingly two-toned, with both types of cuticle being shiny in reflected light. Light- to medium-brown sclerotized cuticle is found on the prodorsum (aspis), epimeral plates, legs and gnathosomal components, and appears darkest on the cheliceral digits and the lateral rib of the prodorsum. As in the adult, this cuticle is porose and mostly smooth, lacking an imbricate surface. By contrast, most cuticle of the hysterosoma is colorless and nearly transparent in life, so that dark food boli, internal organs and the oily, yellow contents of the opisthonotal gland are well visible externally (Fig. 19A, C). In preserved specimens this cuticle is creamy white to slightly yellowish, and is weakly translucent (Fig. 17C, D); it is deformable but seems more elastic than that of the soft, flexible articulations. In transmitted light it appears thick and uniform, and glows conspicuously under DIC or polarized illumination (Fig. 17F; see Remark 4). This part of the cuticle, which lacks apparent porosity or surface ornamentation in juveniles, becomes sclerotized, imbricate and porose in the adult. Small porose tubercles at the base of large setae and a narrow ring around the opisthonotal gland opening are lightly sclerotized and therefore are contrasting brown. The larva is colorless throughout when first eclosed from the egg, and sclerotized parts (the same structures as in nymphs) darken only slightly as it matures. Its structure is nearly identical to the larva of *C. gigantea*, which was described and illustrated by Grandjean (1966), and his figures are referred to below to illustrate certain features of *C. johnstoni*.

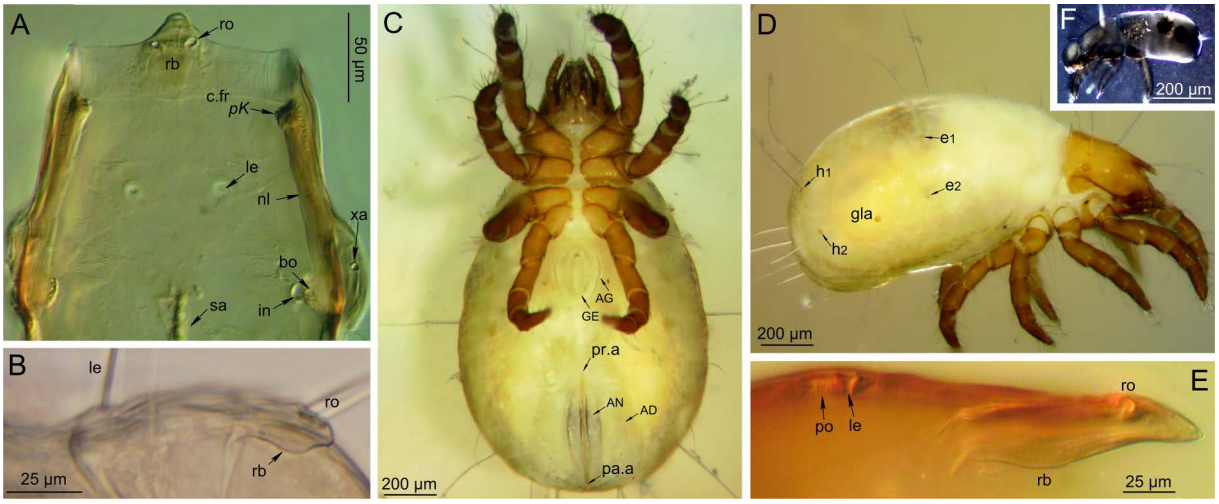


FIGURE 17: *Collohmannia johnstoni* **n. sp.** immatures, light micrographs, DIC (A, B, E) and incident (C, D) illumination: A – protonymph, separated prodorsal shield, ventral view; B – larva, anterior part of prodorsum, lateral view; C-E – tritonymph: C – ventral view, D – lateral view, E – anterior part of separated prodorsum, lateral optical section. Abbreviations: AD – adanal segment, AG – aggenital region, AN – anal segment (paraproctal valves), *c.fr* – cheliceral frame (line *bt* of Grandjean 1966), GE – genital valves, *gla* – orifice of opisthonotal gland, *pK* – prodorsal condyle, *nl* – lateral rib (nervure), *po* – porose area, *pa.a* – postanal apodeme, *pr.a* – preanal apodeme, *rb* – rostral bulge, *sa* – sagittal apodeme; *bo*, *in*, *le*, *ro*, *xa* – prodorsal setae or their alveoli; *e*, *h* – gastronotic setae. Each image layered and color- and sharpness-enhanced (see Material and Methods).

As in the adult, there are porose areas and associated dermal glands positioned near setae; their distribution is noted below.

Prodorsum — The general form of the aspis is similar to that of adults except for the limbless rostral tectum, which occupies only a narrow distal portion (ca. 15 %) and is short enough to leave all but the base of each chelicera exposed (Figs. 17A, D, 18H, K). The aspis is therefore broadly truncate anteriorly, except for a medial projection that bears the rostral setae (*ro*). Seen flat in dorsal aspect, the projection is broadly convex in the larva, hardly long enough to contain the alveoli of *ro*; it becomes somewhat triangular in the Pn, but is a larger and nearly an equilateral triangle in the Dn and Tn, with the alveoli of *ro* near its base. As in *C. gigantea* (Grandjean 1966, his Figs. 4C, D), the lower wall of the tectum (rostrophragma) projects ventrally between the chelicerae to form a purse-like pouch, narrowly V-shaped in cross section, that he considered a naso. In nymphs, the presence of a larger medial projection alters the shape of the optical section (cf. Fig. 17B, E), and the width of the 'naso' increases, until in the Tn its form is more that of an inverted dome or swelling. In the medial region of the rostral tectum both surfaces are pigmented and distinctly porose (Fig. 17A), but in lateral regions the distal margin becomes hyaline and lacks distinct porosity. In all immature instars the lateral rib (*nl*) and exobothridial lobe are similar to those of the adult, except that the ventral marginal thickening is less distinct than in the adult, and the lobe is less extensive posteriorly, such that seta *xp* is not on the aspis (Fig. 18K). The cuticle in which *xp* inserts is not sclerotized, but it seems somewhat stiff, lacking the fine striation of the soft cuticle that otherwise surrounds the aspis and forms the sejugal groove. There is no occipital phragma; the posterior margin of the aspis curves slightly downward before attaching to the sejugal cuticle but otherwise is simple. The thin, blade-like sagittal apodeme (*sa*, Fig. 17A) is present in all immature instars, similar in form and relative size to that of the adult (see Remark 5). Except for the absence of the phragma, muscle insertions seem similar to those of the adult, with sigilla in approximately the same locations; the latter are more clearly marked in nymphs than in the larva. The macula lying immediately posterior to each lamellar seta, which is conspicuous in the adult, was not

discerned in the larva or Pn; it is weak, but present in the Dn and Tn (Fig. 17E; see Remark 1). Except for the bothridial seta, prodorsal setae of all immature instars are similar in form to those of the adult, but some have slightly different relative lengths. Most noticeable is that the rostral seta is about twice as long in immatures as in the adult, relative to the other prodorsal setae. The bothridial seta (*bo*) is similar in length to *ro* in immatures (becoming 2-3 times as long as *ro* in adults), and its shape changes significantly during ontogeny. In the larva *bo* is narrowly lanceolate, usually with a single strong tip but subterminal large barbs can make it appear bifid or trifid. Barbs are relatively numerous in the distal half, being minute on the shaft but several times larger on the head; as in the adult they are formed in the hyaline, isotropic external layer. The birefringent core appears hollow throughout, but conspicuously so only in the expanded head region. In the Pn the head is narrower, sometimes indistinguishable, and has fewer barbs (Fig. 18H); in the Dn and Tn seta *bo* is filiform, tapering only very close to the tip, as in many adults (Fig. 18K). The gentle sigmoid curve immediately distal to the bothridium may be less distinct than in the adult, especially in the larva. The bothridium is similar in structure to that of the adult, but the outpockets in the middle two portions are few in the larva, becoming more numerous in successive instars.

Gastronotic region — This region accounts for about two-thirds of the total length in nymphs but slightly less (about 60 %) in well-expanded larvae. Anteriorly, in the region of the sejugal groove, the cuticle is flexible and finely, transversely striate in all immature instars (Fig. 18H); this allows a limited degree of retraction of the prodorsum, probably similar in extent to that of the adult. Its posterior extent is probably what Grandjean (1966) designated line *as* (his Figs. 1A, 2), though he did not mention cuticular striations. This dorsosejugal band of soft, striate cuticle continues into the podosomal region above the coxisternum. Two transverse grooves are present dorsally in all immature instars, but efface mid-laterally (Fig. 18H). The anterior groove (*r2* of Grandjean 1966) passes between setal pairs d_1 and d_2, and is usually inconspicuous. The other (*r3*) lies posterior to setal pair e_1 and is usually conspicuous even at low magnification. In the more contracted preserved nymphs, the region anterior to *r3* and above the legs is concave, and the region posterior to *r3* is somewhat depressed in lateral view. Setal development is normal and holotrichous, except that f_1 is vestigial, appearing like a minute pit with distinct walls, in all immature instars. Setal pairs e_1, e_2, h_1 and h_2 are flagellate and notably larger than others in all instars; proportionally they are at least as long as in the adult. Seta p_1 is of medium length (similar to p_2) when first joining the gastronotic complement in the Pn (Fig. 18H), but it enlarges in the Dn to become one of the five long pairs. As in the adult, other setae are short and thin in all immature instars, with c_3 and f_2 being smallest. Other than the normal shifts in posterior setae from larva to Pn, as segment PS is incorporated into the gastronotum, the relative positions of gastronotic setae remain similar throughout ontogeny, with the exception that pair e_1 migrates anterolaterally: it is posterior to d_2 in the larva, posterolateral to d_2 in nymphs, and anterolateral to d_2 in the adult (see Remark 6). Lyrifissures are all cupular in form and have the normal ontogeny: *ia*, *im* and *ip* have similar positions in all instars; *ih* and *ips* lie off the anterolateral corner of the paraprocts in the larva and Pn, respectively, then shift anterolaterally as the next paraproctal segment appears (Fig. 18B-E). The opisthonotal gland opening (*gla*) lies closely dorsal to *ip* in all immature instars (becoming more nearly aligned between *ip* and seta f_2 in the adult).

No porose areas were seen in the gastronotic region of larva or nymphs. However, after short treatment (one day) in cold lactic acid, clusters of cells can be seen that – based on their shape and locations – appear to be homologues of the adult dermal glands. In the Dn and Tn, all the setae accompanied by porose areas in adults are underlain by similar umbrella-like clusters of elongated cells (including seta *le* of the prodorsum). This condition appears to develop gradually: in the larva the elongated cells are clustered near the setae, but do not form well-circumscribed umbrella-like formations-rather, they occupy broader expanses, including all the subcuticular space in the posterior part of the

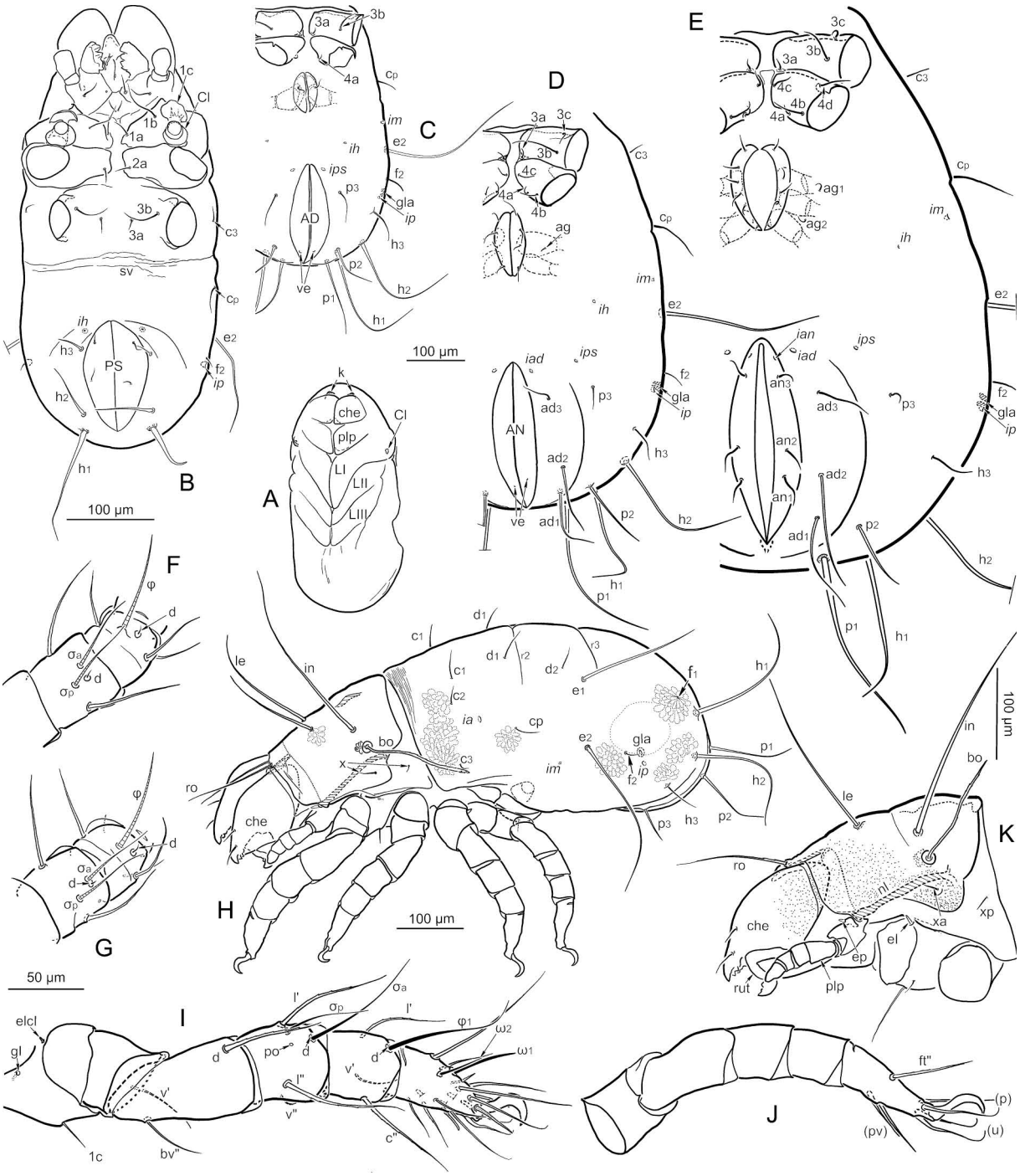


FIGURE 18: *Collohmannia johnstoni* **n. sp.** immatures: A – prelarva, ventral view; B – larva, ventral view, legs omitted; C-E – partial ventral views of the hysterosoma with legs omitted: C – protonymph, D – deutonymph, E – tritonymph; F, G – larval genu and tibia, dorsal aspect, showing variations of setae *d* in specimens extracted from eggs (see text for other cases): F – setae *d* of both segments separate from solenidia (abnormal), G – genual seta *d* associated with solenidion σ (normal), tibial seta *d* independent from solenidion (abnormal); H-J – protonymph: H – oblique lateral habitus, I – right leg I, posterior (abaxial) view, J – left leg IV, anterior (abaxial) view; K – prosoma of tritonymph, lateral view, legs omitted. A, C-E to same scale; F-J to same scale. Notations explained in text.

hysterosoma. A similar arrangement is seen in the Pn, but posterior clusters are more differentiated (Fig. 18H). Apart from these tight clusters, similar elongated cells were observed dispersed under the cuticle of body and legs in the prelarva, larva and Pn, but only of legs in the Dn and Tn. Whether any of these elongated cells are truly glandular could be determined only with appropriate histological study.

Coxisternum — The form of the coxisternum differs little from that of the adult. Moving posteriorly, each successive epimere is narrower and the coxisternum is divided into four sclerotized units by soft, striated cuticle by the combination of a deep ventrosejugal furrow and a sagittal scissure; the latter is broader than in the adult. The plates of epimere I do not fuse anteriorly in the larva or Pn, but a small bridge of sclerotized cuticle like that of the adult is present from the Dn. The triangular region posterior to epimeral plates IV seems unsclerotized in all nymphs. In all instars epimeral plates are porose, but their pigmentation and the distinctness of borders and apodemes increases during ontogeny. There is no vestige of epimere (or leg) IV in the larva. The epimeral setation (pairs on I to IV) usually develops as follows: larva (3-1-2, including seta *1c*); Pn (3-1-2-1); Dn (3-1-3-3); Tn (3-1-3-4). Variations were mostly noted in the Tn: of 18 plates (nine individuals) studied, one plate III lacked *3c*, and four plates IV lacked *4d*; on one Tn, *4b* was doubled and on another *3c* was doubled, each unilaterally. In nymphs, the relative sizes of setae are as in the adult. In the larva, Claparède's organ (*Cl*, Fig. 18B) and its scale-like protective seta *1c* have the usual form, with no secondary annulation (identical to that of *C. gigantea*; Grandjean 1966, his Figs. 1-3). The supracoxal seta and coxal gland opening on epimere I are like those of the adult, but no clear flange was observed on the dorsal edge. Epimere III does not extend dorsally as it does in the adult.

Anogenital region — This region lacks distinct sclerites in all immature instars. The larva has a noticeable transverse groove with soft, striated cuticle situated behind the coxisternum but it is well removed from the posterior margin of epimere III (*sv*, Fig. 18B). There is no such isolated groove in nymphs, but the same relative position is occupied by a transverse depression between epimere IV and the genital valves. In nymphs the genital valves are small and well-removed (by more than their length) from the paraprocts (Fig. 18C-E). Their usual setation (Pn, Dn, Tn) is 1-4-7; variations were usually asymmetrical and included: Dn may have 3 setae (3 of 12 valves studied) and Tn may have 5 or 6 (1 each of 18 valves studied). The first aggenital seta forms in the Dn, and the second is added in the Tn; one anomalous individual had 3 on one side (ag_1 doubled) and 1 on the other (ag_2 absent). The paraproctal valves are elongated in all immature instars, with the pair collectively lens-shaped, tapered at each end (Fig. 18B-E). The larva lacks transcupular (inguinal) seta h_4 and there are only two setae on each paraproctal valve (segment PS). Because of their positions, we interpret the missing third seta as p_1, as did Grandjean (1966) for *C. gigantea*; p_1 first forms in the Pn, as does cupule *ips*. In the Pn and Dn, paraproctal valves (segments AD and AN, respectively) are glabrous, so in the terminology of Grandjean (1949a) *C. johnstoni* exhibits paraproctal atrichosy at two levels. Marks in the paraproctal cuticle of some Pn and Dn specimens seem to represent setal vestiges; these may include vestiges (*ve*, Fig. 18C, D) of only ad_1 (in Pn) or of both an_1 and an_2 (in Dn). Setal rows *ad* and *an*, as well as their respective cupules (*iad*, *ian*), appear fully developed in the subsequent instar (Dn and Tn, respectively). Segment AD retains a convex, valve-like, 'parenthetic' appearance around the paraprocts in the Dn and Tn, being separated from the gastronotic region by a shallow groove. Genital papillae are similar in form to those of the adult.

Gnathosoma — Few changes occur to the gnathosoma during ontogeny. The larva lacks adoral seta or_3, which is present from the Pn in its adult form and location. The second seta of the palp-femur, *inf*, is added in the adult. In all immatures, palp-tarsus seta *su* forms as a small, non-eupathidial branch from the ventral side of eupathidial seta *ul'* (as illustrated for *C. gigantea* by Grandjean 1966, his Fig. 4B, or slightly longer and thinner); in the adult *su* enlarges to the size of *ul'* and becomes eupathidial, still fused with *ul'* proxi-



FIGURE 19: *Collohmannia johnstoni* **n. sp.** biology and habitat: A – tritonymph on skeletonized red maple (*Acer rubrum* L.) leaf; B – egg with larva visible inside, recently deposited on maple leaf in culture; C – nymphs feeding on red maple leaf; D – adult female feeding on unidentified leaf; E – type locality and typical habitat: riparian mixed forest with overstory of red maple, yellow birch (*Betula alleghaniensis* Britton), white spruce (*Picea glauca* (Moench) Voss) and eastern hemlock (*Tsuga canadensis* (L.) Carr.), and dense understory of rhododendron (*Rhododendron maximum* L.).

mally. Seta *acm* is normal until the Tn, when it becomes eupathidial but otherwise does not change shape or position. The dark pattern on the ventral surface of the adult pharynx, described above, develops gradually; it is narrow and without apparent reticulation in the larva, then increases in darkness, relative width and degree of reticulation in successive nymphs. No structural change in the chelicera during ontogeny was detected.

Legs — The structure of legs in immatures is generally like that of adults, except most segments become relatively longer and thinner with successive instars (cf. Fig. 18H, Fig. 14). The most conspicuous ontogenetic change is the steady increase in relative size of leg IV. When first formed in the Pn, it appears small and weak, with length ca. 0.8 times that of leg I; it is about equal to leg I in length (though thinner) in the Dn, and about 1.1 times leg I in the Tn (becoming $\sim$ 1.2 times leg I in adult). All pretarsi are monodactylous, and the ambulacrum articulates by means of a condylar rib at the distal extreme of the tarsus, as in the adult. Sclerotized cuticle is porose throughout ontogeny, but this porosity becomes more noticeable in successive instars, as the cuticle darkens. The lines of luminous pores are present in nymphs, though less obvious and less extensive than in the adult. No porose area (such as those associated with ventral setae in the adult) was observed in the larva or in early nymphs but they can be vaguely discernible in the Tn. All immature instars have genual pores on legs I-III, with the same distribution as in the adult.

Solenidial ontogeny (Table 1) does not vary. For legs II-III, the adult complement is present from the larva and for leg IV it appears abruptly in the Dn. The ontogeny of leg I solenidia is more complex, and the following formulas apply (genu-tibia-tarsus): larva (2-1-1), Pn (2-1-2), Dn (2-2-3), Tn (2-2-4); the third tibial solenidion, φ_3, appears in the adult.

The ontogeny of leg setae is more complicated and variable (Table 1); it is discussed separately below, with reference to both immatures and adult, but salient traits include the following. Seta *d* is minute and coupled to the respective solenidion on all genua and tibiae, as in the adult, though in the larva the nature of the coupling is variable (see below). Iteral setae are added to tarsi I-III in the Tn, but are absent from tarsus IV. The setal formula for leg IV in the Pn is typical of oribatid mites: 0-0-0-0-7, with the tarsal setae being *ft"*, (*p*), (*u*) and (*pv*). From the larva legs I and II bear the primilateral pair (*pl*), tarsus III bears only *pl'* and tarsus IV lacks primilateral setae (see Remark 7). Only the proral pair (*p*) are eupathidial in the larva; for other eupathidia, transformation from a normal seta occurs in a specific nymph or adult (see below).

Prelarva

The prelarval instar is a typical calyptostase, remaining fully within the egg. It has neither setae nor projecting appendages, but has relatively well-formed vestiges of chelicerae, palps and all three pairs of legs, with the pairs meeting in the midline (Fig. 18A). The leg vestiges are strongly angled, forming chevrons. The chelicera has a clear egg-tooth (*k*), and a vestige of Claparèdes organ (*Cl*) is at the base of leg I. The general form is that commonly seen in middle-derivative oribatid mites, being most similar to those of Desmonomata, particularly Nothrina and early-derivative Brachypylina such as Neoliodidae (Sitnikova 1960; Grandjean 1962b).

Material examined and distribution

The holotype male and allotype female of *Collohmannia johnstoni* were collected by R.A. Norton from the Monongahela National Forest in Randolph County, West Virginia, north of US Rt. 33 near the towns of Bowden and Alpena, on 2-XI-2013. The type locality (38°56.505'N, 79°40.084'W; elevation 930 m) is the trailhead that leads into the Otter Creek Wilderness, accessible from National Forest Rt. 91. The site is a riparian mixed forest with overstory of red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), white spruce (*Picea glauca* (Moench) Voss) and eastern hemlock (*Tsuga canadensis* (L.) Carr.), with a dense understory of rhododendron (*Rhododendron maximum* L.); mites were collected from the thick layer of leaf litter. These and 10 paratypes (3 females, 3 males, 4 immatures) from the same collection are preserved in

alcohol in the collection of the Acarology Laboratory, Museum of Biological Diversity, the Ohio State University (Columbus, Ohio). Thirty other adult paratypes were designated from material collected from the same site, on various dates (9-IX-1980, 22-X-1983, 30-V-1999, 13-VI-2003, 24-V-2005, 13-VI-2006, 1-V-2009); the earliest collection was by M.O. Johnston, the others by R.A. Norton. Four of these paratypes (2 males, 2 females) along with several juveniles have been deposited in each of the following collections: the Canadian National Collection, Agriculture and Agri-food Canada (Ottawa, Canada); the Senckenberg Museum of Natural History (Görlitz, Germany); the Siberian Zoological Museum (Novosibirsk, Russia); and the collection of the Tyumen State University Museum of Zoology (Tyumen, Russia). The remainder of paratypes and several dozen non-type specimens are in the personal collections of the authors. Several additional specimens were collected from non-riparian hardwood forest litter, several hundred meters from the type locality.

The species has been collected from only two other sites, both also within the Monogahela National Forest. (1) West Virginia, Pocahantas Co., 19.3 km E. Richwood; col. S. O'Keefe, 23-VIII-1990, 5 females, 2 males from sifted hardwood litter by log. (2) Same, but Forest Trail 150, 23.7 km S. junction with Trail 55; col. S. O'Keefe, 17-V-1991, 1 female, 1 male from sifted litter, moss, and rotten wood at base of tree.

Etymology

The species epithet *johnstoni* is a double patronym. It is named with respect to honor the memory of the late Prof. Donald E. Johnston, long a principal figure at the Acarology Laboratory of the Ohio State University. Don had a major positive influence on the early career of R.A.N. and on the careers of many other acarologists who passed through that unique program over several decades. It is also named for his son, Prof. Mark O. Johnston (Dalhousie University), who as a student made the initial collection at the type locality.

Development and Variability of Leg Setation

Basic terminology and concepts

Setal priorities — In the evolutionary models of leg setation developed by Grandjean (1946), the 'priority' of a particular seta on a given leg and segment is an indication of its evolutionary persistence: its resistance to variation, ontogenetic delay and regressive loss. Priorities are not random, and usually conform to Grandjean's (1961a) Law of Parallel Homology: they depend on whether the seta is on the anterior (′) or posterior (″) face of a leg oriented in its hypothetically ancestral position, *i.e.*, artificially directed laterally. Usually priorities do not reflect analogy, *i.e.* they are not determined by whether the pair member is on the abaxial (= antiaxial) or adaxial (= paraxial) face of a leg in its natural position (I-II forward, III-IV backward).

Disjunctions — A pseudosymmetrical pair comprises two setae opposing each other on a single leg (e.g. *l*′ and *l*″, or *v*′ and *v*″), in contrast to true, bisymmetrical pairs (e.g. *l*′ on left and right legs). It is common in oribatid mites for one member of a pseudosymmetrical pair to be inserted more distally than the other, and Grandjean's (1958b) terminology indicates which seta is the more distal of the two. Descriptors can be based on homology: a prime (′) disjunction when the distal seta is on the anterior face, a double-prime or second (″) disjunction when on the posterior face. Or, they can reflect analogy: an abaxial or adaxial disjunction indicates that the distal seta is on the outer or inner face, respectively, when a leg is in its natural position.

Disjunctions are often present and consistent on oribatid mite tarsi, and Grandjean (1958b) has used them to help identify setae. On leg tarsi, if a particular pair has a disjunction strong enough to be clearly distinguished, a common pattern is for it to be similar on all legs, conforming to parallel homology. Disjunctions are commonly ″, except for pairs of the ventral rows (including the primiventral pair) which are commonly ′. Even though the subject is little studied, a number of exceptions are known (Wauthy and Fain 1991 and cited papers).

When studying tarsus I of some early-derivative oribatid mites, particularly some Enarthronota and

Parhyposomata, the identification of disjunctions can be complicated by the presence of seta *m″* (monotrope), between *pv″* and *s*. But this seta is rather easily identified and accommodated if ontogeny is known, since *m″* is always larval (Grandjean 1962a). It is much more difficult to be certain about identities and disjunctions if *m′*, the rare adaxial member of the pair, exists because it is always postlarval; *i.e.* it forms anterior to *pv′* at the same time that an accessory ventral seta, *v′*, might be forming posterior to *pv′*. These difficulties do not hamper our study of *C. johnstoni*, because *m″* does not exist in the larva, and *m′* is not known to form in the absence of *m″*.

Amphistasic and eustasic setae — Amphistasic setae are those not linked to a particular instar (or stase). They vary among species in their instar of first formation, and often vary among individuals of a species. Except for tarsi, most setae on legs of oribatid mites are amphistasic. The only amphistasic setae on leg tarsi are the iteral pair (*it*), which are always post-larval (*i.e.*, formed in a nymph or adult) but show great variation in presence and ontogeny (Grandjean 1964).

By contrast, eustasic setae are those strongly linked to a particular instar; if a seta does not form at the 'correct' time it never appears subsequently on that individual. Well known examples include all typical setae present on tarsi of an oribatid mite larva: fastigials (*ft*), tectals (*tc*), prorals (*p*), unquinals (*u*), primiventrals (*pv*), antelaterals (*a*), primilaterals (*pl*) and the unpaired subunguinal, *s*. These, as well as their metameric homologues on tarsus IV, are referred to as fundamental setae. All post-larval setal additions to leg tarsi in oribatid mites, except for the amphistasic iteral pair (and one or two rare exceptions that do not apply to *C. johnstoni*) are also eustasic, and form what Grandjean (1940, 1958b) referred to as 'posterior accessory setae'. Usually, these are added in discrete rows (files) that correspond to the lateral (*l*) and ventral (*v*) pseudosymmetrical pairs of the typical verticil of five setae (Grandjean *op. cit.*), and they respectively align proximal to the fundamental primilateral (when present) and primiventral setae. 'Posterior' was an unfortunate choice in a morphological sense: they are more appropriately called *proximal accessory setae*, though some can be positioned in rather distal parts of the tarsus, especially when numerous (see below).

Eustasy seems a counter-intuitive property of proximal accessory setae. Collectively they are the most variable component of tarsal setation in terms of presence, both among higher taxa and within species, but any particular seta is stable in its development. Grandjean (1958b), in one of the most laudable studies of oribatid mite morphology, convincingly showed this by painstakingly following the development of these setae in *Platynothrus peltifer* (C. Koch) through rearing individual mites and studying their exuviae.

A single verticil (*l′*, *v′*, *l″*, *v″*) of proximal accessory setae is potentially added at each post-larval molt, and while members of a pseudosymmetrical pair may appear together, asymmetrical appearance is common. Grandjean (*op. cit.*) considered the four setae of a verticil to be independent in terms of variation, both between the legs of a pair and among individuals. In a few early-to middle-derivative taxa, and only on tarsus I, a third pair of rows can be present, positioned between rows (*l*) and (*v*) and running proximally from the fundamental antelateral pair; these rows represent pair (*c*) in the presumably more ancestral verticil of seven setae (Grandjean 1940, 1958a). Rarely (e.g. some Palaeosomata and Perlohmanniidae) a ventro-medial row of accessory setae forms proximal to the subunguinal seta, and in a single instance known to us – *Perlohmannia coiffaiti* Grandjean – there is an additional pair of rows (*r*) between (*c*) and (*l*) (Grandjean 1957b, 1961b).

Variability of Leg Setation in Collohmannia johnstoni

Our analysis of leg setal development was based on the study of 10 haphazardly selected specimens (20 legs) of each instar of *C. johnstoni*; the 10 adults were female. Table 1 indicates the instar of appearance for all setae known from adult mites, and Table 2 gives the frequency of variable setae.

Types of observed variation — Only two instances of what we consider anomalies in presence/absence were observed on legs. One adult

had an obviously doubled seta *v′* on one trochanter I; no known oribatid mite has more than one seta on trochanter I in normal individuals. One larva unilaterally lacked tibial seta *v′*; this is otherwise a very stable seta in larvae of oribatid mites.

By contrast, numerous setae exhibit vertitional variation in the sense of Grandjean (1952, 1972, 1974), *i.e.* the seta has some measurable and heritable probability of occurrence in a given instar. Such variation is 'all-or-nothing': the seta is present in normal form or entirely absent. In his conceptual model, only the probability of the seta's occurrence is heritable, such that absence in parents does not preclude presence in offspring. Two members of a bilateral setal pair would be developmentally independent under this model, with each member following the same laws of chance. Grandjean (*op. cit.*) perceived evolutionary importance in vertitions, particularly as an indicator of an evolutionary trend toward regressive loss of the variable seta from the population in question. The probability of absence would be an indicator of progress toward this end. Wauthy *et al.* (1991; see also Leponce *et al.* 2001) presented another view, that vertitions reflect fluctuating asymmetry and by themselves lack such portent.

Overview, and vertitions in amphistasic setae — Not counting solenidia, the famulus, or anomalies mentioned above, 178 different setae were noted collectively on the legs of adult *C. johnstoni*; these are distributed among legs I-IV as: 63:45:38:32. Of these, 16 setae ($\sim$ 9 %) have variable presence in the adult (7:5:2:2), and all but one (tibia II seta *v″*) are on tarsi. Eleven other vertitional setae (6 %, 5:2:1:3) are constantly present in the adult but vary in the instar at which they appear; all but one of these 11 (tarsus I seta *it″*) are non-tarsal *v* or *l* setae. The 11 setae of this second group are amphistasic, and the cell into which they are placed in Table 1 indicates the most common instar of first appearance, while Table 2 indicates the probability of this seta appearing either one instar earlier or one instar later. Vertitions in amphistasic setae were most common among setae added in the Dn and Tn; none were observed in either the larva or Pn. The pattern of development in iteral setae shown by *C. johnstoni* – formation as complete pairs in the tritonymph on tarsi I-III and absence from tarsus IV – is rather rare according to the summary of Grandjean (1964), and we observed only one vertition: a single Dn formed *it″* on one tarsus I. We did not consider it an anomaly, since this particular variation is consistent with his conceptual model, in which 'resistance' to regression (ontogenetic delays and losses) of iteral setae decreases from I to IV.

Vertitions in proximal accessory setae of tarsi — *Collohmannia johnstoni* develops proximal accessory setae on all legs: ventral and lateral setae are added to all tarsi, and setae of row *c* appear on tarsus I (Table 1). These account for all 15 of the tarsal setae that show variable presence in the adult. We did not follow the development of individual mites, but considering the limitations of sample size our data are consistent with Grandjean's (1958b) model of eustasy.

This is perhaps best illustrated by the development of ventral pairs (Fig. 15). All protonymphs showed one of two patterns: either one (v_1″, Fig. 15D) or two (v_1′, v_1″, Fig. 15F) ventral setae formed in the Pn, proximal to fundamental pair (*pv*). When v_1′ was absent, the space that it would have occupied was usually vacant (Fig. 15D). In a single instance (Fig. 15E) the space was occupied by *pv′*. One could interpret pattern 15E as having pair (v_1) present and *pv′* absent (as an anomaly), but we doubt that this is true. Seta *pv′* is a fundamental, eustasic seta that was present on all 20 larval legs of the initial study, and to be certain we studied 30 additional larval tarsi I for this single character: *pv′* was never absent. Pair (*pv*) usually has a disjunction in the larva (see below), with *pv″* being slightly more distal, and we interpret pattern 15E as representing its extreme manifestation. Each subsequent instar also had a variation in which the space was vacant (patterns H, L, O), suggesting that if v_1′ was not formed in the Pn, it was absent for the rest of the individual's development. Frequency data are consistent with this interpretation. By direct observation v_1′ formed on only 5 of 20 protonymphal legs, and the number in successively later instars (inferred from patterns J, M and P) was respectively 4, 2 and 5 legs (Table 2). No examined protonymph

lacked v_1″, but we infer from the absence of both members of pair (v_1) in a single Dn (Fig. 15I) and a single Tn (Table 2) that it does rarely occur. In this interpretation, pairs (v_2), (v_3) and (v_A) are consistently added in the Dn, Tn and adult, respectively; only the protonymphal pair (v_1) is vertitional and they account entirely for the variation in ventral accessory setae of later instars.

On tarsus II, protonymphal pair (v_1) never forms; instead, deutonymphal pair (v_2) is vertitional (Table 1), with frequencies (Table 2) that well match those inferred in subsequent instars, except v_2′ is less frequent than expected in the studied tritonymphs. Pairs (v_3) and (v_A) always form in the Tn and adult, respectively. On tarsus III, ventral accessory setae develop like those of tarsus II, with frequencies of vertitional pair (v_2) being similar from Dn to adult (Table 2). Tarsus IV develops no ventral accessory setae until the Tn, and this pair is only weakly vertitional. Seta v_3″ was consistently present and v_3′ was absent from a single Tn; neither seta was absent in any adult leg studied.

All observations of ventral setae are consistent with Grandjean's (1958b) idea that more proximal ('posterior') verticils of accessory tarsal setae are more resistant to vertition and regressive loss. In other words, if vertitions occur in a given row, they usually are restricted to its most distal (most 'anterior' in Grandjean's terminology) member, the seta that forms earliest in ontogeny. By contrast, we observed no variation in setae of the *c*-rows, which occur only on tarsus I. Pair (c_2) was consistently present in the Dn, pair (c_3) was always added in the Tn, and pair (c_A) was always added in the adult.

With the partial exception of tarsus I, the development of lateral accessory setae is also consistent with Grandjean's ideas. Tarsus II (Fig. 16G-I) first formed lateral setae (l_3) in the Tn (Table 1), and this pair was vertitional; the frequency of l_3″ was the same in Tn and adult (Table 2), but that of l_3′ was not, which we interpret as sampling error during our selection of individuals to study. Pair (l_A) always appeared in the adult. Tarsus III consistently formed a single lateral seta, l_A′, in the adult. Tarsus IV also formed this adult seta, but l_3′ was vertitional in the Tn, with a low frequency similar to that seen in adults (Table 2).

Development of the lateral accessory setae of tarsus I is consistent with Grandjean's ideas until the adult instar. Pair (l_2) was vertitional in the Dn (Table 1), with low frequencies that are mirrored in the Tn (Table 2), and the Tn consistently added pair (l_3). If the adult consistently added only pair (l_A), then we would expect to see 2 or 3 lateral setae (depending on whether the respective l_2 seta had formed) on each face of the tarsus, aligned more-or-less longitudinally proximal to fundamental pair (*pl*) as in, e.g., Fig. 15N. In fact, the complement range is broader and more variable, and the setae have various positions (e.g. Fig. 16A-F; *l*-setae are those without labels), such that none of the 20 adult tarsi I studied were precisely alike. Considering the low frequency of both setae of pair (l_2), most tarsi I should have 2 lateral setae (the respective l_3 and l_A) on each face if a single pair was added to the adult. In fact, no anterior face had 2 lateral setae: there were 3 (6 legs), 4 (11 legs), 5 (1 leg) or 6 (2 legs). The posterior face had 2 (8 legs), 3 (11 legs) or 4 (1 leg) setae. Those of the posterior face were usually aligned proximal to *pl*″ in a straight or arching row, while those of the anterior face were typically in an irregular, vaguely zigzag pattern that encompassed much of the height between the level of *ft*′ and the *c*′-row. In several cases one of these setae (l_x′; Fig. 16A, D) aligned well with the *c*′-row, but we consider it an *l*′ seta for three reasons: (1) in other patterns with a similar number of anterior setae the apparent counterpart is higher, away from row *c*′ (cf. B, F); (2) normal vertitions in accessory setae are found in the distal pairs, not the proximal pairs; and (3) following the pattern of other *c*-row setae, c_A would be eupathidial if l_x′ were actually a *c*′-row seta. One might also argue that if *c*-rows follow the same general priorities as ventral and lateral rows, the anterior (′) seta should have been lost from the presumed pair before the posterior (″) seta.

We conclude that more than one pair of lateral setae are added to tarsus I between Tn and adult; *i.e.*, there is a low level of adult neotrichy. On the anterior face this is obvious, since 14 of 20 legs had 4 or more *l*-setae, at least one more than the number of instars would account for (which is 3: one per instar

from Dn through adult). The variable positioning is also suggestive of neotrichy. On the posterior face neotrichy is obvious in only one instance (Fig. 16D), where there are 4 lateral setae (unlabeled). But considering the rarity of pair (l_2) in the Dn and Tn (Table 2), even a complement of 3 lateral setae (on either face) might include one neotrichous adult seta. We suspect that the unlabeled setae in Figs. 16A-F all derive from the lateral row of accessory setae, but considering both spatial variation and the vertitional variation in pair (l_2), we cannot establish homologies.

Setal priorities — In *C. johnstoni*, the anterior (′) member of a pseudosymmetrical pair in ventral and lateral rows usually has priority over the posterior (″) seta. As examples: trochanters of *C. johnstoni* lack setae *v″* and *l″*, regardless of whether this face is abaxial (I, II) or adaxial (III, IV); primilateral seta *pl″* is absent from tarsus III; and on femora and tibiae the posterior seta of pairs (*l*) and (*v*) is either delayed to a later instar, relative to the anterior seta, or lost altogether. Exceptions are rare: one is seta *c″*, which is fundamental (present from the larva) on tibiae I and II, while *c′* never forms. But the most striking exceptions relate to vertitional setae of the ventral accessory rows on tarsi: setae of the *v′* row are (with a single exception) less frequent than the respective *v″* seta, and usually the difference is large (Table 2).

Disjunctions — Disjunctions of setae on tarsi of *C. johnstoni* usually do not conform to parallel homology. Most clear disjunctions are adaxial, *i.e.* ′ on legs I and II, but ″ on legs III and IV. Fastigial setae, in which *ft″* is more distal regardless of leg, are an exception. It is rare for a disjunction to change during ontogeny, but this was observed in pair (*pv*) of tarsus I. Pair (*pv*) usually have a small ″ disjunction in the larva (Fig. 15A, B), which is itself rare for this setal pair among oribatid mites (see Wauthy and Fain 1991). In the Pn the disjunction of (*pv*) differs according to the presence of vertitional seta v_1': if absent, then (*pv*) retains the ″ disjunction, which can be accentuated (Fig. 15D, E); if both setae of pair (v_1) are present, then (*pv*) assumes the ′ disjunction that characterizes ventral accessory setae of tarsi I and II. We did not observe a Pn that lacked both members of (v_1), but we predict (*pv*) would in this case retain the initial disjunction. In later instars all possible arrangements of pair (*pv*) were observed (Fig. 15), but they had a ″ disjunction only in the absence of v_1'.

When pseudosymmetrical pairs are unbalanced – one member present, the other absent – disjunctions can be accentuated or even reversed. This seems to relate to limiting or balancing gaps (uneven spacing) in sensory coverage. Fig. 16 shows another example: when lateral pairs on tarsus II are balanced, the ′ disjunction is small (G, I), but when l_3' is absent the other setae on the anterior face appear to spread to occupy the vacant space (H), resulting in strong disjunction of (l_A) and a reversed disjunction in pair (*pl*).

Eupathidia — In addition to variation in presence-absence of setae, there is variation in the transformation of some setae of tarsus I from normal, mechanoreceptive form to eupathidia, which are probably contact chemoreceptors (Alberti 1998). Usually eupathidia are easily distinguished by their hollow shaft, the absence of barbs, and tapered tip that bends slightly ventrad. As with *C. gigantea* (see Grandjean 1966; Pfingstl *et al.* 2005), an unusually high number of setae transform from the normal form to eupathidia during the development of *C. johnstoni*. The exact number depends on the presence of pair (v_1); there are 17 if both setae are present (Figs. 15P, 16A) and 16 if v_1' is absent (Fig. 15N, O); we saw no adults that lacked v_1'', but they would likely have the minimal number of 15.

All eupathidia are consistent in the instar of their transformation from normal setae. These include five fundamental setae (present from the larva): the proral pair, (*p*), which are eupathidial from the larva; the unpaired subunguinal, *s*, which transforms in the protonymph; and the primiventral pair, (*pv*) which transform in the Dn. Post-larval setae include the iteral pair (*it*) which transform together in the adult; this pattern is known from species in diverse macropyline families (Grandjean 1964). Among accessory setae, pairs (c_1) and (c_2) transform in the Tn and adult, respectively. If they exist, setae of pair (v_1) transform in the Dn, along with (*pv*). Pairs (v_2) and (v_3) transform in the Tn and

adult, respectively. Pairs (v_A) and (c_A) are never eupathidial, nor are any lateral accessory setae, antelaterals, primilaterals, fastigials or tectals.

In papers on the mixonomatan genus *Perlohmannia* (Perlohmanniidae), Grandjean made two generalities about eupathidial transformation in accessory setae of rows *v* and *c* that also apply to *C. johnstoni*. They can be paraphrased as follows: (1) if transformation to a eupathidium occurs at a particular instar, then the seta itself formed in the previous instar (Grandjean 1958a); (2) the most proximal seta in a row containing eupathidia is always normal, *i.e.* it remains a mechanoreceptor (Grandjean 1961b). Both generalities apply to rows *v* and *c* of *C. johnstoni*. The first also applies to the iteral and subunguinal setae, but neither generalization can be extended to include primiventrals: pair (*pv*) are not transformed until the Dn and unlike ventral pairs they do not transform as soon as setae form proximal to them (Fig. 15E, F).

Variation in larval 'duplex setae' — Unexpected variation in the minute seta *d* of genua and tibiae was observed among nine larvae of *C. johnstoni* that were taken from eggs of gravid females. In five of these larvae, still tightly packed in their prelarval cuticles, some genual and tibial setae *d* were not coupled to respective solenidia as they are in other larvae (and in all other instars observed) but were inserted instead in a separate alveolus adaxial to and (on the tibia) somewhat distal to the solenidion. Some were only minute vestiges but others were well-formed setae, half as long as the respective solenidion (Fig. 18F, G). Grandjean (1966) noted a surprising level of variation in the presence or form of leg setae and solenidia among larval *C. gigantea* that were reared in culture, but we saw none of his specific examples in *C. johnstoni*.

Species Comparisons in *Collohmannia*

Collohmannia gigantea — Adults of *C. johnstoni* n. sp. (Cj) are distinguishable from those of *C. gigantea* (Cg) in the following characters. *Prodorsum*: bothridial seta tapering distally, without terminal barbs (Cj) vs. untapered distally, blunt with several minute terminal barbs (Cg; Alberti *et al.* 1994). *Notogaster*: dorsoventrally more compressed, height/width 1.2-1.5 (Cj) vs. 1.1-1.2 (Cg; 1.2 is rare in each species); with 5 pairs of very long setae, including e_2 and h_1 (Cj) vs. with 3 pairs of very long setae, e_2 and h_1 shorter (Cg). *Spermatopositor*: tongue-apodeme laterally flattened, freely projecting (Cj) vs. antero-posteriorly flattened, not projecting. *Legs*: tarsus I not distally swollen, similar relative size in both sexes (Cj) vs. swollen distal to articulation with tibia, that of male relatively larger (Cg); tarsus I with four solenidia (Cj) vs. six (Cg); setation of tarsus I similar in both sexes, with only several neotrichous lateral setae of normal shape (Cj) vs. male with hypertrichy of ribbon-like setae on adaxial face (Cg); male with hypertrophied seta *v″* of genu IV in form of flattened, asymmetrical diamond (Cj) vs. thick, slightly flattened, distally curved like thumb, or banana (Cg); male tibia IV unmodified (Cj) vs. basally thickened and with region of adaxial pustules (Cg); pore of genu I differently positioned than those of II and III, near middle of segment (Cj) vs. proximal, near articulation as on genua II, III (Cg). Other differences certainly exist. The leg setation of adult *C. gigantea* has not been described, other than Grandjean's (1966) illustrations of tarsus I. The latter has more setae in both sexes than it does in *C. johnstoni*, but no count is available; in particular, accessory rows (*v*), (*l*) and (*c*), which usually are clearly defined in *C. johnstoni*, are not discernible among the richer setation of *C. gigantea*. The accessory setation of all leg tarsi may be richer in *C. gigantea*: for example, we studied several examples of tarsus IV on both males and females, and all had developed pair (v_3), which we never saw on tarsus IV of *C. johnstoni*.

Based on Grandjean's (1966) description of the larva and that of nymphs by Pfingstl *et al.* (2005) juvenile instars also show differences. The bothridial seta tapers at the tip (Cj) vs. being blunt, with terminal barbs (Cg); the long gastronotic setae (e_1, e_2, h_1 in larva, plus h_2 and p_1 in nymphs) are truly flagellate like those of the adult (Cj) vs. attenuate, proportionally shorter than in the adult (Cg); tarsus II forms seta *pl″* in all juveniles (Cj) vs. *pl″* absent from all juveniles (Cg); seta *d* of genua and tibiae are minute, but setiform in all instars (Cj) vs. only a dot-like vestige (Cg).

Comparing our Table 1 with the descriptions of nymphs by Pfingstl *et al.* (2005), there are many apparent differences in setal ontogeny. However, based on our study of two Dn and three Tn of *C. gigantea*, some aspects of their work should be reinvestigated. For example, they considered the most proximal ventral pair of all tarsi to be (*pv*), but our *C. gigantea* nymphs had accessory ventral setae proximal to (*pv*) on all legs, as in *C. johnstoni*. They indicated that pair (*it*) is absent from tarsi II and III in the Tn, but these setae were symmetrically present on each of our three *C. gigantea* Tn; *C. johnstoni* Tn consistently form them on these tarsi. They indicated that the seta they designated *pl'* (see Remark 7) of tarsus IV forms in the Dn of *C. gigantea*, but it was not present on our Dn of this species. Also on tarsus IV, their figures show no ventral setae forming in the Tn, but our three specimens symmetrically had pair (v_3), like *C. johnstoni* usually does. Another apparent difference relates to the setation of tarsus IV in the Pn. Pfingstl *et al.* (2005) described and illustrated nine setae in *C. gigantea*, contrasting with the more typical setation of seven in *C. johnstoni*. This was an error, however: Dr. Pfingstl (pers. commun. 2014) kindly reexamined specimens and found only the usual seven setae.

Collohmannia asiatica — At present, literature about this species includes only the published description (Christov 1970). This is not detailed enough for careful comparison with *C. johnstoni*, except that it has a distally swollen, barbed bothridial seta (tapered, essentially smooth in Cj). Also, based on our brief study of a type specimen, three pairs of notogastral setae (e_1, h_2 and p_1) are flagellate or nearly so (five pairs in Cj).

Collohmannia schusteri — This fossil species from Baltic amber also is known by few traits, but it is easily distinguished from *C. johnstoni*. The bothridial seta does not taper distally (tapered in Cj). Only three pairs of notogastral setae (p_1, h_2 and e_1; the latter mistakenly called d_2 by Norton 2006) are flagellate (five pairs in Cj). Male leg IV is very different: genual seta v'' is thickly spine-like and both genu and tibia are densely tuberculate (v'' a flat asymmetrical diamond; genu and tibia without tubercles in Cj).

Redescription of *Collohmannia* and Family Diagnosis

Several diagnoses in the literature relate specifically to *Collohmannia* (Sellnick 1922, 1960; Bulanova-Zachvatkina 1975) or to its inclusive family-group taxa Collohmanniidae (Weigmann 2006) or Collohmannioidea (Bulanova-Zachvatkina 1975; Balogh and Mahunka 1983; Sergienko 1994; Norton and Behan-Pelletier 2009). When first proposing the family, Grandjean (1958a) gave no diagnosis. Later (Grandjean 1969) he proposed Collohmannioidea as new, again without a diagnosis, but by international rule both family-group names were made available in 1958. The fossil genus *Embolacarus* was proposed as a member of Collohmanniidae (Norton 2006), but the described structure of its coxisternum and adanal plate of its type species, *E. pergratus* Sellnick, 1918 are unlike those of *Collohmannia*, which indicates the mites may not be congeneric. Until *E. pergratus* is recollected and carefully examined, the reality of these differences will remain in doubt, so *Embolacarus* is not considered further here. Therefore, Collohmanniidae and Collohmannioidea are functionally monobasic and their diagnoses can be considered equivalent.

The redescription of *Collohmannia* and new diagnosis of Collohmanniidae presented below are an extension of that by Norton and Behan-Pelletier (2009) for the superfamily, complemented by our study of *C. johnstoni* and new observations on *C. gigantea*. They are consistent with what is known about the fossil *C. schusteri* and with new, preliminary examinations of four other species that will be treated in a subsequent study, viz. *C. asiatica* and three new species (one in amber) from Eurasia. Juvenile traits are known only from *C. gigantea* and *C. johnstoni*.

Collohmannia Sellnick, 1922 (type species *C. gigantea* Sellnick, 1922 = *C. nova* Sellnick, 1932). Adult. Dichoid Mixonomata (see Grandjean 1969) with sejugal furrow wide dorsally, narrow ventrally. Large ($\sim$ 1200-2000 μm total length), medium to dark brown, overall shape ovate; convex dorsally, flatter ventrally. Sclerotized cuticle porose throughout, with superimposed imbricate pattern on notogaster and plates of anogenital region.

Prodorsum — Stegasime, with independent aspis, isolated from coxisternum by soft cuticle; in dorsal aspect broadly rounded anteriorly, gradually broadening posteriorly to equal anterior breadth of notogaster; aspis with large, semicircular exobothridial lobe extending ventrally from bothridial region, and internal supporting rib ('nervure') starting near bothridium and extending obliquely anteroventrad to end as articulating condyle for subcapitulum; entire sejugal border projecting internally to form transverse occipital phragma, connecting exobothridial lobes; with short sagittal apodeme projecting in front of phragma. Bothridial seta tapered or slightly broadened distally, with tight sigmoid bend inside bothridium; bothridium with multiple chambers, including one with several dozen contiguous, sausage-shaped outpockets but without extended brachytracheae or tracheae. Setation normal, with long interlamellar and lamellar seta; two pairs of exobothridial setae on exobothridial lobe. With small porose area posterior to each lamellar seta, appearing as macula in transmitted light.

Notogaster — Convex, elliptical in dorsal aspect, extending well onto somewhat flattened venter; without lateral carinae or suprapleural scissure. With 15 pairs of setae, simple but heterogeneous in size, plus alveolar vestiges of pair f_1; three to five pairs long, flagellate. Opisthonotal gland and normal five pairs of lyrifissures present; *gla*, *ip* and seta f_2 clustered laterally; *ips* located in plicature region. With multiple round or oval porose areas, distinct from general porosity and representing dermal glands; most porose areas at or near base of setae, with size somewhat inversely related to setal size (largest around vestige of f_1, flagellate setae with at most narrow ring of pores around insertion).

Coxisternum — Separated from notogaster and anogenital sclerites by soft cuticle. Divided into four parts by ventrosejugal furrow and nearly complete sagittal furrow; tapering posteriad, with epimere IV only about half as wide as I, such that legs IV unusually close together. Supracoxal region of epimere I with spinose seta *eI*; that of III with large, triangular dorsal extension.

Anogenital region — Genital plates elongate, appearing subrectangular or tapered at ends, according to view; with 7-9 setae longitudinally aligned on medial margin. Anal plates longer than genital plates; narrow, elongated, lens-shaped as pair; with small lyrifissure *ian* near anterior margin followed posteriorly by three pairs of aligned anal setae. Blade-like preanal apodeme present, appearing in ventral aspect as subsurface, dark medial line running anteriorly from anal valves. Respective aggenital and adanal plate fused in lateral half, separated medially by oblique incision; aggenital portion broadly rhomboid, similar in length to genital plate and bearing two longitudinally aligned aggenital setae in posterior half; adanal portion tapering posteriorly, bearing three pairs of longitudinally aligned setae. Infolded plicature region between anal and adanal plates with narrow intercalary sclerite and lyrifissure *iad*. With separate, small porose areas on anal and adanal plates, without separate porose areas on genital or aggenital plates. Ovipositor of female normal, with three pairs of coronal setae; three distal lobes short, each with normal four setae. Spermatopositor of male atypical, similar to ovipositor in length but directed slightly posteriorly when fully extended; with two pairs of coronal setae, both on anterior face; anterior distal lobes partly fused to form U-shaped receptacle for movable, scale-like posterior lobe when retracted; anterior lobes with four pairs of setae, posterior lobe with two pairs.

Gnathosoma — Subcapitulum stenarthric, mentum triangular; pharynx with conspicuous, pigmented ventral sclerite, narrow at attachment to mid-ventral commissure, then broadening posteriorly. Capitular apodeme large, with inverted V-shape in cross-section and scissure along sagittal line. Supracoxal seta of palp spiniform. Lateral lips with three pairs of setae, or_1 distally bifurcated. Rutellum atelobasic, distally broad, with five strong teeth; dorsal face without ciliary brush but with two (usually) hyaline, isotropic spines. Palp five-segmented; setation (trochanter-tarsus) 0-2-1-3-9(+ω). Chelicera strong, chelate-dentate; attachment of cheliceral sheath well onto principal segment, basal fifth of which thereby inserted into body; cuticle porose, including inserted portion.

Adaxial face with small spicules, well-developed Trägårdh's organ and lamellated organ; abaxial face with two setae.

Legs — Tubular in general structure; sclerotized cuticle with fine porosity, but setae v' of femora, genua and tibiae insert eccentrically in small, rounded, luminous porose area similar to those of notogaster. Pretarsal ambulacrum tridactylous, claws similar. Genual pore present on I-III, absent from IV. Tibiae I and II with seta c'' present; all tibiae and genua with minute seta *d* closely coupled to solenidion; tarsus I with 4-6 solenidia. All tarsi with proximal accessory setae in ventral, and usually lateral rows; tarsus I with setae in row *c*; tarsus I with numerous eupathidia, including *s* and pairs (*p*), (*pv*), (*it*) and distal members of rows *v* and *c*; famulus spiniform with rugose surface. Male tarsus I with or without adaxial hypertrichy of ribbon-like setae. Male leg IV with modified genu, seta v'' hypertrophied; cuticle of tibia (also sometimes genu) with or without dense small tubercles (pustules).

Immatures — All juvenile instars with colorless, unsclerotized gastronotic and anogenital regions, contrasting with sclerotized prodorsum, epimeral plates and legs; brownish color of sclerotized cuticle increases with successive instars. Prodorsum truncate anteriorly, with very narrow rostral tectum having convex naso remnant on ventral wall, below rostral setae; lateral rib conspicuous; seta *xp* inserted posterior to border of exobothridial lobe. Gastronotic region with weakly defined transverse grooves anterior and posterior to setal row *e*; seta f_1 represented only by vestige, nymphs with enlarged setae distributed as in adult; no porose areas evident, but at least some homologous clusters of glandular cells present. Coxisternum structured as in adult; Claparède's organ without secondary annulation, protective seta *1c* with usual scale-like form. Anogenital region without defined sclerites. Genital papillae large, similar in size; setation of genital valves (proto- to tritonymph) commonly 1-4-7, but latter two numbers variable; two aggenital setae form in deuto- and tritonymph respectively (see Remark 8). No inguinal (transcupular) setae in larva; seta p_1 first forms in protonymph; paraprocts without setae (vestiges may be present) or cupules in proto- and deutonymph (see Remark 9).

Collohmanniidae Grandjean, 1958. Adult. Large ($\sim$ 1200-2000 μm), dichoid Mixonomata of overall ovate form; sclerotized cuticle porose throughout, with superimposed imbricate pattern on notogaster and in anogenital region. Prodorsum: with isolated aspis; rostrum strongly stegasime; laterally with large exobothridial lobes and posteriorly with internalized occipital phragma; sagittal apodeme and lateral supporting rib present; bothridium with chamber having dense, contiguous outpockets; with pair of porose areas posterior to lamellar setae. Notogaster: with vestigial seta f_1 and 15 pairs of setae, of which 3-5 pairs enlarged, flagellate or nearly so; with many small dermal glands associated with small porose areas, most at or near setal insertions. Coxisternum: epimeres successively more narrow posteriorly; plates divided into four units by sejugal furrow and narrow sagittal furrow; independent from prodorsum, notogaster and plates of genital region. Anogenital region: genital and elongated anal plates almost contiguous; with blade-like preanal apodeme extending anteriorly from anal vestibule; aggenital and adanal plates fused laterally, separated by oblique, narrowly V-shaped incision medially; spermatopositor directed posteroventrally when extended, longer than ovipositor. Gnathosoma: subcapitulum stegasime; rutellum broad, atelobasic, with strong terminal teeth; chelicera robust, chelate-dentate, with Trägårdh's organ and lamellated organ; palp five-segmented, with forked distal eupathidium, seta *acm* independent of solenidion. Legs: ambulacrum homotridactylous; tarsi with numerous accessory setae, including row *c* on tarsus I; latter with numerous eupathidia; leg IV dimorphic, male with hypertrophied genual seta v''. Juveniles: prodorsum with very weak rostral tectum; gastronotic region unsclerotized; coxisternum structured as in adult; anogenital region without sclerites, proto- and deutonymph with glabrous paraprocts, sometimes bearing vestiges of setae.

Relationships of *Collohmannia*

Ideas about the phylogenetic relatives of *Collohmannia* – most of which are implied by classifications

– have varied, but have focused on dichoid families of middle-derivative oribatid mites that were eventually grouped by Grandjean (1969) as the unranked taxon Mixonomata. The latter was ranked as an infraorder by Schatz *et al.* (2011), though it is clearly paraphyletic (Norton 1998; Schaefer *et al.* 2010; Pachl *et al.* 2012). Sellnick (1922) assigned *Collohmannia* to no family when it was first proposed, but he noted resemblance to Lohmanniidae; the genus name also implies a connection (*col* - Latin prefix meaning together), though he did not explain the etymology. Vitzthum (1931) seems to have made the first formal family assignment, by including *Collohmannia* (and *Perlohmannia*) in a broad concept of Lohmanniidae, and this was followed in Radford's (1950; misspelled as *'Callohmannia'*) checklist of mite genera. While Grandjean's original sense of Mixonomata included Lohmanniidae, this family has since been transferred to Enarthronota, specifically to Hypochthonioidea, based on both morphological (Norton 2010) and molecular (Pachl *et al.* 2012) characters. Baker and Wharton (1952) tentatively included *Collohmannia* instead in the mixonomatan family Eulohmanniidae, but this seems to have been subsequently ignored. It appears that neither these latter authors nor Vitzthum studied specimens, nor were their actions supported by discussion. When Grandjean (1958a) proposed Collohmanniidae, he compared it mainly with Perlohmanniidae but not as a close relative; soon after (but without referring to his paper), Bulanova-Zachvatkina (1960) included *Collohmannia* in Perlohmanniidae. Again, it seems that neither author had studied specimens at that time. The idea that Collohmanniidae and Perlohmanniidae are closely related survives in some recent catalogues (Subías 2004, Shtanchaeva and Subías 2010, Subías *et al.* 2012), in which the two families comprise the Perlohmannioidea.

A different idea focused on the similarity of Collohmanniidae to ptychoid mixonomatans. This was first suggested by Sellnick (1918), who thought the fossil species *Embolacarus pergratus* Sellnick was ptychoid, but – surprisingly – in 1922 he did not suggest any relationship with *Collohmannia* (see Norton 2006). Štorkán (1925) specifically compared *Collohmannia gigantea* to 'phthiracarid' mites, even though he saw it alive and knew it was not ptychoid. He discussed *C. gigantea* at the end of the section on 'Phthiracarinae' (sensu lato, essentially = modern concept of Ptyctima), which could be interpreted as his intention to include *Collohmannia* in the group. However, he made no clear statement in this regard and also discussed similarities with *Lesseria* (now = *Epilohmannia*; Epilohmanniidae). Štorkán's (1925) uncertainty probably is captured best by the supposed junior synonym that he claimed to have published in 1923 – *Phthiracaroides incertus*. He gave no reference and we can find no paper proposing this name; it is not the Štorkán (1923) paper about mites in mole's nests, as is sometimes suggested. Therefore, we consider it unavailable: a nomen nudum. In describing *C. nova* (later synonymized with *C. gigantea*), Sellnick (1932) also noted similarities with *'Phthiracarus'* (used in a very broad sense) but considered *Collohmannia* a genus of Lohmanniidae. Looking beyond the similarity in facies between *Collohmannia* and Ptyctima, Grandjean (1966, 1969) examined specific characters, particularly five that in cladistic terminology could be considered synapomorphies supportive of a close relationship between *Collohmannia* and Ptyctima. These are summarized below, followed by five others.

1. Coxisternum — This is unusually structured in *Collohmannia*; it is independent of surrounding sclerites, divided by a cross of articulating furrows (scissures) into four plates (each formed from plates of two fused demi-epimeres), and the epimeres narrow from front to back, such that legs IV are unusually close together. It is the same in all Ptyctima and is necessary for folding of the coxisternum during retraction of the podosoma (Sanders and Norton 2004).

2. Aggenital and adanal plates — On either side these plates are fused laterally, leaving only a medial incision to separate the plates. Sellnick (1932) illustrated these plates as independent, but this may have been an artifact of dissection. The partial fusion exists in all specimens of *Collohmannia* we examined, and Grandjean (1969) considered this the most common situation in *C. gigantea*, while allowing that plates may be separate in some individuals.

Among Ptyctima fusion of these plates characterizes most Euphthiracaroidea, some of which retain a plesiomorphic incision marking the plate boundary. No such fusion exists in the highly derived euphthiracaroid subfamily Temburongiinae (Synichotritiidae; Norton and Lions 1992), or in Phthiracaroidea.

3. Sagittal apodeme — This unpaired apodeme ('nervure sagittal') in the posterodorsal part of the aspis is unknown outside *Collohmannia*, Phthiracaroidea and most Euphthiracaroidea. Of the few euphthiracaroids that lack it as adults, their juveniles (if known) have a distinct sagittal apodeme (Grandjean 1969 and cited papers).

4. Bothridium — In *Collohmannia*, a large section of the bothridium has numerous sausage-shaped, contiguous, smooth-walled locules. Grandjean noted that a bothridium of similar form was known only in Ptyctima, but some large Epilohmanniidae, e.g. *Epilohmannia praetritia* Berlese and some undescribed species, also have such structures (R.A.N., unpublished).

5. Famulus — The spine-like shape seen in *Collohmannia* is common, but a rugose surface is known only in *Collohmannia* and Ptyctima. Outside the infraorders Enarthronota and Palaeosomata, it is rare for any oribatid mite to have a famulus with discernable surface structure, but Nehypochthoniidae, a family proposed as a possible near-outgroup of Ptyctima, has a distinctly annulate famulus (Norton and Metz 1980).

6. Preanal apodeme — This narrow, blade-like apodeme extends anteriorly from the anal valves of *Collohmannia* to lie in the ventral midline and provide the origin for some of the genital adductor muscles and part of the extensive set of lateral compressor muscles that insert at the lateral edge of each adanal plate (see also Norton 2006). Grandjean (1969) noted this similarity, but did not include it as support of his idea. The blade-like preanal apodeme is unique to *Collohmannia* and Euphthiracaroidea. In the latter group this apodeme seems to be a 'kingpost' for a laterally acting compressor system that controls hemolymph pressure (Sanders and Norton 2004; Schmelzle *et al.* 2009). As with character 2 (above), an apodeme of this form is not present in Phthiracaroidea, and seems absent from temburongiine Synichotritiidae as well.

7. Lateral rib — Juvenile *Collohmannia* and Euphthiracaroidea possess a paired lateral rib ('nervure laterale'), which borders the aspis and ends distally in a condyle that articulates with the subcapitulum. It is present in all instars of *Collohmannia*, but is most conspicuous in juveniles, where its pigmentation and thickness contrast with the paler surrounding cuticle of the aspis. Travé (1975) viewed this similarity as support for a relationship between the groups, but a similar rib exists also in endeostigmatid mites and Palaeosomata (Grandjean 1954). We know of no examples from Enarthronota or Parhyposomata, nor do we know examples in Mixonomata, outside of *Collohmannia* and Euphthiracaroidea (see Remark 10). Considering its taxonomic distribution (absent from Parhyposomata and other Mixonomata), we think the rib re-evolved in a common ancestor of *Collohmannia* and Euphthiracaroidea, but such homoplasies are weak support for a phylogenetic hypothesis.

8. Transverse hysterosomal lines in juveniles — In both *Collohmannia* and Ptyctima there are transverse lines (linear grooves) in the cuticle of the gastronotic region of juveniles (Travé 1975). These are in addition to the indistinct line *as* of Grandjean (1966), which simply marks the posterior boundary of flexible, striated cuticle extending from the sejugal furrow (we presume the notation *as* relates to the aesthenic zone of Grandjean 1954). Two lines are present in *Collohmannia* juveniles, designated *r2* and *r3* by Grandjean (1966); he did not discuss the notations, but they seem to relate to his hypothetical demarcation of primitive segments (*ar2*, *ar3* of Grandjean 1947b). Line *r2* would presumably mark the boundary between segments D and E, and *r3* that between E and F. It is a reasonable idea, considering the apparent segmentation of the endeostigmatid genus *Terpnacarus*, thought to represent a close outgroup of Oribatida (Grandjean 1939; Norton *et al.* 1993). Mixonomata are quite phylogenetically distant from endeostigmatid mites, and many intervening taxa lack such transverse lines. Disregarding the complicated cases of transverse scissures between sclerites in

Enarthronota (Norton 2001), simple transverse lines can be found in some soft-bodied members of the most primitive infraorders, e.g. Pediculochelidae (Enarthronota), Aphelacaridae (Palaeosomata) and Parhypochthoniidae (Parhyposomata). Transverse lines that occur in juveniles of a few species of the derived infraorder Brachypylina (e.g. *Pirnodus detectidens* Grandjean, 1956) cannot reasonably be attributed to primitive segmentation boundaries.

Regardless of their origin, the lines of *Collohmannia* differ from hypothetical boundaries in one important respect: seta d_2 lies between *r2* and *r3*, whereas only row *e* should be present if the lines marked segments. This is exactly the situation in those Ptyctima with juveniles that possess line *r2*: the phthiracaroid genera *Phthiracarus* and *Steganacarus* (Grandjean 1950; Webb 1977) and the euphthiracaroid genus *Paratritia* (Travé 1975). Besides *Collohmannia* and Ptyctima, we know of no taxon with such an arrangement of lines and setae. In this case, d_2 could have migrated posteriorly across the primitive boundary or (perhaps less likely) the lines (at least *r2*) may have a different origin. In either instance the similarity is synapomorphic. Its significance is somewhat compromised by our poor general knowledge of juvenile Ptyctima, some of which have apparently lost *r2* and retain only *r3* or else have neither line (e.g., Walker 1965; Schubart 1967; Travé 1975; Ermilov 2011b).

9. Plicature zone — There is an extensive infolded plicature zone (*pz.1*) between notogaster and adanal plates in *Collohmannia*, a trait also of all Euphthiracaroidea other than Temburongiinae (Norton and Lions 1992). In *Collohmannia* the cuticle of this zone is of the transitional type (imbricate and porose, but unpigmented) and anteriorly it bears lyrifissure *ips*. In Euphthiracaroidea the plicature zone is moderately hardened, but *ips* is on the notogaster, indicating that the zones are not precisely homologous and making the synapomorphy somewhat equivocal. Members of Perlohmanniidae have a placement of *ips* similar to that of *Collohmannia* (Grandjean 1958a) but Grandjean (1969) argued effectively against the close relationship of these two groups.

10. Posterior notogastral sinus — Posterior to the valves, the plicature zone of *Collohmannia* diffuses to become a large expanse of pale transitional cuticle, best seen in posterior view (Fig. 10B). The sinus may allow the notogaster to flex during contraction of the lateral compressor muscles, performing the same function as the terminal sinus or terminal fissure in Euphthiracaroidea (Märkel 1964; Sanders and Norton 2004). Its form is consistent with Märkel's observation that a sinus, rather than a fissure, is typical of those euphthiracaroid taxa having a broader notogaster.

Collectively the ten morphological traits discussed above seem convincing for a close relationship with Euphthiracaroidea, even that of sister-group. Half (#2, 6, 7, 9, 10) are not shared by Phthiracaridae or (except for #7, since juveniles are unknown) by temburongiine Synichotritiidae, but these differences can be explained as being masked by further derivations. Both groups appear to have been derived within Euphthiracaroidea as the latter is usually conceived. Morphological data support the case for Temburongiinae (Norton and Lions 1992) and molecular data support that for Phthiracaridae (Pachl *et al.* 2012). At least for Phthiracaridae, all but #7 appear to relate to the evolution in that family of a hemolymph-pressure control system of plates and muscles that act dorsoventrally, rather than laterally as in most euphthiracaroids (Schmelzle *et al.* 2009).

Recently an interesting similarity between *Collohmannia* and Phthiracaridae has emerged that is not shared by any euphthiracaroid mite. The New Zealand species *Austrophthiracarus notoporosus* Liu and Zhang, 2014 appears to possess numerous notogastral porose areas, although they have no obvious association with setae. It would be unreasonable to list this as a synapomorphy, but it does emphasize that the distribution of notogastral dermal glands is rather mosaic (Norton and Alberti 1997).

While molecular data help clarify the origin of Phthiracaridae, they paint an equivocal phylogenetic picture regarding *Collohmannia*. Analyses of the 18S ribosomal RNA gene by neighbor-joining (Lee *et al.* 2006) and maximum-parsimony (Dabert *et al.* 2010) algorithms produced trees consistent with *C. johnstoni* (as *Collohmannia* sp.) and *Ne-*

hypochthonius porosus Norton and Metz (as predicted by Norton and Metz 1980) being the closest outgroups of Ptyctima, but not with strong statistical support. The maximum-likelihood tree of Lee *et al.* (2006) had *C. johnstoni* and *Steganacarus magnus* (Nicolet) as sister-taxa, but *N. porosus* was distant. By contrast, maximum-likelihood and Bayesian analyses of Dabert *et al.* (2010) included *C. johnstoni* in the midst of Nothrina (Desmonomata), as sister-taxon to *Nothrus* sp. (Nothridae). Statistical support for this relationship was weak, but the similar result of a Bayesian analysis by Pachl *et al.* (2012) – a grouping of *C. johnstoni* (as *Collohmannia* sp.) with *Nothrus silvestris* Nicolet – had strong support.

We can identify no morphological support for this latter relationship – no synapomorphies of *Collohmannia* and *Nothrus* – but *Collohmannia* does have a chelicera with apomorphic traits of the infraorder Desmonomata as a whole (sensu lato, Schatz *et al.* 2011). One is the encroachment of the cheliceral sheath onto the face of the principal body, resulting in an 'inserted' chelicera (Norton 1998). Ptyctima and other mixonomatans have the plesiomorphic state, in which the sheath attaches proximally. Another cheliceral trait is the presence of a large, well-defined Trägårdh's organ, which also characterizes Desmonomata. There is some evidence that a small, inconspicuous and delicate Trägårdh's organ is present in Ptyctima but its evolutionary polarity relative to the large structures noted above is equivocal (Lions and Norton 1998 and cited papers). On the dorsal face of the rutellum, *Collohmannia* species lack the ciliary comb (= brush) common to nearly all desmonomatans outside Astigmata, but they do possess adjacent hyaline 'spines', usually two, in this position. Grandjean (1966) considered the spines a special form of the comb, but their form is quite different from that of desmonomatan cilia. We know only one family currently classified in Mixonomata that does have a well-formed rutellar brush – Eulohmanniidae (R.A.N., unpublished) – but the relationships of this strange mite are poorly understood.

Three other characters are interesting, if not conclusive. First, the prelarva of *Collohmannia* is quite similar to that of Nothrina, but their shared retention of relatively large leg vestiges is an obvious symplesiomorphy. Prelarvae of Ptyctima are more regressive, *i.e.* more derived, in all known instances (Sitnikova 1960; Grandjean 1962b; Lions 1973). The second relates to sperm ultrastructure, studies of which have been illuminating in recent decades. According to Alberti and Schuster (2005) mature sperm of *C. gigantea* are more similar to those of brachypyline oribatid mites than to the unique, small, lens-like sperm of Phthiracaridae (the only Ptyctima that have been studied in this regard). However, developing spermatids of *C. gigantea* are unique among mites in their length and highly coiled chromatin, and the presence of a cuff ('manchette') of microtubules accompanying chromatin condensation is shared only with Phthiracaridae among studied species. The third trait relates to general body form. *Collohmannia* is dichoid, but the ventral part of the sejugal articulation is narrow – little more than a hinge to allow dorsoventral flexing – and the dorsal part merges with the broad articulation surrounding the notogaster. As such, it approaches the holoid body form of Desmonomata.

While the gnathosomal similarities seem significant, we see no other morphological support for grouping *Collohmannia* with Nothrina or with any particular family in that group. Nothridae do have bothridial outpockets, but they are quite different in form (Calugar and Vasiliu 1979). For now, *Collohmannia* must join the sizeable list of taxa exhibiting conflicts between morphological and molecular data.

Remarks on Morphology and Nomenclature

1. Porose organs — In contrast to Brachypylina, macropyline oribatid mites rarely have discrete porose areas on the main body. *Collohmannia* adults are unusual in having more such areas than any oribatid mite other than certain Lohmanniidae (Enarthronota), which have a large number of unusual, innervated dermal glands on the prodorsum and notogaster (Alberti *et al.* 1997, Norton *et al.* 1997). Sellnick (1932) had observed porose areas on the prodorsum, adanal plates and legs of *C. gigantea* (as *C. nova*), but did not mention the many ar-

eas on the notogaster. Without having seen them, Grandjean (1934) assumed the porose areas of this species were respiratory surfaces, but probably that function is served by the general cuticular porosity. Instead, the discrete porose areas on the main body appear to represent dermal glands; those on legs may as well, but confirmation will require ultrastructural studies.

Most of the dermal glands of *Collohmannia* are adjacent to setae. No other macropyline group shows this association so clearly, but it is common in various Brachypylina adults and immatures. As reviewed by Norton and Alberti (1997), such juxtaposition has been considered either apomorphic or plesiomorphic by various authors, but a scattered taxonomic distribution suggests that it is evolutionarily labile. The essential connection is a developmental one: dermal glands appear to derive from secretory cells that envelop receptor cells of the associated seta. So, while the potential for dermal gland formation adjacent to setae may be ancestral, the specific pattern of expression may reflect multiple derivations. Among acariform mites, *Collohmannia* species have the greatest proportion of setae with associated dermal glands, and their further study should help illuminate developmental and evolutionary aspects of juxtaposition.

2. Spermatopositor — Grandjean (1966; his Fig. 8) drew the spermatopositor of *Collohmannia gigantea* in habitus, and it appears similar to that of *C. johnstoni*. Woodring (1970) described cuticular and histological features of the spermatopositor ('penis') of a variety of oribatid mites, including *C. gigantea*. He studied and illustrated the latter only in retracted form, surprisingly without reference to Grandjean's study, and apparently was unaware of the mobility (or even the presence) of the posterior lobe, which he envisioned as part of a 'central pleat'. Woodring characterized the spematopositor of *C. gigantea* as a 'weak penis', one of only two he classified that way, the other being that of the brachypyline species H*ydrozetes thienemanni* Strenzke (Hydrozetidae). Both are long and rather weakly constructed, contrasting with the short, well sclerotized, conical form ('strong penis') in most oribatid mites. Both short and long types exist in the genus *Ameronothrus* (Ameronothridae; Schubart 1975).

Hydrozetes species – those for which males are known – are sexually dimorphic in that males have modified setae on the anterior face of tarsus I. Grandjean (1966), noting the analogy with *C. gigantea* male tarsi, encouraged study of mating behavior in *Hydrozetes*, particularly to see if it involved a similar courtship. *Collohmannia* species use the large spermatopositor to deposit nuptial food, but its direct role in fertilization is unproven. The fact that *Hydrozetes* (at least *H. thienemanni*) also has a long, weakly sclerotized spermatopositor is a second morphological correlation between these very distantly related mites.

The similarity of the *Collohmannia* spermatopositor with the female ovipositor is striking: both are long, double-walled tubes with a movable unpaired distal lobe and coronal setae distributed at a mid-length fold. It is tempting to view such a spermatopositor as plesiomorphic: minimally derived from the female genital organ. But even the very early-derivative palaeosomatan family Acaronychidae shows the typical oribatid mite genitalic dimorphism, with a short, 'strong' spermatopositor (Grandjean 1954). It seems likely that the long, 'weak' spermatopositor of the middle-derivative genus *Collohmannia* (as well as those of *Hydrozetes* and *Ameronothrus* species) represents an evolutionary reversal, a genetic 'shortcutting' of a phylogenetically old developmental divergence.

3. Porosity of chelicera — In *Collohmannia*, the principal cheliceral segment inserts a short distance into the body wall, such that the flexible sheath attaches along line *en* (Fig. 11A). This seems to be an adaptation that allows more diverse orientations and strengthening of retractor-adjustor muscles, associated with the reduction of the trochanter and the more horizontal orientation of the principal segment. Previously, inserted chelicerae were known only from the Desmonomata (*sensu lato*, Nothrina, Brachypylina and Astigmata) and the distantly related enarthronote superfamily Hypochthonioidea (Norton 1998, 2010), which suggests two independent evolutions. In Desmonomata the principal segment typically has a porose cuticle external to line *en*, but lacks pore canals internal to *en*, which is con-

sistent with the idea that porosity serves a respiratory function (Alberti *et al.* 1997). In *Collohmannia* the porosity continues inside the body wall, where it would appear to have no function. This suggests that *Collohmannia* exhibits a rather plesiomorphic form of insertion, consistent with being a close outgroup of Desmonomata (see above).

4. Properties of unsclerotized cuticle — Under polarized transmitted light, the unsclerotized cuticle of preserved immatures, such as that of the gastronotic region, has a distinct glow (Fig. 17F). Because the cuticle is supple, the glow probably does not derive from minerals, and it is not as intense as the birefingence of the so-called actinopilin that is found in setae and structures derived from them. Whatever its cause, the cuticular layers are quite distinct in such illumination, and *C. gigantea* immatures show the same trait. We have not surveyed all oribatid mites, but these features are not unique to *Collohmannia*. Immatures of *Perlohmannia* species show the same glow and distinctive layering, as do those of *Eulohmannia*, various Nothrina (e.g. *Platynothrus*, *Trhypochthonius*) and the early-derivative brachypyline genus *Hermanniella*. We have not seen such birefringence in immatures of more derived Brachypylina that are superficially similar to those of *Collohmannia* (e.g. *Scheloribates*).

Grandjean (1966) noted that the clearing of immature *C. gigantea* with lactic acid causes separation of cuticular layers, with fluid filling the intervening space. We found the same artifacts in *C. johnstoni*, whether lactic acid or Nesbitt's agent was used for clearing, but the effect was somewhat weaker with the latter and often was manifested as wrinkling and the production of artificial surface patterns. Since his specimens were reared in the laboratory, Grandjean questioned whether field-collected specimens would suffer the same artifacts; in *C. johnstoni*, they occur consistently, and regardless of a specimen's origin or the duration of storage (if any) in alcohol.

A similar separation was seen in articulating cuticle between leg segments of adults and immatures, shown as an apparent double-cuticle in Fig. 14. This is certainly an artifact, as we observed the stages of separation over the course of several hours of treatment in lactic acid. Grandjean (1966; his Fig. 17) illustrated such separation, but did not discuss it. This artifact is not unique to *Collohmannia*: Grandjean (1958b, his Figs. 6-9) illustrated it for *Perlohmannia dissimilis* (again, without discussion) and we have seen it in that genus as well.

5. Sagittal apodeme — In all instars of *C. johnstoni* the sagittal apodeme projects internally as a small blade (Figs. 7G, 17A). It serves as the origin for part of the cheliceral retractor muscles, others of which originate from sigilla adjacent (mostly anterior) to the apodeme. In his study of the larva of *C. gigantea*, Grandjean (1966) called this a 'nervure' (which we translate as 'rib') and neither described nor illustrated a blade-like apodeme descending from it. We have not studied a larva of *C. gigantea*, but our several deuto- and tritonymphs of this species have a blade-like apodeme, like that of *C. johnstoni*, and Grandjean may have overlooked it in the larva. Though he used the term 'nervure' for both the sagittal apodeme and the lateral rib, they seem to be quite different structures. Both are internally projecting sclerotized surfaces, but the former is for muscle insertion while the latter is a supporting strut (see Remark 11).

6. Identity of notogastral setae d_2 and e_1 — Grandjean (1966, his Fig. 8) interpreted the enlarged seta dorsal to e_2 in the male of *Collohmannia gigantea* as d_2 and a small seta posteromedial to d_2 as e_1. We feel these latter two notations should be reversed. In the larva of *C. gigantea* seta e_1 is large and inserted directly posterior to the smaller d_2 (Grandjean 1966, his Figs. 1, 2). In the nymphs, these two setae retain their size difference, but their positional relationship is different: e_1 is displaced to become distinctly posterolateral to d_2 (Pfingstl *et al.* 2005, their Figs. 1, 15). By contrast, in the adult the large seta is anterolateral to the smaller seta. Grandjean's interpretation would require that between tritonymph and adult: (1) seta e_1 changes from a large to a small seta and is displaced far medially, and (2) d_2 changes from a small to a large seta and is displaced far laterally. It is not unusual for setae to undergo dramatic changes from one instar to the next, but these instances usually relate to specialized posterior setae that become normal when their

segment is displaced during anamorphic addition, and a non-homologous seta assumes its place and form. Grandjean (1964) referred to this as 'anhomologous tautergy.' However, we know of no examples of such ontogentic changes to setae in the middle of the body, where relative positions are usually stable.

Instead, we interpret the large seta to be e_1, as it is in the larva and all nymphs, rather than d_2, This would require a seta from segment E to have a slightly more anterior position than one derived from the segment in front of it (D), but on the whole it seems a more parsimonious interpretaton, requiring a simple continuation of a gradual displacement that started in the protonymph. This same displacement of enlarged seta e_1 occurs in *C. johnstoni*.

7. Primilateral setae on tarsus IV — Primilateral setae are fundamental, eustasic setae on the lateral face of leg tarsi. In a review of their morphological and taxonomic distribution, Grandjean (1959a) noted their absence from tarsus IV of all oribatid mites he had studied. Since that time, there have been at least two reports of their presence.

Travé (1967) wrote that *pl'* formed on tarsus IV in the tritonymph of *Phyllochthonius aoutii* Travé, and Fuangarworn (2010) reported the same development in *P. ovatosetosus* Fuangarworn. Neither author discussed this unique setation, but it is a reasonable hypothesis. Leg IV has an unusual development in all acariform mites: several setae that are fundamental and eustasic on legs I-III typically are delayed to the deutonymph (Grandjean 1946), or even to the tritonymph (Wauthy and Fain 1991). Phyllochthoniidae are rather early-derivative oribatid mites, and it should not be surprising if they retained another such fundamental seta, one that was fully suppressed on tarsus IV of more derived taxa. Also, it seems unlikely to be accessory lateral seta *l'* because proximal accessory setae are totally absent from the vast majority of Enarthronota, and this is true of tarsi I-III of *Phyllochthonius* species. In Grandjean's (1958b) conceptual model (see above) the priority of accessory setae decreases from anterior to posterior, so tarsus IV should be the first tarsus, not the last, to lose a particular seta.

The second case is quite different. Pfingstl *et al.* (2005) indicated that seta *pl'* is added to tarsus IV in the deutonymph of *Collohmannia gigantea*, but we believe this is an error. Their Fig. 14 shows labels for 14 setae, including pairs (*ft*), (*tc*), (*p*), (*u*), (*a*), (*pv*) plus setae *s* and *pl'*. However, only 13 setae are illustrated, which is the number indicated in the setal formula given in their text. The latter number is identical to that consistently seen on deutonymphs of *C. johnstoni* (Table 1), which do not form *pl'* or any lateral accessory seta on this segment. Each tarsus IV of our two *C. gigantea* deutonymphs has a setation identical to that of *C. johnstoni*. We believe the seta labeled *pl'* in their Fig. 14 is actually *a'*, with *u'* having been mistaken for the real *a'*. For the tritonymph, their Fig. 19 shows 15 setae on tarsus IV, including the same labels as indicated for the deutonymph, plus one unlabeled seta in the middle of the reverse side of the figure. Most *C. johnstoni* tritonymphs also have 15 setae on this segment, having added accessory pair (v_3) to the protonymphal complement, and the same setation exists on both legs of our *C. gigantea* tritonymph. As with the deutonymph, we believe that the seta labeled *pl'* by Pfingstl *et al.* is actually *a'*, with the unlabeled seta being *a"*. Collectively, the setae they labeled (*a*) and *s* are instead *s* and (*pv*), with the setae they labeled (*pv*) being (v_3).

Like most members of the infraorder Mixonomata and the hyporder Nothrina, *Collohmannia* tarsi are replete with proximal accessory setae in both ventral and lateral rows, but it seems that Pfingstl *et al.* (2005) did not include this possibility in their analysis. Since accessory laterals are present on tarsi I-III, it is almost certain that any seta on the anterior lateral face of tarsus IV is also an accessory lateral, not a primilateral.

8. Aggenital setation in *Collohmannia gigantea* — According to Pfingstl *et al.* (2005), two pairs of aggenital setae first form in the deutonymph of *C. gigantea*, which would be exceptional. In his early summary of development, Grandjean (1949a) found a maximum of one pair in deutonymphs of oribatid mites; many data were subsequently published but we know of no others that indicate a larger complement in this instar. Further, we have studied two deutonymphs of *C. gigantea* from Austria (where their material originated) and each exhibits

the typical single pair of aggenital setae. Dr. Pfingstl (pers. commun. 2014) kindly reexamined his deutonymphs and found the original observation to be in error: his deutonymphs, like ours, have a single pair.

9. Paraproctal atrichosy — According to Pfingstl *et al.* (2005), in the deutonymph of *C. gigantea* the paraproctal valves (anal segment) appear with their entire complement of setae (see their Fig. 2), but in our two deutonymphs they are glabrous, as in *C. johnstoni*. Dr. Pfingstl (pers. commun. 2014) kindly reexamined his nymphal specimens of *C. gigantea* and found the original observation to be in error: the paraprocts of both proto- and deutonymphs are glabrous and anal setae do not form until the tritonymph. Two-level paraproctal atrichosy appears to be a family-level character state.

10. Lateral rib — In his classic study of Palaeosomata, Grandjean (1954) characterized this rib as 'apodematique', marking the boundary between cheliceral and palpal segments. However, there is no evidence that it is an apodeme in the sense of serving for muscle attachments. Rather, it seems to be a reinforcing strut that stiffens the lateral region of the aspis in support of prodorsal condyle *pK*, which articulates with the subcapitulum. A similar, but not identical rib exists in immatures of some Brachypylina, notably Liacaridae (Costeséque and Taberly 1961; Trávníček 1977), but also some others, e.g. *Pirnodus cryophilus* Fernandez (Fernandez 1989); as Grandjean (1970) noted, these are differently positioned and do not terminate in a condyle.

11. Equivalence of Ptyctima and Euptyctima — Grandjean (1967) proposed the name Euptyctima for an unranked grouping of ptychoid oribatid mites that included only the superfamilies Phthiracaroidea and Euphthiracaroidea (*i.e.*, the ptychoid mixonomatans). He excluded the ptychoid enarthronote families Mesoplophoridae and Protoplophoridae, which together formed his complementary group Arthroptyctima. These proposals seem somewhat inconsistent and unnecessary. His intention was to dismantle the taxon Ptyctima, which according to common usage at that time was polyphyletic, as it included unrelated members of two of his major groups, Mixonomata and Enarthronota. Yet, he created another polyphyletic group (Arthroptyctima) despite noting that Mesoplophoridae and Protoplophoridae had evolved ptychoidy independently (see also Norton 2001, Pachl *et al.* 2012). Subsequently, Arthroptyctima has been mostly ignored, but Euptyctima remains widely used.

Euptyctima is unnecessary for two reasons. First, we believe it is equivalent to the initial sense of Ptyctima. The latter name was proposed by Poppe and Oudemans (1906) to distinguish ptychoid oribatid mites (Ptyctima), at least as they were known to exist in the vicinity of Bremen, from nonptychoid groups (Aptyctima; lapsus spelling 'Aptyetima'). These authors provided neither a diagnosis nor explanation of concept, but no enarthronotes were included; rather, Ptyctima contained only Phthiracaridae, which at that time had a broad sense, including both modern Phthiracaroidea and Euphthiracaroidea. No protoplophorid species had been described at that time, and Mesoplophora had not been formally incorporated into Phthiracaridae; on proposing the latter genus, Berlese (1904) only noted a general similarity to 'Hoploderma'. The enarthronotes were included in Phthiracaridae (= Hoplodermatidae) when Ewing (1917) proposed the subfamilies Protoplophorinae and Mesoplophorinae. The second reason is procedural: rather than propose a new name for the monophyletic part of a polyphyletic Ptyctima (if it were perceived that way), one could simply remove the few 'offending' taxa (the enarthronotes) and retain the original name for the large and otherwise monophyletic group (the ptychoid mixonomatans).

There is some irregularity regarding authorship and date of the name Ptyctima. The article in which it first appears is commonly cited as Poppe and Oudemans (1906), but the publication lists the author as S.A. Poppe, with Oudemans' contributions indicated only in parentheses. According to Jacot (1929), Heft 1, containing the article, was published in September of 1906, and this year appears on reprints even though the volume (XIX) is associated with 1907. Separately, and after Poppe's death, Oudemans (1907) explained that he alone was responsible for the nomenclature used in that work.

With no reason to doubt this, we follow Willmann (1931) in using the attribution Ptyctima Oudemans, 1906 (in Poppe and Oudemans 1906).

Notes on Biology

1. Habitat, abundance, and associates — *Collohmannia johnstoni* is common in the thick litter of dense rhododendron thickets at the riparian type locality along Otter Creek. The 10 quantitative samples (totaling 4,000 cm^2), collected in November, 2013 yielded 38 specimens (98 per m^2), but these were highly aggregated. One sample contained 60 % of the mites (23), three had no mites, and the other six had 1-5 mites each. No adult *C. johnstoni* specimens were collected from the underlying A1 horizon, but one of the five samples had three juveniles (see Note 4 for population structure). Within the riparian forest, *C. johnstoni* was rarely encountered in samples of cushion mosses and never from sphagnum or from the rather homogeneous litter directly under hemlock trees. It is not restricted to rhododendron-rich litter, however. Specimens were found at low density in samples of general litter from nearby non-riparian forest (less than 1 km distant) that had similar overstory trees but little or no rhododendron. Also, the forests from which two collections were made in Pocahontas Co. (see above) were not riparian, and rhododendron is not mentioned in the available collection data.

Collohmannia johnstoni was always accompanied in Otter Creek samples by the cyphophthalmid harvestman *Siro exilis* Hoffman, which was present in much greater numbers. An undescribed species of *Perlohmannia* was also present in riparian samples, but it was often collected in general non-riparian litter samples that lacked *C. johnstoni* and *S. exilis*. Both *Siro* and *Perlohmannia* are also present in the forested habitats of Styria, Austria where *C. gigantea* is found (Schuster 1960, Alberti and Schuster 2005). In the Nearctic Pacific North West, different species of *Siro* and *Perlohmannia* can be abundant in forest litter, but *Collohmannia* has never been found there.

2. Feeding biology — We have examined gut contents of many field-collected specimens of *C. johnstoni*, both adults and juveniles, and found boluses to contain mostly small leaf fragments. Fungal hyphae and spores were seen, but not in abundance and they may have been ingested with leaf material. We maintained adults and juveniles in the laboratory, in small chambers with a plaster-charcoal substrate. Always they ignored offerings of fungi (hyphae or fruiting bodies of various species) and unicellular terrestrial algae (*Protococcus* sp.) that have proven attractive to various other species of oribatid mites. Juveniles fed readily on aged dead leaves of deciduous trees – *Betula alleghaniensis* and *Acer rubrum* – removed from the samples after extraction of the mites, and over a few days several nymphs could fully skeletonize a leaf fragment (Fig. 19A, C). On one occasion, a small group of larvae fed actively on a decayed hemlock needle, despite the presence of small deciduous leaf fragments in the study chamber. Adults fed on the same materials, but at a slower rate, and they never fully skeletonized a leaf fragment under similar conditions. Similarly, *C. gigantea* was maintained in the laboratory by Alberti and Schuster (2005) on rotting leaves of *Fagus sylvatica* L. and *Carpinus betulus* L.

3. Courtship behavior — Relatively few oribatid mite species exhibit significant sexual dimorphism (Grandjean 1966; Norton *et al.* 1997; Behan-Pelletier and Eamer 2010 and cited references) and other than a modest dimorphism in some Epilohmanniidae (Wallwork 1962) *Collohmannia* includes the only examples known outside the Brachypylina. This dimorphism is strong enough that males and females of *C. gigantea* were originally described as different species (Schuster 1962). Courtship and associative mating have been observed and described for only a few of the dimorphic oribatid species, though it may be a common feature among them.

The initial stages of courtship behavior in *C. johnstoni* were observed numerous times in the laboratory. The behavior is generally similar to that of *C. gigantea*, as described by Schuster (1962) and Alberti and Schuster (2005), whose images also suffice to illustrate courtship in *C. johnstoni*, except for slightly different body forms. When moving about the observation dishes, males usually carried legs I in front of them, above the substrate in antenna-like fashion, but used them for walking when climbing over irregular surfaces, such as a leaf fragment.

Upon encounter with a female, the male touched and stroked her long posterior setae with his tarsi I. If she moved away, as usually happened at first, he followed closely behind her with legs I raised in what Schuster (1962) called 'chain walking'. The contact appeared to be only between the male's first tarsi and her setae, in contrast to *C. gigantea*, in which the male applies his first tarsi directly to the flanks of the female during chain walking (Fig. 1 of Alberti and Schuster 2005). The long, ribbon-like neotrichous setae on the adaxial face of tarsi I in male *C. gigantea* may assist in maintaining physical contact with the female's notogaster, but males of *C. johnstoni* have no setae of this form.

At some point, the *C. johnstoni* female stopped walking and the male moved to her side, often nuzzling underneath her (cf. Fig. 3 of Alberti and Schuster 2005). If she did not move away, he positioned himself in front of her, turned his posterior to her, elevated his hysterosoma while standing on legs I-III, and extended both legs IV toward her in parallel with each other and approximately parallel to the surface (cf. Fig. 1 of Schuster 1962). Then, his elongated spermatopositor was extended and a secreted drop of thick, clear fluid was deposited between the closely adjacent genua IV, where it was held by the opposed pair of enlarged setae *v″*. If the female remained, she fed on the fluid held by the male. In most observed courtships, the female walked away after several minutes, leaving the male still in an erect position.

After courtship, the male usually remained erect for at least several minutes, with legs IV crossed at the tarsi and remaining stuck together by the fluid. When he eventually moved away, often still in an erect posture, legs IV were dragged behind him for some minutes, even as much as a half-hour. Eventually the legs were pulled apart by rubbing them together, then they were groomed one at a time with the respective leg III. Uneaten fluid could become smeared on the substrate, and we often observed this being eaten by the male himself, by the original female, or by another passing adult (no juveniles were in the chambers).

Other behaviors were observed less frequently. If a female did not stop after chain-walking, the male sometimes moved rapidly in front of her, assumed the erect posture and presented legs IV, and repeated this multiple times if she avoided him; in one instance this behavior continued over a distance of 2 cm. Several times, erect, displaying males moved backwards into females that did not approach them. Several times, while a female was feeding, we observed the male lifting legs III from the substrate, extending them to the side, and waving them in unison, up and down, at a rate of once or twice per second.

Rarely, we observed interactions among multiple individuals. Once, two males were seen erect, but without legs IV extended, on either side of the same female. Also once, two females were seen apparently competing for fluid from the same male; one, a lighter, teneral female, pushed and displaced a darker female that had started eating the fluid held by the male.

Males usually seemed to encounter females haphazardly, and often this occurred at the edge of the observation chamber as mites of both sexes followed the chamber wall. On a single occasion we tracked the wandering path of a female across the substrate, and a male appeared to follow the same path; we had no opportunity to repeat this observation. Males sometimes were seen alone with hysterosoma erect but legs IV not extended, either walking or unmoving for several minutes, as if dispersing a volatile pheromone. These behaviors hint at the possible existence of sex pheromones, but we have no further evidence for such communication. It is also possible that the extended period of dragging legs IV after courtship is purposeful, *i.e.*, in effect laying a scent trail. Sometimes females were seen following a leg-dragging male, eating the nuptial fluid smeared on the substrate, and the male intermittently squeezed new clear fluid onto his legs.

As in the studies of *C. gigantea* by Schuster (1962) and Alberti and Schuster (2005), we failed to observe sperm transfer. If the vessel were tilted or light increased in order to see details in lateral view, the courtship ceased. We examined some of the thick fluid smeared on the substrate, and like the above authors we found no sperm or other particles within it. It seems certain that the extruded clear

fluid is not a spermatophore, but rather serves as an enticement, an endogenous nuptial gift in the classification of Lewis and South (2012). Like Alberti and Schuster (*op. cit.*), we never found a free-standing spermatophore in culture vessels.

It seems that sperm transfer must occur while the female is in feeding position, but only two observations directly support this. During courtship, one feeding female broke away briefly from the male, allowing us to see that the male had deposited between his genua a drop of material that appeared more opaque than the usual nuptial fluid. It may have been a stalkless spermatophore but we had no opportunity to examine it. The female immediately returned and moved under his erect body, further in than we had observed previously, and this may have been the time of transfer. When she pulled away after a short time, his legs were almost clean, which was quite unusual. But some of the material – with the consistency of a silicone sealant – was stuck to the substrate. After the female left, the male quickly ate the remains, and we had no opportunity to examine it for spermatozoa. In another instance, courtship that was well along was accidentally disrupted. The female was examined closely, and her genital plates were smeared with a milky, cream-like material. We speculate that the male deposits a stalkless spermatophore on the substrate beneath the female after she has fed for some time, and she squats over it to take it into her genital vestibule.

Most of our observations seem to have involved aborted courtships that stopped during or after nuptial feeding. This could simply be an artifact of the observational conditions, or may have related to the state of females. Previously fertilized females might feed but not complete the process, and respond less aggressively to the nuptial fluid than do teneral, virgin females (see above). Similar incomplete courtships of the brachypyline mite *Mochloribatula* sp. were observed by Oliveira *et al.* 2007; males of this mite produce an attractant from specialized dermal glands at which the female nibbles, but no sperm exchange was observed.

If observations of *C. johnstoni* in the laboratory reflect natural behavior, males seem rather wasteful with the nuptial fluid, and with the energy needed for courtship. Males seem to display for any female, receptive or not, and even for other males. Multiple times, we opened holding jars that contained only males, to find a male in its display posture with legs IV extended and smears of the nuptial fluid on the substrate, or two males nuzzling underneath and displaying (erect hysterosoma) for each other.

4. Eggs, parity and population structure — Preserved, field-collected females commonly carried a dozen or more eggs, with 15 being the maximum observed. Eggs taken from three preserved females were measured (mean and range; n = 32): length 357 μm (300-430); width 209 μm (180-240). These eggs varied in state of development, from being an apparently mature egg, to containing a prelarva, to containing a fully formed larva. This range suggests that the oviducts serve as brood pouches, as was demonstrated for the nothrine *Archegozetes longisetosus* Aoki (Bergmann and Heethoff 2012). At least under culture conditions, *C. johnstoni* females retained eggs within their body until the larva had developed. Eggs deposited on the culture substrate were shiny and nearly transparent, without noticeable chorion, and the larva could be discerned within, most conspicuously by the pigmented parts of the gnathosoma (Fig. 19B). Despite dozens of larvae having been produced by several females in culture vessels over several weeks, we saw few eggs during the daily observations. Most often, the first evidence of reproduction in cultures was the presence of a rather shriveled-looking (unexpanded) larva lacking gut contents, which indicates that hatching is quite rapid after parity.

These observations point to *C. johnstoni* being an ovoviviparous species. The prelarva was observed only in eggs within the oviducts of preserved females, although we assume that its cuticle surrounded any unhatched larva. Egg retention to the development of the larva is considered facultative in some oribatid mites (Haq *et al.* 1991; Norton 1994; Hubert 2000), but we have no evidence that this is true of *C. johnstoni*. A single exception to ovoviviparity was noted: in a dying culture with the single remaining living female in obviously poor health, an egg was found that contained only a prelarva (sacrificed to confirm its state

of development). Søvik (2003) discovered an analogous situation with *Ameronothrus lineatus* (Thorell), a brachypyline oribatid mite that is usually ovoviviparous: declining conditions (in this case colder temperature) seemed to lead to deposition of less developed eggs, which seldom completed development.

Three collections were large enough so that population structure can be roughly estimated. The population sex ratio probably does not differ significantly from the 1:1 that is expected from a bisexual species in Oribatida (Norton *et al.* 1993). In September, 1983 the 55 adults collected were 55 % female; in September, 2002 the 34 adults collected were 56 % female; and in November, 2013 the 65 adults collected were 46 % female. Juveniles of all instars were present at all collection times, but collectively were always less numerous than adults in samples: in September, 1983 juveniles comprised 41 % of the 93 individuals collected (10 larvae, 14 proto-, 6 deuto- and 8 tritonymphs).

Alberti and Schuster (2005) reported an absence of larvae from winter samples of *C. gigantea*. We have no winter collections of *C. johnstoni*, but the November, 2013 sample included larvae, all nymphs, and females containing larvae. Considering the cold fall and winter at this location, we doubt that larvae present in November would molt to protonymphs before spring, which also is probably when overwintering gravid females would lay their eggs. Therefore, we believe all instars are present throughout the year.

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