Acaronemini n. tribe and *Praeacaronemus rackae* n. sp., n. gen., proposed for mites from the family Tarsonemidae (Acari: Heterostigmae)

MAREK KALISZEWSKI and WOJCIECH MAGOWSKI
(With 7 figures)

Abstract

Acaronemini, a new tribe of Tarsonemidae is diagnosed. *Praeacaronemus*, a new genus is described, and its type species *Praeacaronemus rackae* is described and figured. Taxonomic and phylogenetic position of the new taxa are discussed and estimated.

Acaronemini n. tribe


Diagnosis: Adult mite of this tribe differ from others in having subunguinal seta s rather setiform than spine-like; tarsus I and tibia I not fused or retaining discernible sutures, femur I with less than 4 setae, presence of unguinal setae u, u" flanking pretarsus I and u" pretarsus II and III partly; claws barely developed. Sejugal apodeme not developed or initially formed, poststernal apodeme not developed. Tegula broadly rounded, not tongue-shaped; all idiosomal setae smooth, slender.

Gnathosoma roundish-triangular, slightly elongated, beak-like. Cheliceral styles moderately long; postpalpal pair of setae absent.

At the present time the new tribe contains two genera: *Acaronemus* LINDQUIST & SMILEY and *Praeacaronemus* n. gen.

Praeacaronemus n. gen.

Type species: *Praeacaronemus rackae* n. sp.

Diagnosis: Adult female of this genus is distinguish from other tarsonemid mite in having subunguinal seta s setiform and in having unguinal setae u" (on tarsi I, II and III) and u' (on tarsus I). Leg I lacks pl" tarsal seta, and t; the smallest solenidion of tibial I sensory cluster. Femur I with only 3 setae, (d absent); femur II with only two setae, (d absent). Tarsus II with 5 setae (excluding the u" and s); tarsus III with 4 setae (excluding the u" and s setae). Tarsus and tibia of leg I not fused, (female) with conspicuous suture in dorsoventral view.

Gnathosomal capsule subtriangular, slightly beak-like with moderately distinct and large palpi. Sejugal apodeme completely undeveloped. Presternal apodeme well distinguished.
Scapular sc₂ setae little longer than distance between their insertions. Apodemes I and II normally developed, apodemes III and IV weakly developed.

**Praeacaronemus rackae** n. sp.

*Female:* (all measurements in μm)

**Gnathosoma** (Fig. 1, 2): Gnathosomal capsule nearly as long as wide (length 30, width 27.3), with arch-like base (in dorsal view), slightly elongate, roundish subtriangular shape. Dorsomedian apodeme well developed, conspicuous, extending from base to anterior end of gnathosomal capsule. Palpi distinct, moderately large, straight, slightly convergent anteriorly, each distally with 2 minute setae and three inconspicuous processes. Cheliceral stylets distinct, straight, relatively large, but their basal levers rather small, oval, oriented obliquely, nearly longitudinally (in dorsal plane). Pharyngal pump rather large (length 13, internal part 5,2), with well-sclerotized lateral walls (6,5 wide); at its posterior extremity a pair of small adjacent, oval gland-like structures. Ventral gnathosomal setae smooth and slender; dorsal pair of gnathosomal setae also smooth, but somewhat stouter, less than twice as long as ventral ones. Postpalpal pair of gnathosomal setae absent.

**Idiosoma** (Fig. 1, 2): Elongate ellipsoidal shape, rounded posteriorly (192.4 long and 119.6 wide). Prodorsal shield subtriangular, with rounded lateral extensions, less than 1.5 times as wide posteriorly as long medially; anteriorly terminated by distinct, broadly rounded, subcircular peak over base of gnathosoma; conspicuously divided from the rest of shield. A pair of vertical setae (each 19.5 long) inserted 22.1 apart.

Stigmata inserted in angle of outline of prodorsal shield, connected with tracheal trunks, forked posteriorly, ending medially at half of length of prodorsal shield. Near stigmata small, sac-like extensions. Scapular pits located about two-thirds between scapular and vertical setae, aligned longitudinally obliquely with insertions of latter. Bothridia near scapular pits but located more medially; sensilli (about 14.3 long) rounded and capitate, pilose, covered by fringe of prodorsal shield. Scapular setae (40) nearly as long as distance between them (41.6), and a little more than twice as long as vertical setae. Distance between bases of vertical and scapular setae on each side 26. Length of setae c₁ 14.3, c₂ 26; distance between c₁ (48.1) a little greater than between sc₂, and more than half of distance between c₂, which is 88.4. Distance between bases of c₂ and c₁ 28.6 (on each side). Two pairs of setae on tergite EF aligned transversely: f 15.6 long and e 16.9; length of setae d on tergite D 16.9. Distance between setae f (22.1) about a third of that between e (65) and less than between d on tergite D (32.5). Setae h of tergite H 16.9, located 37.7 apart.
Figs. 1, 2: Praeacaronemus rackae n. sp., female. - Dorsal side (1), ventral side (2).
All setae of dorsal side smooth, slender. Dorsal shielding not granulated.

Propodosomal plate medially 50.7 long and posteriorly 107.9 wide. Apodeme I distinct, 15.6 apart between lateral ends and connected with conspicuous prosternal (anteromedial) apodeme; this well developed, extended out of apodemes II, and forked near their medial ends. Coxal setae 1a about two-thirds as long as 2a, located a little posteriorly to middle of apodemes I. Setae 2a located nearly on apodemes II. Sejugal apodeme completely undeveloped. Coxal setae 3b slender, 3a a little stouter and longer than 3b. Tegular flap broadly rounded with somewhat undulating edge near trochanters IV, about three times as wide (16.9) as long (5.2). Metapodosomal apodemes weakly developed, poststernal (posteromedial) apodeme absent. Aggenital plate widely rounded, with sharp posterior end. Pseudanal plate trapeziform with ps setae as long (16.9) as distance between them.

Pharynx connected with long sclerotized pipe reaching mid-level between medial ends of apodemes III and IV, ending at funnel-shaped extension, and easily seen in ventral view medially.

Legs (Figs. 3, 4, 5, 6): Pretarsus of leg I without em- podium, with discernible though not strong claw. Tibia and tarsus of leg I distinct, separated by well retained and clear suture. Pretarsus I flanked by two unguinal setae u', u" and subunguinal seta s setiform, inserted apically. Three eupathidia located apically on tarsus I: p', p" and tc' sub-equal in length; eupathid tc" inserted lower, about 1.3 times longer than others; tarsal seta pl" absent. Tarsal solenidion ω (4) larger than tibial φ1. Tarsus I (excluding pretarsus) about 1.2 times as long as tibia, other segments of leg I of normal proportions. Tibial sensory cluster lacking smallest φ, solenidion; clavate φ1 (2.4 long) and rod-like eupathid k (4 long) present. Femur I with three setae (d absent). Length of leg I, excluding trochanter, 55.9. Total length of tibia and genu of leg II equal to length of tarsus II (including pretarsus). Of the two unguinal setae on leg II, u' reduced; subunguinal seta s setiform. Tarsal solenidion strong, relatively large, clavate (4 long). Tarsus II with 6 (excluding remaining u"), and femur II with 2 setae (d absent). Seta 1' of femur II and genu II stout but shorter than others, and pilose. Leg II (excluding trochanter) 49.4 long. Segments of leg III nearly equal in length (tibia a little shorter than tarsus and femurogenu). Trochanter of leg III sub-elliptical, nearly as long as combined length of femurogenu and tibia III. Tarsus of leg III with 5 setae (excluding u"), full length of leg III 5.5. Pretarsi of leg II and III with paired, not well developed claws and membranous pulvilli. Femurogenu IV (24.7 long) with femoral seta (13.6) and genual seta somewhat longer (16.9); femoral seta slender, genual much stouter. Tibiotarsus IV (11.7 long) with thick tibial seta v', stout (26 long), about 1.2 times as long as femurogenu IV, and twice as long as tibiotarsus IV. Apical seta atten-
u rate and smooth, 67.6 long, i.e. nearly twice as long as leg IV (36.4).

Chaetotaxy and solenidiotaxy respectively for femur, genu, tibia, and tarsus as follows: (number of solenidia excluded from number of segmental setae given in parenthesis)

- leg I: 3 - 4 - 6 (1φ) - 7 (1ω);
- leg II: 2 - 3 - 4 - 5 (1ω);
- leg III: 1 + 3 - 4 - 5. Counts do not include unguinal setae u' and u", because of their indiscernibility (and for other reasons explained later). Except for setae l' on femur II and l' on genu II, all legs setae smooth and slender.

Males and larvae unknown.

Figs. 3-6: Praeacaronemus rackae n. sp., female. - Leg I (3), leg II (4), leg III (5) and leg IV (6).
Etymology

Respecting the priority of LINDQUIST & SMILEY (1978) in the description of the first taxon of the new Tarsonemidae branch, the authors consider that the proposed new tribe should be nominated as Acaronemini. Features such as the number of setae on femur I, tarsus II, III; the structure of oral appendages, pharynx and others, indicated that the new genus is very closely related to the direct ancestor of Acaronemus LINDQUIST & SMILEY. This conclusion provided the reason for naming the new genus Praeacaronemus, i.e. to present a precedence relationship to Acaronemus.

The authors decided to name the new species "rackae" in order to emphasis the merits of Dr. G. RACK, through whose kindness the description of the new taxa was possible.

Material and methods

The holotype of Praeacaronemus rackae n. sp. was collected on August 11th, 1965 from a beech stump in Hamburg by G. RESPONDEK. The mite was mounted in Hoyer's medium (slide N° A 12/65) and deposited in the Zoological Museum, University Hamburg, West Germany.

The nomenclature, terms and notation applied to the idiosomal and leg chaetotaxy and solenidiotaxy are based on LINDQUIST & SMILEY (1978) and LIDQUIST (1978). Only the female is known.

Discussion

At the present very little is known about the biology of the above described new species. Using only available circumstances, the indirect conclusion is that Praeacaronemus rackae is a fungivorous mite. The chelicerae of Praeacaronemus are surprisingly small and therefore probably incapable of piercing the thick egg chorion of others mite or insects. This is cotrary to the case for mites of the genus Acaronemus (LINDQUIST & SMILEY, 1978). Moreover, especially the other primitive characters of the morphology make it possible to attribute fungivorous feeding, especially also the fact that this appears also to be one of the most primitive way of feeding in Tarsonemidae (KRANTZ & LINDQUIST 1979).

The phylogenetic position of the new genus is very interesting. Apart from a number of features (such as the shape and structure of the gnathosoma, the body proportion, tegula shape, similar development of the apodemes, presence of unguinal u', u" setae and subunguinal seta s setiform, retention of tibio-tarsal suture on leg I and similar reductions of setae on tarsus I, tibia I, femur I and femur II) which place the genus close to Acaronemus, it also possesses numerous features which distinguish it from Acaronemus. These are the lack of sejugal apodeme, small cheliceral levers, a greater number of setae retained on the leg segments and particulary the existence of four unspecialized setae each on tarsus II and III.

Nevertheless the new genus appears to be most closely related to Acaronemus, with both probably related close to the Tarsonemus waitei group. This group is itself relatively primitive, with however some evidences of specialization. A relationship to any other group of Tarsonemidae should be considered cautiously (detailed discussion of this problem is in preparation W. MAGOWSKI, PhD thesis).
The examination of the *T. waitei* group and the taxa under consideration, has made the attempt to reconstruct the phylogenesis of the Acaronemini possible. Among variants of cladograms considered, the most probable accepted was that shown in Fig. 7. In order to present this schematic diagram of relationships as faithfully as possible, it was necessary to show the *T. waitei* group as a unit consisting of three evolutionary lines.

Some problems exist in relation to the evaluation of usefulness of such features as the presence or absence of unguinal setae \( u' \) and \( u'' \). The omission of these in SUSKI's drawings and in the descriptions of *T. lobosus*, *T. pauperosetus* and *T. idaeus* (SUSKI 1965, 1967, 1968) and the consideration of them out of the basis of general leg chaetotaxy by LINDQUIST (1978), indicate caution. Nevertheless in this work, full homology between apical setae arrangement on tarsi I, II, III of Praeacaronemus with that of Acaronemus is accepted, but without the certainty that this is in fact so. Analysis and counts of characters allow the claim that Acaronemus and Praeacaronemus (particularity the last) exhibit features which are remnants of an unknown, very primitive ancestral group of Tarsonemidae from which have been derived probably most groups of this family (*Tarsonemus* CANESTRINI & PANZAGO, 1876, *Iponemus* BEER & NUCIFORA, 1965, *Steneotarsonemus* BEER, 1954, *Xenotarsonemus* BEER, 1954, *Heterotarsonemus* SMILEY, 1969, *Suctarsonemus* MAHUNKA, 1974, *Neotarsonemoides* KALISZEWSKI, 1984, *Daidalotarsonemus* DE LEON, 1956, *Fungitarsonemus* CROMROY, 1958). In our opinion this sufficiently justifies the grouping of Praeacaronemus n. gen. and Acaronemus LINDQUIST & SMILEY, 1978 into a taxon of tribal rank.

Appendix

Proposed opinions on the value of characters (plesiomorphic-apomorphic) are discussed here for gnathosoma, idiosoma and legs.

1. Shape of gnathosoma

Morphological properties of gnathosoma undergo selection pressure connected with recognition, obtaining and taking of food. Basal width, internal musculature of the pharynx, size, form and location of appendages appear to determine the shape and sclerotization of the gnathosoma. From the features mentioned above, the easiest to observe is the location and direction of the palpi. Roundish or ellipsoidally shaped gnathosoma are considered to be the plesiomorphic character here. This is connected with a moderately broad arrangement of the palp bases and their convergent direction. It means that probably the most primitive type of gnathosoma (mentioned above) may have evolved in various directions, with the most common transition to an outline similar to a isosceles triangle, in which palps are placed close one to another at the top and directed almost parallel. Such a type of gnathosoma is considered here an apomorphic character, and is represented in both the Acaronemini, new tribe, and a number of species of the genus *Tarsonemus* sensu CANESTRINI & PANZAGO. In that case the gnathosoma of *Steneotarsonemus*, round in shape, with palpi placed opposite one another and
with their ends directed perpendicularly to the long body axis, would constitute the opposite direction of that divergence. The biology and anatomy of the Tarsonemidae is too little known to draw far reaching conclusions concerning the correlation between feeding preferences and the shape and structure of the gnathosoma.

2. Postpalpal pair of setae

Fully developed in species of the Tarsonemus waitei group, they undergo complete reduction among the Acaronemini.

3. Cheliceral levers

The chelicerae against the background of the gnathosoma, are often invisible. Their levers are then a good diagnostic character. These latter structures are responsible for the power with which the cheliceral stylets pierce cell membrane or egg chorion to reach the nourishment lying behind them.

The transition from a fungivorous way of feeding - here considered the more primitive way - to parasiting the eggs of mites, manifests itself by increasing the cheliceral levers; this motivates the accepted character state polarity.

4. Palpi

Here the longer ones are considered as plesiomorphic, the shorter ones, as apomorphic character. Generally palpi should be considered like others appendages of the body, and therefore shortening should be treated as a common trend. The palpal length surely depends also on the way of feeding. However this relationship is unknown so far.

5. Rostral shield

A wide rostral shield is considered here as the initial form. The tendency to become narrow occurs independently in several evolutionary lines, e. g. in some genera of the Tarsonemidae, in particular Steneotarsonemus.

6. Prodorsal apodeme

It can be assumed that the existence of a prodorsal apodeme is a plesiomorphic character, in contrast to other apodemes which must be considered as apomorphic character acquired later by the Tarsonemidae.

It is highly likely that the prodorsal apodeme is one of a few remnants of a primary body division (KALISZEWSKI in press). The transverse part of this apodeme may mark the boundary between tergites of the cheliceral and palpal segments. In this context, the prodorsal shield consists of three primary tergites:

- a palpal one, without setae, posterior to the prodorsal apodeme,
- a cheliceral one, with a pair of simple setae, a pair of sensili and a pair of scapular pits, and
- a rostral shield (naso) which is the remnant of a precheliceral segment, or segments with one pair of setae.
In such a case, podosomal tergites have undergone full reduction (GRANDJEAN 1969, COINEAU 1971, KALISZEWSKI in press). These relations make it possible to compare or even to discretely establish homologies with similar structures which have been recorded in primitive families of Endeostigmata, i.e. the Micropsammidae COINEAU & THERON, 1983, Sphaerolichidae GRANDJEAN (THERON & RYKE 1975) and Alicorhagidae GRANDJEAN (THERON, MEYER & RYKE 1970). The primitive relationships are especially shown in Micropsammus litoralis THERON & COINEAU, 1983, where even the arrangement of sculpture of the integument is in part similar to the shape of the prodorsal apodeme. The prodorsal apodeme is best developed among members of the relatively primitive Tarsonemis waitei group and is often retained in the form of a short line, parallel to the long axis of the body, as in various advanced species of Tarsonemus, or a weak, weaveform vortex or thickness, as in some of the Pygmephoridae.

It is possible that all apodemes on the ventral and dorsal side are an evolutionary, secondary feature among Tarsonemidae, together with the increase of general body sclerotization in places where primary body segment boundaries in ancestral forms occurred. This view is consistent with the dependence which units apodeme development with general body sclerotization: i.e. the more sclerotized body, the greater mass and smaller mobility. To cope with these difficulties, muscle groups, responsible for a few or only particular parts of the body, increase in size and thus bring with them a thickening of apodemes which provide their attachment. In such a case, the existence of a prodorsal apodeme can be explained by the same mechanism as was applied to explain the increase of apodemes on the ventral side (see points 9-14). Nevertheless the case given here is considered more possible, due to the fact that prodorsal apodeme often occurs in early derived groups of Heterostigmata sensu LINDQUIST (KALISZEWSKI in press). However, it cannot be excluded, that the prodorsal apodeme may be the attachment for an unknown group of muscle, its degree of expression, depending on the degree of development of the muscle.

7, 8. Idiosomal setae
The simple, smooth, slender and tapered setae are assumed here to be the most original form. Every deviation from this form, i.e. thickening, pilosity, shortening, or projection as spikes, can be assumed to be a modification and expression of advancement.

9-13. Presternal, sejugal and poststernal apodemes
Contrary to earlier authors (SCHAARSCHMIDT 1959, BEER 1954, LINDQUIST 1978) the existence of these apodemes, as against their absence (points 8, 9, 12) and their relatively good as against a weak development (8, 9, 11), is here considered as an apomorphy. The polarity that more primitive forms (close to Endeostigmata) of Tarsonemidae were weakly sclerotized, with soft, baglike body covering, has been accepted. With the increase of sclerotization in
the evolutionary process (thickening of covering), the secondary body segmentation in Tarsonemidae originated. This secondary body division occurs on the dorsal side as the prodorsal shield (see 6) and a series of tergites; on the ventral side, solid plates have originated from the adhesion of legs coxae. The greater solidity of the podosomal parts (coxae) and the greater sclerotization can cause a greater conspicuousness of the boundaries (apodemes) between them.

Simultaneously, the tendency to enhance primary sternite remnants, which are recognized as the breast platelet, i.e. the area between apodemes II and the presternal apodeme, part limited by anterial edge of metapodosomal plate and bifurcation of anterial extremity of the poststernal apodeme can be observed.

14. Tegula

The extension of the tegula in comparison with the segment joining trochanters IV, is assumed to be an apomorphic character, according to this character state in different high advanced Tarsonemidae (e.g. Xenotarsonemus BEER or Neotarsonemoides KALISZEWSKI). Correlation between degree of extension and shape of the tegular lobe with secondary body segmentation and sclerotization should be evaluated very carefully, because tegula may participate in reproductive actions of tarsonemid (e.g. ovipositing).

15, 16. Tibiotarsal suture of leg I

Full or partial retention of the tibiotarsal suture of leg I testifies to the high degree of primitiveness and uniqueness of the Acaronemini females among other tarsonemid females, if this feature is considered. The polarity accepted of this feature is discussed in KALISZEWSKI (in prep.).

17. Claws

The weakness of claws of all legs in Acaronemini as opposed to their good development among Tarsonemidae as observed, can be considered as an apomorphy.

18, 23. Form of setae on leg segments

The opinion assumed here is the same as in point 7. The simple, slender and tapered form of the subunguinal setae of tarsi I-III among Acaronemini, unique among Tarsonemidae, confirms the great primitiveness of this group.

19-22, 24-26. Number of setae on leg segments

Reduction of setae on different leg segments is a character which is to interpret as a apomorphy, whereas a greater number of them as a plesiomorphy. Due to the fact that setae on particular leg segments are reduced in different ways in various evolutionary lines and due to the difficulties in observing correlations between particular reductions of setae on legs or leg segments, the great plasticity of these features and tractibility to the selection pressures of habitat may be inferred.
Explanations for marks used in cladogram of considered taxa shown in fig. 7

<table>
<thead>
<tr>
<th>Plesiomorphic characters</th>
<th>Apomorphic characters</th>
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<tbody>
<tr>
<td><strong>Gnathosoma</strong></td>
<td></td>
</tr>
<tr>
<td>1. Gnathosoma ellipsoidal shape</td>
<td>Gnathosoma subtriangular shape</td>
</tr>
<tr>
<td>2. Postpalpal setae present</td>
<td>Postpalpal setae absent</td>
</tr>
<tr>
<td>3. Cheliceral levers smaller</td>
<td>Cheliceral levers larger</td>
</tr>
<tr>
<td>4. Palpi longer</td>
<td>Palpi shorter</td>
</tr>
<tr>
<td><strong>Idiosoma</strong></td>
<td></td>
</tr>
<tr>
<td>5. Rostral shield (naso) broad</td>
<td>Rostral shield narrow</td>
</tr>
<tr>
<td>6. Prodorsal apodeme present</td>
<td>Prodorsal apodeme absent</td>
</tr>
<tr>
<td>7. Idiosomal setae smooth</td>
<td>Idiosomal setae differentiated</td>
</tr>
<tr>
<td>8. Idiosomal setae d, e slender tapered</td>
<td>Idiosomal setae d, e modified not tapered</td>
</tr>
<tr>
<td>9. Sejugal apodeme poorly developed or absent</td>
<td>Sejugal apodeme well developed</td>
</tr>
<tr>
<td>10. Sejugal apodeme discontinuous</td>
<td>Sejugal apodeme continuous</td>
</tr>
<tr>
<td>11. Sejugal apodeme absent</td>
<td>Sejugal apodeme present</td>
</tr>
<tr>
<td>12. Presternal apodeme does not extend out of apodemes II</td>
<td>Presternal apodeme extends out of apodemes II</td>
</tr>
<tr>
<td>13. Poststernal apodeme poorly development or absent</td>
<td>Poststernal apodeme well developed</td>
</tr>
<tr>
<td>14. Tegular flap shorter</td>
<td>Tegular flap longer</td>
</tr>
<tr>
<td><strong>Legs</strong></td>
<td></td>
</tr>
<tr>
<td>15. Tibiotarsal suture of leg I retained</td>
<td>Tibiotarsal suture of leg I reduced fully</td>
</tr>
<tr>
<td>16. Tibiotarsal suture of leg I fully retained</td>
<td>Tibiotarsal suture of leg I reduced ventrally</td>
</tr>
<tr>
<td>17. Claws on legs I-III unspecialized</td>
<td>Claws on legs I-III weak</td>
</tr>
<tr>
<td>18. Seta s on tarsus I setiform</td>
<td>Seta s on tarsus I spinelike</td>
</tr>
<tr>
<td>19. Tarsal seta pl&quot; on leg I present</td>
<td>Tarsal seta pl&quot; on leg I absent</td>
</tr>
<tr>
<td>20. Tarsus II with 4 normal setae</td>
<td>Tarsus II with 3 normal setae</td>
</tr>
<tr>
<td>21. Tarsus III with 4 normal setae</td>
<td>Tarsus III with 3 normal setae</td>
</tr>
<tr>
<td>22. Solenidion ψ2 on tibia I present</td>
<td>Solenidion ψ2 on tibia I absent</td>
</tr>
<tr>
<td>23. Setae d on genu II and femur II smooth</td>
<td>Setae d on genu II and femur II pilose</td>
</tr>
<tr>
<td>24. Femur I with 4 setae</td>
<td>Femur I with 3 or 2 setae</td>
</tr>
<tr>
<td>25. Femur I with 3 setae</td>
<td>Femur I with 2 setae</td>
</tr>
<tr>
<td>26. Femur II with 3 setae</td>
<td>Femur II with 2 setae</td>
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</table>
Fig. 7: A cladogram of relationships among Praeacaronemus n. gen., Acaronemus LINDQUIST & SMILEY, 1978 and species from Tarsonemus waitei group (T. setifer sensu KARL, 1965; T. ideus SUSKI, 1968; T. waitei BANKS, 1912; T. lobosus SUSKI, 1965; T. bakeri EWING, 1939). Plesiomorphic character state marked as a light square. Apomorphic character state marked as a dark square.
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