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NORTH AMERICAN SYNICHOTRITIIDAE (ACARI : ORIBATIDA)

1. **APOTRITIA WALKERI N.G., N. SP., FROM CALIFORNIA**

BY ROY A. NORTON * and J.-C. LIONS**

SYNICHOTRITIIDAE

**ABSTRACT:** Apotritia walkeri, a new genus and species of oribatid mite in the family Synichotritiidae, is based on adult specimens from leaf litter in California. The family Synichotritiidae is redefined, with emphasis on the unique structure of the sagittally attached genital plates, the anteriorly directed ovipositor, and associated modifications. Two subfamilies are recognized: Synichotritiinae, including Sabahtritia and Synichotritia; and Temburongiinae, including Temburongia and Apotritia. A relictual distribution is suggested by the representation of each subfamily in North America and Borneo, and Synichotritia is first reported from the eastern United States (Florida).

SYNICHOTRITIIDAE

**RéSUMé:** Un nouvel Oribate, *Apotritia walkeri* n. gen., n. sp., est décrit à partir d'exemplaires adultes d'une litière de feuilles de Californie. La famille des Synichotritiidae est redéfinie en insistant sur la structure particulière des plaques génitales jointes, l'ovipositeur orienté en avant et des modifications associées.

Deux sous-familles sont reconnues: Synichotritiinae comprenant les genres Sabahtritia et Synichotritia, et Temburongiinae avec les genres Temburongia et Apotritia.

Une nouvelle distribution relictuelle est suggérée par la présence de chaque sous-famille en Amérique du Nord et Bornéo, et *Synichotritia* est pour la première fois signalé à l'Est des États-Unis (Floride).

On August 23, 1960, N. A. WALKER mailed adult specimens of two unusual species of ptychoid oribatid mites to F. GRANDJEAN, seeking his opinion on their relationships. The material was collected from California during WALKER’s doctoral research on the Euphthiracaroidea of *Sequoia* litter. After a brief study, GRANDJEAN responded in two letters (3 Nov., 14 Nov., 1960) which supported WALKER’s idea that each might represent an undescribed family, and highlighted some interesting aspects of their morphology. One of these species was clearly a euphthiracaroid, and WALKER eventually (1965) proposed the name *Synichotritia caroli* for this mite, which is the type-species of the genus *Synichotritia* (Synichotritiidae).

The second species was represented by a single female, which GRANDJEAN dissected and eventually returned to WALKER. GRANDJEAN was impressed by the uniqueness of this mite, in particular the presence of an unpaired genital “plastron,” but...
suggested that it was not a euphthiracaroid, since the ano-adanal plates were fully independent from plates of the genital region. Rather, he thought its affinities were with the Phthiracaridae, either as a derivative of that family or one of its close relatives. It is probably on the basis of Grandjean’s comment that this species was not included in Walker’s (1965) study.

The mite has remained undescribed, and most of Walker’s original 12-15 specimens have been lost, including that dissected by Grandjean. We independently learned of the species’ existence more than a decade ago (from Walker and Grandjean, respectively) and each traveled to California, guided by information from Walker, in unsuccessful attempts to recollect it (J.C.L. in 1981, R.A.N. in 1986). When Walker’s collection was donated to R.A.N. in 1981 only two specimens remained, both of which had been dissected and labeled by M. Sellnick during his visit with Walker in 1960. They have since been remounted.

Our purpose is to describe and illustrate this mite as fully as possible, given the constraints of the two available specimens. We also propose a new genus, and show that it is indeed a member of the Euphthiracaroida, closely related to Synichotritia, Sabahtritia and Temburongia. Aspects of the phylogeny, biogeography, and unique features of this group will be discussed herein, while subsequent papers in this series will treat the genus Synichotritia. Morphological terminology follows that developed by F. Grandjean (see Trévé and Vachon, 1975 for references).

**APOTRITIA** N. GEN.

Type species: *Apotritia walkeri* n. sp.

Diagnosis: Temburongiine Synichotritiidae (see below) having unpaired genital shield elongated, with posterior tectum (bearing one pair of setae) overhanging ano-adanal valves. Notogaster with terminal fissure. Three pairs of adanal setae in normal position, laterad of anal setae. Rostral setae in normal position, well anteriad of lamellar setae. Seta *d* lost from both femur and genu IV. Palp 4-segmented, femur and genu fused; supracoxal seta forked. Leg pretarsi heterotrdactylous.

*Apotritia walkeri* n. sp. (Figs. 1-4)

**Etymology.** The latinized Greek generic prefix *apo* refers to its derived nature; *Tritia* was an early generic name in this group. The specific epithet is in honor of the collector, Neil A. Walker, author of an important monograph on euphthiracaroid mites.

**General.** The cleared, slide mounted parts (opisthosoma, aspis) are light-colored. Based on birefringence in polarized light and an irregular refractive pattern in bright-field illumination (Norton and Behan-Pelletier, 1991) the cuticle of the middle and posterior regions of the single available notogaster is mineralized; the region anterior to a line approximately between setae *d* and *cp* is not mineralized. There is little evidence of mineralization on the aspis and none on the genital shield or ano-adanal plates, but this may be an artifact of specimen preparation. Exposed cuticular surfaces are shiny and weakly foveate, with foveae largest and most dispersed (separated by more than their 4 µm diameter) in the middle regions of the notogaster. Foveae become smaller and more dense (i.e., punctate rather than foveate) in the anterior, posterior and marginal regions of the notogaster, as well as on the aspis and ventral plates.

**Aspis** (Figs. 2B, 2C, 4C, 4G). The aspis is damaged in both of the available specimens, but it has typical euphthiracaroid form: about 200 µm long, 137 µm wide, and 80 µm high at center. There is one well defined lateral carina (*ca*) originating dorsad of the bothridium and running anteriad, blending with the rostral rim. The sagittal apodeme (*as*, = *ns* of Grandjean, serving for attachment of adaxial cheliceral retractor muscles, is long and conspicuous. The paired inferior apodemes (*ai*),
Fig. 1. *Apatrissa walkeri* n. sp.

A. — Holotype, ventral aspect of opisthosoma (asps and podosoma removed). B. — Schematic cross-section of articulation between notogaster and genital shield (gs). C. — Schematic longitudinal section (anterior to left) of articulation between genital shield and ano-adanal plate (an). Borders of tecta and sclerites labeled as follows: *bap* - lateral border of the fused ano-adanal plate; *bgs* - lateral border of the genital shield; *bgt* - base of the posterior genital tectum; *bng* - ventral margin of notogaster; *bnt* - base of notogastral tectum; *t* - posterior margin of posterior genital tectum. Other labels explained in text.
associated with aspis retractor muscles, are large.

The well defined bothridial scale (bs), which inserts into the tectonotal notch of the notogaster (Fig. 2A ; tn) during enpychosis (closure of the ptychoid mechanism ; SANDERS, 1982) lies postero-dorsad of the bothridium. The bothridium has the typical euphthiracaroid form ; no brachytracheae are discernable. A narrow band of fine ridges traverses the region between bothridia. The sensillus (ss) is about 70 µm long, nearly smooth (a few minute barbs in its distal half), thickened slightly in its distal half, then finely attenuate. All observed aspal setae are smooth. The exobothridial seta (ex, homologue of anterior seta in Synichotritia) is fine, simple, about 20 µm long ; there is no trace of the posterior exobothridial seta. The lamellar seta (le) is about 75 µm, the rostral (ro) about 85 µm long ; the interlamellar setae are broken from both specimens, but based on the size of their alveoli (just medially of bothridium) are probably similar to the other two setae (a faint image of in can be seen in Fig. 4G). The insertions of in le and ro are nearly in a straight line, with le less than half as distant from in as from ro.

Notogaster Figs. 1, 2A, 4A, 4B, 4F). The notogaster has the elongated, laterally compressed proportions typical of euphthiracaroid mites, with a length of 396 µm, width of 214 µm, and height of 240 µm. The ventral notogastral margin bears a well-developed tectum (Fig. 1A, 1B) that protects the articular area of the genital shield and ano-adanal plates ; it is broad, ranging from about 25 µm anteriorly to over 40 µm in the anal region, and solid throughout its length. A broad zone of soft cuticle connects the base of the tectum (bnt) to the plates of the anogenital region. The notogastral border (bng) is unusual in ventral aspect, with a large, rounded emargination in the posterior quarter that accommodates the protruding ano-adanal plates. Posteriorly a long terminal fissure (Fig. 4B, arrow), reaching dorsad to the level of setal pair h₁, interrupts the tectum. The tectonotal notch (tn) is well developed. There are 14 pairs of notogastral setae, all of which are smooth, finely attenuate, about 70-90 µm long. They emerge through a rather straight invaginated channel, with the actual insertion being deep in the cuticle. Neither lyrifissures nor the alveolar vestiges of setae f₁ or f₂ that are typical of euphthiracaroid mites could be located, but their absence is uncertain since these minute structures are difficult to discern when cuticle is heavily mineralized. The opisthosomal gland is absent.

Anogenital Region (Figs. 1, 4A, 4B, 4D). The most striking feature of this species is the unpaired genital shield generally shaped like an elongate trapezoid in ventral aspect (Fig. 1, gs) ; approximately 250 µm long, 110 µm wide anteriorly, and 75 µm wide posteriorly. There is no trace of its presumed ancestral construction (paired valve-like genital and aggenital plates), except for medial incisions at its anterior and posterior extremes. In cross-section the shield gradually changes from highly convex anteriorly to nearly flat posteriorly (Fig. 4A). Its anterior border has a strongly reflexed lip (rl) that is completely divided by the medial incision. Posteriorly the shield is extended as a large tectum (Fig. 1C) that covers the anterior region of the paired ano-adanal plates ; the tectum is solid in its distal third, with a posterior border that is very thin and difficult to see in ventral aspect. The shield bears eight pairs of setae, one of which (about 8 µm) inserts on the posterior tectum. Others are concentrated in the anterior quarter of the shield ; one pair (15 µm) inserts in a shallow groove in the reflexed lip, four evenly spaced pairs (5-10 µm, the more lateral setae smallest) are in a transverse row immediately posterior to the lip, and two pairs have a rather medial position in the anterior fifth of the plate. The latter two are the longest of the genital shield setae, with the medial pair (30-35 µm) thin, smooth, and the lateral pair (50 µm) relatively thick and barbed. Homologies with the genital setae of other Euphthiracaracidae could not be established.

The paired ano-adanal plates are very broad, appearing nearly semicircular in ventral aspect. No suture or other separation delineates the anal from adanal regions. The lateral third to half of these plates is covered by the notogastral tectum, and the anterior region is covered by the thin posterior tectum of the genital shield. Anteriorly (hidden under the genital shield tectum) the medial margins of the plates continue dorsad as a preanal apodeme.
FIG. 2: *Apotrita walker* n. sp.

A. — Lateral aspect of holotype opisthosoma, showing partially extruded ovipositor (ov). B. — Dorsal aspect of aspis, with broken central region outlined by dashed line. C. — Right lateral aspect of aspis.
of uncertain structure (see Remark # 3). The postanal apodeme (not illustrated) is well developed; at its juncture with each ano-adanal plate there is a series of weak dorso-ventrally directed ridges, forming an inconspicuous posterior zone of coaptation. Neither anal nor adanal lyrifissures were observed. Two pairs of nearly smooth anal setae are inserted near the medial margin of the plates, at approximately midlength. The three pairs of adanal setae are distinctly larger, with small but distinct barbs.

The ovipositor (Fig. 2A, ov) emerges between the anterior border of the genital shield and the posterior border of coxisternum IV. It is of normal form, but has a highly regressive setation. Coronal setae are absent, and only six setae are present on the distal lobes: two pairs on the dorsal lobe, and one pair on the ventral lobes. Homologues of the two pairs of microsetae on the ovipositor of Synichotritia spinulosa (Walker, 1965, Pl. 48) are absent.

The nearly horizontal position of the progenital chamber and ovipositor causes the genital papillae to be aligned more vertically than usual. The anterior two pairs of papillae are normal in form, with a narrow un sclerotized band separating the distal cap from the stalk. Their retractor muscles are directed obliquely, with origins in the normal position on the notogaster. The posterior pair (vp) is very unusual, with each papilla reduced to less than half its normal size and terminating in a conical cap. The pair is distinctly separated from the anterior pairs, being adjacent in the sagittal plane and positioned well ventrad, just above the genital shield. The retractor muscles leave the posterior papillae in a nearly posterior direction, but their point of origin could not be determined.

Coxisternal Region and Legs. The coxisternal setal formula (I to IV) is 3-0-1-3. Setae 1a and 1c (about 4.5 µm) are minute, inconspicuous except for their alveoli; the others are barbed and finely attenuate, with 1b being longest (about 52 µm, compared to about 35 µm for coxisterna III and IV setae).

The form of the legs is typical of euphthiracaroid mites. All pretarsi are heterotridactylous. The genual pore is present posterodorsally on genua I and II, but could not be discerned on genua III or IV. The following are respective setal formulas: (legs I-IV, famulus included): trochanters (1-1-2-2); femora (3-2-2-1); genua (5-4-2-1); tibiae (5-4-3-2); tarsi (18-12-11-10). Setal homologies are given in Table 1. Several aspects of the setation are interesting. Seta d is absent from femur and genu IV (Fig. 3A); the former absence is present in eupathidial mites (Marx, 1964), but the latter is rare. Genua III and IV each have a single abaxial seta, but they do not seem to be metameric homologues; it is 'p' on III but v' on IV, unless some major positional modifications have occurred. Seta pv" is absent from tarsus II, despite its presence on other tarsi. The famulus (e) of tarsus I is isodiometric, distally truncate and nearly smooth, with the annulation typical of Ptyctima only vaguely defined. Only tarsus I exhibits iter al setae; these are eupathidial, as are four other setae (p', pv", a' and s).

Solenidia formulas are: genua (2-1-1-0); tibiae (1-1-1-1); tarsi (3-2-0-0). All genunal and tibial solenidia are imperfectly coupled (in adjacent but separate alveoli) with setae, the latter being d, with

| Table 1: Leg setation of Apotritia n. sp. (parentheses around setae denote a pair; parentheses around seta and solenidion denote coupling). |
|---|---|---|---|---|
| trochanter | femur | genu | tibia | tarsus |
| Leg I | v' | d, bv", v' | (da"), (f's), v", (v) | (v)', (v), (v) |
| Leg II | v' | d, bv" | (da), (v), v" | (v)', (v) |
| Leg III | I', v' | d, ev" | (da), v" | (v)', (v) |
| Leg IV | I', v' | ev" | v" | (v) |

TABLE 1 : Leg setation of Apotritia n. sp. (parentheses around setae denote a pair; parentheses around seta and solenidion denote coupling).
Fig. 3: *Apotritia walkeri* n. sp.
A. — Left leg IV, abaxial aspect. B. — Subcapitulum and palp, partial right lateral aspect. C. — Right chelicera, abaxial aspect.
one exception (noted below). Seta \( d \) of each tibia is flagellate, weakly barbed, and nearly as long as its flagellate coupled solenidion \( \varphi \); the respective lengths of \( d/\varphi \) decrease from about 130/130 \( \mu \text{m} \) on tibia I to about 70/80 \( \mu \text{m} \) on tibia IV. Solenidia \( \sigma' \) and \( \sigma'' \) of genu I (about 65 and 45 \( \mu \text{m} \), respectively) are piliform and coupled to \( t' \) and \( d \), respectively, typical of Euphthiracaroidea. On tarsus I, solenidia \( \omega_1 \) and \( \omega_3 \) (about 65 and 30 \( \mu \text{m} \), respectively) are ceratiform and inserted at approximately the same longitudinal level on the segment; flagellate solenidion \( \omega_2 \) (about 90 \( \mu \text{m} \)) is the middle structure in a nearly linear arrangement with the famulus (basad), and seta \( ft'' \) (distad).

**Gnathosoma.** The subcapitulum (Fig. 4E) is mostly typical of euphthiraracoid mites (e.g. MÄRKL, 1964; WALKER, 1965); it is stenarthric, with one pair of hypostomal and two pairs of genal setae in their normal positions, all of which are barbed. Of the three adoral setae, \( or_2 \) and \( or_3 \) are simple, but \( or_1 \) is clearly forked; the latter is unusual for euphthiraracoid mites, though commonly found in other oribatid mite groups. The supracoxal (post-palpal) seta (Fig. 3B, e) is also forked, a condition we have not observed in other Euphthiraracoida but which exists in *Eulohmannia* (GRANDJEAN, 1967, p. 256).

The palp (Fig. 3B) is four segmented, apparently due to a fusion of the genu and femur, but there is no remnant of a suture. The trochanteral sclerotization is absent abaxially, leaving the annular structure of the segment incomplete. Assuming the above-mentioned fusion, the setal formula (trochanter to tarsus) is 0-[1-0]-2-8, plus the usual ceratiform tarsal solenidion. Seta \( acm \) and pair \( ul \) of the tarsus are eupathidial. Seta \( su \) is minute, solid, and directed along the base of \( ul' \).

The chelicerae (Fig. 3C) are normal, chelate-dentate, each digit with four distinguishable teeth in typical arrangement. Setae \( cha \) and \( chb \) are 25-30 \( \mu \text{m} \) long and distinctly barbed. Most of the cheliceral cuticle is strongly porose. Both surfaces have spicules, but those of the adaxial surface (shown in Fig. 3C by transparency in dotted lines) are more abundant (about 15-20) and generally larger; the abaxial surface has 10 or fewer, and these are inconspicuous.

**Egg.** The egg is rather elongated and slightly oval, about 295 x 120 \( \mu \text{m} \). There is no noticeable chorion, nor evidence of prelarval development. The body of the holotype female contains two eggs; an egg from the paratype is on a separate slide. In his unpublished dossier, GRANDJEAN noted the presence of two eggs in the specimen seen by him.

**Material examined.** The holotype and paratype were collected from leaf litter on a forested hillside in Marin County, California, about 0.3 km south of Samuel P. Taylor State Park in April, 1956 by N. A. WALKER. Both are dissected, and mounted on a series of five slides each; the notogaster of the paratype was not included in the material we received. All slides will be deposited in the collections of the Division of Insects, Field Museum of Natural History, Chicago.

### RELATIONSHIPS AND CLASSIFICATION

GRANDJEAN noted in his correspondence and dossier that the relationships of this species to other Ptyctima are not obvious. He implied this was due mostly to the unusual structure of the ventral sclerites, which are unlike those of any mite known to him. Particularly striking were the medial fusion of the genital valves, and the associated modifications of the ovipositor and genital papillae.

**PHTHIRACAROIDEA OR EUPTHIRACAROIDEA?**

Three characters can be interpreted as supporting GRANDJEAN's unpublished preliminary ideas on relationships with the Phthiracaridae (sensu lato). One is the absence of a pair of plicature plates. Although the polarity of this character has yet to be carefully examined, a plicature zone and weakly
FIG. 4: *Apotriaia walkerii* n. sp.

formed plates are present in some non-ptychoid Mixonomata, for example, the Perlohmanniidae and Collohmanniidae (Grandjean, 1958, 1966), and their absence in Apotritia could be interpreted as a loss shared with the Phthiracaridae. Second, anal and adanal plates are fused and indistinguishable, forming a single pair of valves around the anus; this is a derived state similar to that in Phthiracaridae. Third, shared with all known Phthiracaridae, is the absence of the opisthosomal gland; this is certainly secondary, a loss known elsewhere in Ptyctima only in the euphthiracaroid family Synichotritiidae. Yet, Apotritia does not share several seemingly derived states of Phthiracaridae, such as the three large brachytracheae that penetrate the prosoma from the base of each bothridium, or the rather regressed nature of the anterior genital papilla. Also, the famulus of tarsus I in phthiracaroid mites is removed from solenidion a', and its coupled minute seta (ft').

Other characters suggest a relationship with the Euphthiracaroida, usually considered to include the families Oribotritiidae. Euphthiracaridae and Synichotritiidae. One is the presence of a well defined bothridial scale, a solid, sclerotized projection that functions during emptyctosis; it acts as a condyle, fitting into the scale receptacle contained in the tectonal notch on the anterior tectal margin of the notogaster. When in contact, these structures form a precise axis of rotation (Sanders, 1982). Although the mechanism in Phthiracaridae has not been carefully described, there is usually a ridge above the bothridium that fits into a less precise zone of coaptation on the notogastral tectum.

Another character state of Apotritia that is shared with all euphthiracaroid mites is the coupling of solenidion a' with seta I' on genu I; we know of no other oribatid mite taxa in which each of the two solenidia of genu I are coupled with setae. This apparent synapomorphy may not be real, however, if Van der Hammen's (1963) interpretation of setal homologies in Phthiracaridae is correct. He considered seta d to be lost from genu I, and regarded the seta coupled with the large adaxial solenidion (a') to be I'. A regression of seta d may have resulted from a previous coupling with a" in phthiracaroid ancestors (see Remark #2), in which case these ancestors also would have had a double coupling on genu I. Double coupling in Apotritia would then represent a plesiomorphy of all Ptyctima rather than a synapomorphy with Euphthiracaroida, and the character would be useless for studying relationships.

Several structures that are found in some (but not all) Euphthiracaroida are well developed in Apotritia. One is the sagittal apodeme of the aspis. Another is the terminal fissure of the notogaster (Markel, 1964 discussed the distribution of these structures). A tectum developed from the fused posterior margin of the genital plates slightly overhangs the anterior margin of the anal plates in many Euphthiracaroida, and such a tectum is strongly developed in Apotritia.

There is another set of characters, however, which make the relationships of Apotritia with the Euphthiracaroida virtually certain. These are a set of derived states shared only with Synichotritia, Sabahtritia and Temburongia; the former is North American and the latter two are known only from the Malaysian region (Mahunka, 1987, 1990). Each character of the set is associated with the genital region, and seems to relate to the unusual orientation of the ovipositor.

First, mites in all four genera have genital plates that are attached in the sagittal plane, such that the progenital chamber does not open via the normal paired-valve mechanism (see Grandjean, 1969). Instead, the ovipositor emerges anterior to the genital shield, between it and coxisternum IV. The degree of mid-sagittal fusion between the ancestrally separate genital valves varies among the four taxa. Although not noted by either Walker (1965) or Mahunka (1990), in Synichotritia the valves

2. Grandjean (1964, p. 546) stated that the more paraxial (= adaxial) of the two genu I solenidia (a') is coupled to seta d in Rhysotritia ardua. This was an error caused by inadvertently reversing the names of his examples, R. ardua and Synichotritia elegans (Brachychthoniidae), as can be seen by comparing his original papers (1942, p. 41; 1963a, p. 130; 1967, p. 266.) In all euphthiracaroid mites we have studied (representatives of most described genera) it is a', the more abaxial (= antiaxial in Grandjean's terminology) of the solenidia, that couples with d; a", the adaxial solenidion, couples with I'.

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articulate sagittaly by a narrow longitudinal band of unsclerotized cuticle; without dissection of the genital region this attachment is easily overlooked. The sagittal articulation in Sabahtritia is similar. Perhaps it allows for flexing of the genital region during egg passage. In both Apotritia and Temburongia the articulation has been lost, resulting in a single genital shield that is respectively broadly triangular or elongated. Mahunka (1990) discovered this fusion in Temburongia but did not discuss its uniqueness among the Oribatida.

This derived mechanism — in which the genital valves no longer open and the ovipositor emerges nearly horizontally (see Fig. 2A) — is correlated with at least two other modifications unique to these four genera. The first is the migration of genital setae away from the middle region of the ancestral genital valves. Ancestrally in euphthiracaroid mites these setae are arranged in a single row along the medial margin of each valve, providing rather evenly dispersed mechanoreceptive capability for the functional edges of the plates (e.g. Grandjean, 1967; his Fig. 3). With the sagittal fusion and loss of valve-like function, the medial plate margins no longer require such capability. We suggest that the genital setae migrated anteriad, near what is the functional edge of the genital region in these taxa, because that is where mechanoreceptive capabilities are most useful. The somewhat dispersed arrangement of the genital setae makes homologies uncertain, but Synichotritia bears either 10 (S. caroli) or 11 (S. spinulosa) pairs of genital + aggenital setae, Sabahtritia has 7³, as does Temburongia patoi; Apotritia walkeri bears eight, one of which has a posterior position on the tectum. Each has a single seta on the anterior edge of the reflected rim; the four or five larger setae in the cluster well posterior of the rim in Synichotritia have been reduced to two in the other genera. Such regression may relate to the reduced mechanoreceptive requirements away from the anterior edge.

The second modification unique to these four taxa relates to the genital papillae; vp is smaller than the anterior two pairs and well removed from them within the progenital chamber. We know of no other oribatid mites in which this is true. If only one of the three genital papillae is reduced in size or lost, it is habitually the anterior, va. This is true both in early derivative groups (e.g. Cienacarus, Aphelacarus and Phthiracaroidea; Grandjean, 1932, 1954) and Brachypylina (e.g. the Oppioidea and Carabodoidea; Behan-Pelletier, 1991; Grandjean, 1960, 1963b). We suggest that normal sized papillae vp would interfere with the near-horizontal extrusion of the ovipositor. Thus they regressed and their position in the progenital chamber altered.

There are several other derived states shared by these four genera that probably are unrelated to the unique genital structure. In members of each genus the palp genu is fused to the femur (in Synichotritia this is true of S. spinulosa but not S. caroli). It appears to be an independent derivation of the same fusion found in Euphthiracaroidea and most Oribotritiidae (see Mørk, 1964; Mahunka, 1990). Two other derived traits are shared by Synichotritia and Apotritia, but their states in Sabahtritia and Temburongia are as yet unknown. First, adoral seta or 1 is forked, which seems common in early derivative oribatid mites but not in the Ptyctima; it may represent a shared ancestral character or a unique reversal. Second, the ovipositor has a highly regressive setation in which coronal setae are absent. Loss of coronal setae is not unique to these genera, but it is rare in Euphthiracaroidea (the ovipositor of Euphthiracarus also lacks these setae, but it emerges normally).

**GENERIC RELATIONSHIPS**

Much remains to be learned about all four genera, and a thorough cladistic analysis is not intended here, but based on available information we view their relationships as illustrated in Fig. 5. Considering other Euphthiracaroidea and the related genera Collohmannia and Perlohmannia as successive outgroups (see Grandjean, 1958, 1966), our concept of the plesiomorphic ventral plate structure of Synichotritiidae is shown schematically on the cladogram stem in Fig. 5. Apomorphic traits exhibited by this ancestor included the following:

3. Five were originally figured (Mahunka, 1987), but this was later corrected (Mahunka, 1990).
Fig. 5: Cladogram expressing hypothesis on relationships of *Apotritia* and three related genera. Numbers indicate apomorphic character states discussed in text. Figures are of anogenital regions, with all but upper four being hypothetical. Lower right figure represents ancestor of Euphotitisaracoida, having paired and separate genital (g), aggenital (ag), anal (an) and adanal (ad) plates.
1) each aggenital plate was fully fused with its respective genital plate; 2) the sagittal connection between paired genital plates near their posterior extremity that exists in most Euphthiracaroidea was advanced far forward 4, effectively joining the paired genito-aggenital plates into a single unit with a sagittal articulation; 3) the genito-aggenital setation (ancestrally probably 9/2) shifted anteriad; 4) the coronal setae of the ovipositor were lost; 5) the posterior pair of genital papillae were regressed and displaced mediad and ventrad; 6) each adanal plate was fully fused with its respective anal plate (but their transverse articulation with the genito-aggenital plates existed); 7) the opisthosomal gland was lost.

Sabahtritia + Synichotritia appear to represent one branch. They share the apomorphy (8) of having lost the transverse articulation between genito-aggenital and ano-adanal plates, resulting in a single pair of compound ventral plates (not counting plicature plates) which are sagittally articulated in the genital region but unattached in the anal region. Apparent apomorphies of Sabahtritia include: 9) a pair of deep cuticular hollows in the genital region (these need more precise characterization but seem at least superficially similar to those in the protoplophoroid enarthronote genus Bursoplophora; 10) monodactyly by the loss of lateral claws; 11) a regressed genito-aggenital setation (7 pairs). Relative to Sabahtritia, we have as yet identified no apomorphies for the genus Synichotritia; the absence of genital hollows, tridactyly, and 10 pairs of genito-aggenital setae are plesiomorphic.

Apotritia + Temburongia, forming a complementary branch, share several apomorphies, including: 12) fusion of the genital plates across the sagittal articulation, forming a single unpaired "genital" shield; 13) loss of the plicature plates; 14) the development of a ventral notogastral tectum protecting the articulation with plates of the anogenital region; 15) loss of the posterior exobothridial seta; 16) loss of seta v from the palpal femur; 17) loss of at least two pairs of genital setae. Apomorphies of Temburongia include: 18) a short triangular genital shield which apparently rotates posteriorly to some degree to expose the progenital chamber; 19) a pair of medial extensions of the notogastral tectum that nearly join, covering the juncture of the genital shield and ano-adanal plate (there is much soft cuticle that otherwise would be exposed to attack by predators); 20) the alignment of all anal and adanal setae on the medial margin of the plate; 21) monodactyly by loss of lateral claws; 22) posterior displacement of rostral setae. Apomorphies of Apotritia include: 23) development of a thin seta-bearing posterior tectum on the genital shield that overhangs the ano-adanal plates; 24) the loss of seta d from femur and genu IV; 25) a forked postpalpal seta; 26) presence of a long terminal fissure on the notogaster.

Two homoplasious characters were identified in this preliminary analysis. First, there seems to have been a parallel regression in genital setation on both sides of the first branch point. Second, and more interesting, is the fact that the only known species to lack fusion between palpal femur and genu (the ancestral euphthiracaroid state) is Synichotritia caroli. This suggests several alternatives: 1) fusion of the femur and genu occurred independently three times, in Temburongia + Apotritia, in Sabahtritia and in Synichotritia spinulosa; 2) a similar scenario, except the fusion evolved twice, with Sabahtritia having evolved from within Synichotritia; 3) the common ancestor of the four genera had a fused femur-genu, with the plesiomorphic state in S. caroli representing a reversal. The third alternative may seem most parsimonious, but such a reversal is not known in other oribatid mites.

**Family-group classification**

Synichotritia, Sabahtritia and Temburongia each comprised monogeneric families when first proposed (Walker, 1965; Mahunka 1987, 1990). The top-heavy classification results from stressing differences in genital setation.
rences in ventral plate structure, and a comparable approach to *Apotritia* would require the proposal of yet another monobasic family. Instead, we stress the similarities noted above, and suggest that all four taxa forming this monophyletic group be included in the Synichotritiidae. The novel basic genital structure in the common ancestor of this family — in which the progenital chamber opens anteriad of the genital plates rather than between them — set the stage for some striking modifications, but a top-heavy classification with redundant family-group taxa will mask this.

Since appropriate family-group names are already available, we propose recognizing two subfamilies of Synichotritiidae. Synichotritiinae would include *Synichotritia* and *Sabahtritia*; Temburongiinae would include *Temburongia* and *Apotritia*. Mahunka (1990) recently lowered Sabahtritidae to subfamilial rank within Synichotritiidae, but we do not recognize the former family-group taxon as it is redundant in our classification. Suggested preliminary diagnoses are as follows.

**Synichotritiidae Walker, 1965**: Euphthiracaroidea with genital plates connected in sagittal plane, either fused without trace or connected by narrow longitudinal band of articulating cuticle. Genital setae not arranged in medial row; all or most dispersed in anterior genital region. Progenital chamber opening in soft cuticle between genital plates and coxisternum IV. Ovipositor lacking coronal setae. Posterior genital papillae highly regressed, adjacent sagittally and ventrally in progenital chamber. Opisthosomal gland absent. Complete fusion between anal and adanal plates. Aspis with single pair of lateral carinae; bothridial scale posterodorsal to bothridium; no elongate brachythraceae or other tubular structures descending from bothridium; sagittal apodeme well developed. Palp genu free or fused to femur (palp with 5 or 4 free segments). Legs heterotridactylous or monodactylous; genu IV without solenidion; trochanter III and IV with two setae. Eggs without noticeable chorion; prelarvae not developed before parity. Body cuticle mineralized.

**Synichotritiinae Walker, 1965**: Synichotritiidae with ano-adanal plates fused to genito-agenital plates without trace of suture; genital plates articulated sagittally. Plicature plates well developed. Three pairs of anal setae, three pairs of adanal setae. Notogastral margin without tectum; terminal fissure absent; with 15 or 14 pairs of setae (*p, present or absent*). Aspis with two pairs of exobothridial setae; bothridium with short, hollow finger-like lobes ("logettes" of Grandjean, 1967) at its base.

**Temburongiinae Mahunka, 1990**: Synichotritiidae with ano-adanal plates fully articulated with genital shield by soft cuticle; sagittal articulation of genital plates lost, forming an unpaired genital shield without trace of suture. Plicature plates absent; a broad band of soft cuticle connects notogaster with ventral sclerites. Ventral margins of notogaster with a broad tectum; terminal fissure present; with 14 pairs of notogastral setae (*p, absent*). Aspis with one pair of exobothridial setae (posterior seta lost); bothridium without lobes.

**Remarks**

1. **Relationships of Synichotritiidae with other Euphthiracaroidea.** Cladistic relationships of Synichotritiidae (our sense) with Euphthiracaridae and Oribotritiidae have not yet been addressed. Mahunka (1990) conducted a standard phenetic "distance" analysis of Euphthiracaroidea, with and without character-weighting schemes, in which three phenograms (mistakenly called cladograms) were presented. His favored weighted version (his Fig. 5) reflected the standard familial groupings of genera, and both weighted versions showed phenetic relationships among *Synichotritia, Sabahtritia,* and *Temburongia,* that are identical to the cladistic ones expressed in our Fig. 5. The Synichotritiidae

5. Though the analysis was phenetic, Mahunka (1990, p. 43) did present a list of euphthiracaroid traits with suggested plesiomorphic (ancestral) and apomorphic (derived) states. However, his method of determining this polarity was not discussed. Also, many of the legend symbols ("+" for apomorphy, "o" for plesiomorphy) seem to be reversed, since all "normal" states (e.g. 2 pairs of exobothridial setae, 5 pairs of lyrifissures, 5 segmented palps) are marked with "+" whereas their modified states are marked with "o".
clustered with Euphthiracaridae in the favored version. In the other two, not all oribotritid genera clustered together, but Synichotritiidae clustered with a portion of them.

In the cladistic sense, both Synichotritiidae and Euphthiracaridae (sensu stricto) seem to be monophyletic taxa. Synapomorphies of the former family have been described above. The Euphthiracaridae is well defined by at least two synapomorphies: 1) the anterior “interlocking triangle” formed from thickened, coaptive bases of the preanal apodeme; and 2) the presence of a cluster of bothridial “tracheoles” (Markel, 1964; Grandjean, 1967).

In contrast, Oribotritiidae is probably paraphyletic. The family was proposed by Grandjean (1954), who included within it a group of genera removed from the earlier broad concept of Euphthiracaridae. Grandjean (1967) considered Oribotritiidae to be the least specialized of the three families, and in fact none of the diagnostic character states shared by all members can be considered derived. One of these states, the laying of a sculptured prelarva, is not universal. In Maerkelotritia (not studied by Grandjean), the stage of offspring development at parity (“birth”) varies according to species, but it is either egg or larva (Norton, 1992); no species of Maerkelotritia known to us lays sculptured prelarvae. Though cladistic terminology was not used, Markel (1964) appears to have criticized Grandjean’s (1954) proposal of removing Oribotritiidae from the earlier broad concept of Euphthiracaridae for similar reasons.

While Oribotritiidae may be paraphyletic with respect to Euphthiracaridae (sensu stricto), there is at least one reason to believe that the two families together comprise a monophyletic group that is the sister-group of Synichotritiidae. Euphthiracaridae and Oribotritiidae all possess a paired manubrium, a posterovertal apodetic process extending internally from the exobothridial field of the aspis; it serves for the attachment of prodorsal muscles, including lateral adjustor muscles, dorsal endosternal muscles, and one set of dorsoventral muscles (Sanders, 1982). The manubrium is unique (apomorphic) to Euphthiracaridae and Oribotritiidae, being absent (plesiomorphic) in Synichotritiidae and Phthiracaroidea. Thus the similar fusions of ventral plates in Euphthiracaridae (sensu stricto) and Synichotritiidae result from evolutionary convergence.

2. Polarity of the double coupling on genu I.

As noted above, Van der Hammen (1963 and other papers; see also Parry, 1979) considered seta $d$ to be lost from genu I of Phthiracaridae, and regarded the seta coupled with the large adaxial solenidion ($a'$) to be $l'$ (rather than $d$), even though the coupled structures have a near-dorsal position. He labeled $a''$ and $e'$ with an ontogenetic notation ($e_1$, $e_2$, respectively) but this was not based on their ontogenetic appearance, which is unknown. Probably they are both larval, as is true of most oribatid mites whose adults possess two solenidia on genu I. The only known exception is Epilohmanniidae (Grandjean, 1964; Norton et al., 1978).

If this is accepted, there are two alternative explanations that would seem reasonable based on patterns observed in other taxa, and each suggests a different polarity of the double coupling. The most obvious interpretation, cited above, is that seta $d$ has been fully regressed in Phthiracaridae as a result of coupling with the abaxial solenidion $a''$ (see Grandjean, 1946). In such a case, the phthiracarid state can be considered to have been derived from a plesiomorphic double coupling.

However, seta $d$ of genu I has regressed in some oribatid mites without coupling with a solenidion; for example, it is vestigial in the larva of both Eulohmannia and Nehyphochthonius without being coupled to a solenidion in any instar. The phthiracarid state may have evolved directly from such a pattern by neoteny, rather than deriving from a double coupling. This would be consistent with the non-flagellate nature of $a''$ in Phthiracaridae, since the total loss of seta $d$ from an ancestrally coupled structure is usually associated with the enlargement

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6. Norton and Metz (1980) stated that one such solenidion is developmental in Nehyphochthonius but this was an error; both $e'$ and $a''$ are present in the larva, with $e'$ already coupled to $l$. It is seta $d$ that is developmental in the latter genus; it is vestigial in the larva but fully formed, and distant from any solenidion, beginning with the protonymph.
of the solenidion to flagellate form (Grandjean, 1946; Norton, 1982). From this viewpoint the double coupling in Euphthiracaroidea could be considered an autapomorphy. A careful cladistic analysis of the relationships between the two ptychoeid taxa should illuminate this problem.

3. Preanal and postanal apodemes. The preanal region could not be studied satisfactorily in the available specimens of Apotritia walkeri, since we tried to keep the parts of the two available specimens as intact as possible. In Synichotritia the preanal apodeme has the form of a double-walled lamella in the sagittal plane. It is essentially a sclerotized region of the cuticle of the anogenital vestibule, running dorsad from the medial edge of each anal plate. In lateral aspect it is triangular, with its base extending over approximately the middle fifth to third of the combined length of the ventral plates. Walker (1965, p. 40) made special mention of it in his familial diagnosis of Synichotritiidae ("median internal, lamellate structure") but its presence is the rule in Euphthiracaroidea. As described by Sanders (1982), this apodeme serves as the origin of anogenital adductor and compressor muscles in Euphthiracarus. A similar (but smaller) lamelliform apodeme is present in the postanal region of Euphthiracaroidea; the posterior vertical muscles attaching here assist in closure of the ano-adanal valves. It is the ventral bases of these two apodemes that form the interdigitating zones of coaption between plates ("interconnecting triangles" see Mäkel and Meyer, 1959) found in Euphthiracaridae (sensu stricto). In Apotritia a normal postanal apodeme seems to be present, and the vertical ridges mentioned in the description seem to represent a weakly developed zone of coaptation. However, we could not determine the nature of the preanal apodeme; any modifications associated with the evolution of the unpaired shield remain unknown.

4. Geographic distribution of Synichotritiidae. — The known distribution of Synichotritiidae seems incongruent with the relationships proposed herein; one of the two genera in each subfamily is recorded from the temperate coniferous forests of California, the other from forests of the tropical island of Borneo (Kalimantan)7. This pattern is probably relictual, however, and each subfamily probably had a broad historical distribution, as suggested by the following new records (specimens in the collection of R.A.N.).


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7. Mahunka (1990) did not present locality data in the description of Temburongia patoi, but they appear in a subsequent paper (Mahunka, 1991); it is from Brunei.
LITERATURE CITED


