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Title

Molecular phylogeny reveals genital convergences and reversals in the barklouse genus *Trichadenotecnum* (Insecta: Psocodea: 'Psocoptera': Psocidae)

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ABSTRACT

Trichadenotecnum is one of the most diverse genera among the non-parasitic members of Psocodea (Insecta: "Psocoptera"). The genus shows a world-wide distribution (excluding the Australian Region, where only one introduced species is known) with its center of diversity in southern to eastern Asia. Several species groups had been proposed for this large genus based on morphology, but their validity and phylogenetic relationships are still unclear because of great morphological diversity in the genitalia, systematically the most relevant character. In this study, we estimated the molecular phylogeny of the Old World species of *Trichadenotecnum* based on extensive taxon sampling. As a result, the monophyly of morphology-based species groups was very strongly supported in most cases. However, two groups were recovered as non-monophyletic, which had been inadequately defined on the basis of plesiomorphies or convergences of genital characters. First, the monophyly of the *sexpunctatum* group was not supported because the *medium* group was found to be embedded within this group. The simpler genitalia observed in the *medium* group were considered to be derived from the more complicated genitalia present in the *sexpunctatum* group. Second, the monophyly of the *majus* group was not supported for two reasons: (1) It was divided into two distant clades which initially had been united on the basis of convergent similarities of the male genitalia. (2) Two species groups were revealed to be embedded within the main clade of the *majus* group; the initial separation of these groups had been based on reversals to the ancestral genital condition.

Key words: Morphology, Parsimonious reconstruction, Homoplasy, Taxonomy, Old World species, Species groups

Main text

1. Introduction

The barklouse genus *Trichadenotecnum* Enderlein, 1909 is one of the largest genera among the free-living members of the order Psocodea (formerly "Psocoptera"; Yoshizawa & Johnson, 2006). The genus consists of more than 200 species distributed in all zoogeographical regions (summarized in Lienhard & Smithers, 2002; Lienhard, 2011, 2015; Yoshizawa & Lienhard, 2015) except for the Australian Region, where only one introduced species is known (Yoshizawa & Smithers, 2006). Several additional species have been distinguished but are not yet described; some of them are included in the present analyses (see Table 1).

The species of *Trichadenotecnum* are superficially very similar to each other; without examining the genital characters, species identification is difficult even between rather distantly related species. Nevertheless, the species of *Trichadenotecnum* and even the genus itself were once diagnosed only by superficial similarities in forewing markings and venation, which caused much taxonomic confusion (e.g., Roesler, 1943, 1944; Thornton, 1961; New, 1978; Yoshizawa, 1998; Yoshizawa & Smithers, 2006). Recently, the genus was redefined by a combination of apomorphies including male and female genital characters (Yoshizawa, 2001, 2003). Several species groups have been proposed within the genus based mainly on male and female genital structures (Yoshizawa, 2001, 2003; Yoshizawa & Lienhard, 2004, 2015; Yoshizawa et al., 2007, 2008, 2014).

Genitalia are the most widely used morphological characters in insect systematics, from species diagnoses (e.g., Tuxen, 1970) to lower- or higher-level phylogenetic studies (e.g., Yoshizawa & Johnson, 2006; Song & Bucheli, 2010). In contrast, it is sometimes argued that the genitalia may not contain useful phylogenetic information because of the extremely rapid evolutionary rates of the genital structures (Arnqvist & Rowe, 2002; Eberhard, 2004). In the case of *Trichadenotecnum*, some species groups defined by genital structures were tentatively supported by molecular phylogenies (Yoshizawa, 2004). However, taxon sampling for these analyses was very limited. Recent progress in the taxonomic study of the Old World species of *Trichadenotecnum* (summarized in Lienhard & Smithers, 2002; Lienhard, 2011, 2015; Yoshizawa & Lienhard, 2015) has revealed its great diversity in the Oriental to eastern Palearctic regions. Many new species have been

described, which have been either assigned to previously defined species groups or to some newly proposed species groups based on morphological characters (Yoshizawa & Lienhard, 2004, 2015; Yoshizawa et al., 2007, 2014). Therefore, molecular-based tests for the morphologically established taxonomic system are highly desirable.

In this paper, we estimate the molecular phylogeny of the Old World species of *Trichadenotecnum* based on extensive taxon sampling. On the basis of the resulting tree, we examine the morphological evolution of the male genital structures in the genus. The molecular phylogeny also provides new insights for intrageneric taxonomy, but here we focus only on phylogeny and morphological evolution; taxonomic rearrangements will be subsequently proposed along with descriptive taxonomic studies (e.g., Yoshizawa & Lienhard, 2015).

2. Materials and Methods

The specimens used for DNA analyses were collected in various ways. The samples collected by beating or direct searching were freshly killed and stored in 99.5% ethanol. The samples collected by Malaise traps (tagged as Tiger or Sabah, Table 1) were placed in a water-rich preservative for a variable period, then stored in 80% ethanol, and finally preserved in 99.5% ethanol.

Samples were collected from various countries and regions (Table 1) and covered all known species groups from the Old World (Yoshizawa, 2001, 2003; Yoshizawa & Lienhard, 2004, 2015; Yoshizawa et al., 2007, 2014). A total of 72 species (73 individuals) of *Trichadenotecnum* were sampled for phylogenetic analyses (Table 1). Outgroups were selected from other Psocidae, covering all subfamilies and most tribes (Metylophorini not sampled) (Yoshizawa & Johnson, 2008). *Trichadenotecnum* is classified under the tribe Ptyctini, so this tribe was sampled most extensively. The tree was rooted by Kaindipsocinae as suggested by Yoshizawa et al. (2011).

Partial sequences of the nuclear *18S* rRNA, *Histone 3* and mitochondrial *16S* rRNA, *12S* rRNA and cytochrome *c* oxidase subunit I (*COI*) genes were used for analyses. Methods for DNA extraction, PCR amplification, sequencing, and alignment followed Yoshizawa & Johnson (2010) for *18S* and Yoshizawa & Johnson (2008) for the other genes. The aligned data set is available in the Online Supplement. See Table 1 for the GenBank accession numbers.

Using the aligned data set, maximum-likelihood (ML) and Bayesian analyses were performed. The best-fitting model for the ML analysis was estimated on the basis of the hierarchical likelihood ratio test (hLRT) using a BioNJ tree, as implemented in jModelTest 2.1.7 (Darriba et al., 2012). As a result, the GTR + Invariable site + Gamma model was selected (parameters described in the Online Supplementary matrix). ML tree searches were conducted using PAUP*4a142 (Swofford, 2002). Neighbor-joining (NJ), Bayesian and PhyML-estimated (by subtree pruning and regrafting: SPR) ML trees were used as starting trees, and heuristic searches with tree bisection reconnection (TBR) branch swapping were conducted. The tree with the best score was found when the PhyML-estimated ML tree was used as the starting tree. Likelihood-based bootstrap support values were calculated using PhyML 3.1 (Guindon et al., 2010) with 1000 bootstrap replicates. SPR branch swapping was performed for each bootstrap replicate with the GTR + Invariable site + Gamma model (all parameters estimated from the data set).

We used MrBayes 3.2.1 (Ronquist et al., 2012) for Bayesian Markov chain Monte Carlo analyses. For Bayesian analyses, data were subdivided into nine categories (*18S*, *16S*, *12S*, first, second, and third codon positions of *H3* and *COI*), and the substitution models for the analysis were estimated separately for each data category using hLRT as implemented in MrModeltest 2.3 (Nylander, 2004). Detailed settings for Bayesian analyses are described in the data matrix (Online Supplement). We performed two runs each with four chains for 5,000,000 generations, and trees were sampled every 1,000 generations. The first 50% of the sampled trees was excluded for burn-in, and a 50% majority consensus tree was computed to estimate Bayesian posterior probabilities.

In addition to the bootstrap value and Bayesian posterior probability, the robustness of certain clades of interest was tested with an approximately unbiased test (AU test; Shimodaira, 2002) using PAUP* by contrasting the best ML tree with trees estimated by constraining alternative relationships (e.g., monophyly of the *sexpunctatum* group, see below).

A key morphological character causing incongruences between molecular and morphological systematics was mapped on the resulting tree, and the ancestral states were estimated using Mesquite 3.03 (Maddison & Maddison, 2015) under the parsimony and likelihood models. Methods for morphological observations, illustrations and coding followed Yoshizawa et al. (2008).

3. Results

The phylogenetic trees resulting from ML and Bayesian analyses of the five gene regions were well resolved (Fig. 1). These trees were nearly identical except for minor rearrangements of weakly supported branches (see Online Supplementary data). The monophyly of the genus *Trichadenotecnum* was consistently supported, with 88% bootstrap (BS) and 100% posterior probability (PP). The monophyly of almost all species groups proposed previously was also supported with high support values (86–100% BS, 100% PP), except for the paraphyly of the *sexpunctatum* group (the *medium* group embedded within the *sexpunctatum* group) and the polyphyly of the *majus* group (divided into two clades, with two other species groups embedded within one of these clades) (Fig. 1). The monophyly of the *circularoides*, *digitatum* and *vaughani* groups could not be tested because only a single species from each species group was available for the analyses.

Within *Trichadenotecnum*, the *circularoides* group was sister to the remainder of the genus, and the monophyly of the genus, excluding the *circularoides* group, received strong support (88% BS, 100% PP). Arrangements of the four groups (the *marginatum*, *corniculum*, *longimucronatum*, and *spiniserrulum* groups) outside of *Trichadenotecnum s. str.* (*sensu* Roesler, 1943; Thornton, 1961) were unstable, but the monophyly of *Trichadenotecnum s. str.* was well supported (78% BS, 100% PP). Relationships among the species groups within *Trichadenotecnum s. str.* were also unstable. Species-group assignment of *T. germanicum* has not been proposed to date, and this species was placed as sister to the *majus* group II (see below) with low nodal supprt (<50% BS and <70% PP).

As also suggested on the basis of morphological characters (Yoshizawa, 2001, 2004), a close affinity between the *sexpunctatum* and *medium* groups was supported with high support values (88% BS, 100% PP). However, the *sexpunctatum* group was paraphyletic because one species of the group, *T. sexpunctatum*, was placed sister to the *medium* group with fairly strong support (64% BS and 99% PP). In contrast, the monophyly of the *sexpunctatum* group could not be rejected by the AU test (P=0.43).

Monophyly of the *majus* group was not supported for two reasons. First, the group was divided into two distant clades: one contained *T. sibolangitense* and a related undescribed species (*majus* I), and the other contained the rest of the *majus* group (*majus* II). A close relationship between *majus* I and II (keeping the *distinctum* and *vaughani*

groups within the *majus* II clade: Fig. 1) could not be rejected by the AU test (P = 0.36). However, a close relationship between *majus* I and *T*. *arciforme* + *T*. sp.tiger15, as suggested by the similarity of the male genitalia (Fig. 2A1, C8: Yoshizawa et al., 2014), and a close affinity of the species lacking the median tongue in the *majus* group (*majus* I + Clade C: Fig. 2) were both rejected by the AU test (P<0.001). Second, two species groups, the *distinctum* and *vaughani* groups, were embedded within the *majus* II clade (Fig. 1), so that this part of the *majus* group was paraphyletic. Placement of the *distinctum* group within *majus* II was especially robust (Fig. 1). The monophyly of *majus* II excluding the *distinctum* and *vaughani* groups was rejected by the AU test (P<0.001).

The most parsimonious reconstruction of the transformation series of the male hypandrial median tongue was performed. The hypandrium is the 9th abdominal ventral plate, which shows great diversity among species and is thus the most important diagnostic character; its median tongue is a characteristic feature widely observed in the genus *Trichadenotecnum* (Fig. 2 and Supplementary Fig. S1). The presence of the fully developed and movable hypandrial median tongue was estimated as the ancestral condition of *Trichadenotecnum* (Fig. 2 and Suppl. Fig. S1: red). Its reduction and absence were identified as having occurred several times (in the *corniculum*, *spiniserrulum*, *krucilense*, and *majus* groups: Suppl. Fig. S1). A reduced and unmovable median tongue was identified as the ancestral condition for the *majus* II clade (Fig. 2, blue), and the complete absence of the median tongue was estimated to have occurred once in the clade C (Fig. 2, white). Reversals to the fully developed and movable median tongue were only identified within the *majus* II clade: in the *distinctum* group (from its unmovable condition) and *vaughani* group (from its complete absence) (Fig. 2). The likelihood reconstruction provided concordant result with that from the parsimony reconstruction (Suppl. Fig. S2).

4. Discussion

The present molecular phylogenetic analyses using five gene markers sequenced from a wide range of *Trichadenotecnum* species generally supported the validity of the morphology-based taxonomic scheme. For example, the *marginatum* and *longimucronatum* groups were originally described as independent genera, *Cryptopsocus* Li, 2002 and *Conothoracalis* Li, 1997, respectively, which were subsequently synonymized with *Trichadenotecnum* on the basis of morphology (Yoshizawa et al., 2007; Yoshizawa &

Lienhard, 2015). Synonymies of *Cryptopsocus* and *Conothoracalis* with *Trichadenotecnum* were here unambiguously supported (Fig. 1). The monophyly of nearly all morphologically proposed species groups and the close relationship between the *sexpunctatum* and *medium* groups were also strongly supported; suggesting that the male and female genital characters contain sufficient phylogenetic signals, contrary to some previous points of view (Arnqvist & Rowe, 2002; Eberhard, 2004).

In contrast, a significant incongruence between the morphological and molecular phylogenies was also identified in three cases. First, the monophyly of the *sexpunctatum* group was not supported, and the *medium* group was embedded within the group. The close similarity of the male genitalia between these groups has long been recognized (Thornton, 1961; Yoshizawa, 2001, 2004), which was also strongly supported by the present analyses. Species of the *sexpunctatum* group have more developed hypandrial processes than those in the *medium* group (Fig. 2A3, A4), and the *sexpunctatum* group has been diagnosed by the more developed hypandrial processes. However, the present results suggest that the less developed condition, as observed in the *medium* group (Fig. 2A4), is actually derived from the more developed *sexpunctatum*-like condition (Fig. 2A3). The sister relationship between *T*. *sexpunctatum* and the *medium* group is fairly well supported (64% BS and 99% PP; Fig. 1), but monophyly of the *sexpunctatum* group cannot be rejected by the AU test. Further evidence is needed to confirm the morphological transformation in the *sexpunctatum* + *medium* clade.

The second incongruence concerns the monophyly of the *majus* group, which was divided into two separated clades. The reduction or complete absence of the hypandrial median tongue (blue or white in Fig. 2) is recognized as one of the autapomorphies defining the *majus* group (Yoshizawa, 2001, 2004; Yoshizawa & Lienhard, 2004; Yoshizawa et al., 2007, 2014). Placement of *T*. *sibolangitense* into the *majus* group (Yoshizawa et al., 2014) was also based on the complete absence of the median tongue in this species. Its hypandrial structure is especially similar to that of *T*. *arciforme* (Yoshizawa et al., 2014: Fig. 2A1 and 2C8). The AU test could not reject a close affinity between *majus* clades I and II (including the *distinctum* and *vaughani* groups within clade II: Fig. 1), but a close relationship between the *majus* I clade and the species lacking median tongue (clade C in Fig. 2) was clearly rejected. Extensive convergences in the shape of the structures of the hypandrium have apparently occurred in distantly related clades.

The third incongruence also concerns the *majus* group. Two morphologically-defined groups, the *distinctum* and *vaughani* groups, were imbedded within clade II of the *majus* group (Figs 1–2). As mentioned above, absence or reduction of the hypandrial median tongue is consistently observed throughout the *majus* group, but species in the *distinctum* and *vaughani* groups have a fully developed and movable hypandrial median tongue (Fig. 2B6 and C9). In particular, the *distinctum* group was deeply embedded within the *majus* II clade (strongly supported by bootstrap/posterior probability). Exclusion of these two species groups from *majus* group II was also rejected by the AU test. This result strongly suggests that reversal to the ancestral condition occurred at least twice within the *majus* II clade. Independent reductions of the median tongue were identified in several species groups (Suppl. Fig. S1), but reversals were only identified within the *majus* II clade.

In summary, there was a high level of congruence between the molecular phylogeny and a morphologically based classification scheme. However, some notable incongruence was also detected. In particular, previous morphological study suggested the possibility of a close relationship among the *majus*, *distinctum*, and *vaughani* groups based on the arrangement of the hypandrial distal processes (*majus* + *vaughani*; Yoshizawa & Lienhard, 2004) or on the female genital structures (*majus* + *distinctum*; Yoshizawa et al., 2007). Convergent reductions of the median tongue have been identified in several species groups (Suppl. Fig. S1), but, with the exception of *T. sibolangitense* and its relatives (Fig. 2A1), the species concerned were correctly separated from the *majus* group based on other genital characters (Yoshizawa et al., 2007, 2014). These results show that, although convergences and reversals exist, genital characters still contain useful phylogenetic signals. The present molecular tree will help to evaluate the significance of morphological characters for establishing a sound taxonomic system for *Trichadenotecnum*. Uncovering the evolutionary background producing the high diversity and morphological convergences/reversals of genital structures in *Trichadenotecnum* also merits further studies.

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Figure Captions

Fig. 1. Maximum likelihood tree estimated by PAUP* with TBR branch swapping using the tree estimated by PhyML tree as the starting tree. Numbers associated with the branches are ML Bootstrap/Bayesian Posterior Probability values higher than 50% (BP) or 80% (PP).

Fig. 2. The most parsimonious reconstruction of the state of the hypandrial median tongue on the ML tree, including the *majus* group and its relatives (left). Names of the species now assigned to the *majus* group are underlined. Note that *T*. *castum* is parthenogenetic, and its males are unknown (indicated by gray circle). On the right side, the hypandrium of representative species is illustrated (median tongue is highlighted by red or blue). The ancestral condition of the entire tree is "fully developed and movable" (red circle). This condition is also ancestral to Clade A, but "complete absence" (white circle: A1) occurred in *T*. *sibolangitense* and its relatives. *T*. *sibolangitense* was assigned to the *majus* group and is considered to be a very close relative of *T*. *arciforme* and its relatives (C8: Yoshizawa et al., 2014) based on the convergent absence of the median tongue and the triangular shape of the hypandrium. The reduced and unmovable median tongue (blue circle) is the ancestral condition to Clade B, but reversal to the "fully developed and movable" condition occurred in B6 and relatives (the *distinctum* group). "Complete absence" is the ancestral condition to Clade C, but reversal to the "fully developed and movable" condition occurred in C9 and relatives (the *vaughani* group).

Table 1

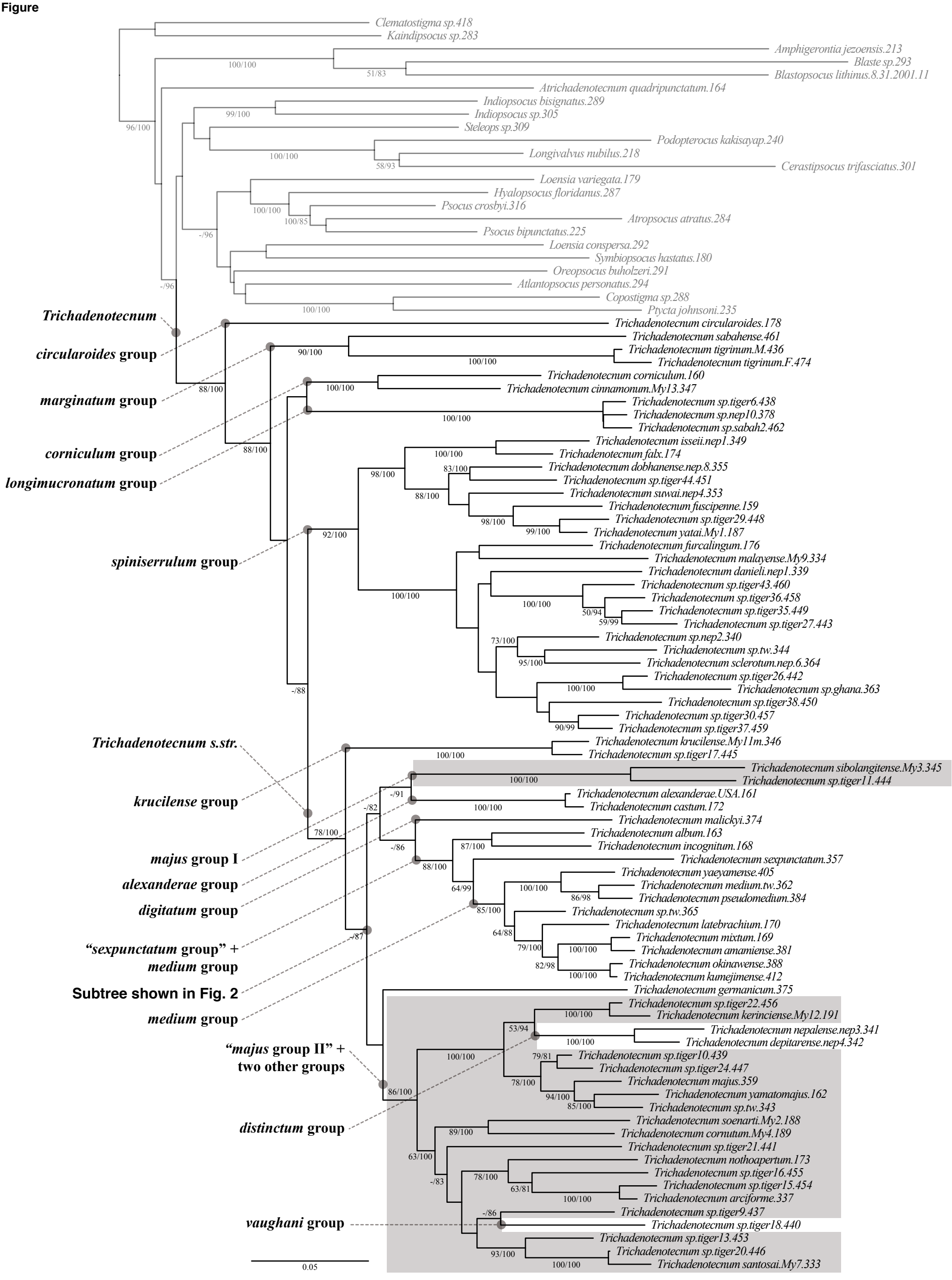
Taxa included in this study; – indicates missing data.

Supplementary Figure.

Suppl. Fig. 1. The most parsimonious reconstruction of the state of the hypandrial median tongue on the entire ML tree. See the caption of Fig. 2 for further explanation.

Suppl. Fig. 2. Likelihood reconstruction of the state of the hypandrial median tongue on the ML subtree. See the caption of Fig. 2 for further explanation.

Figure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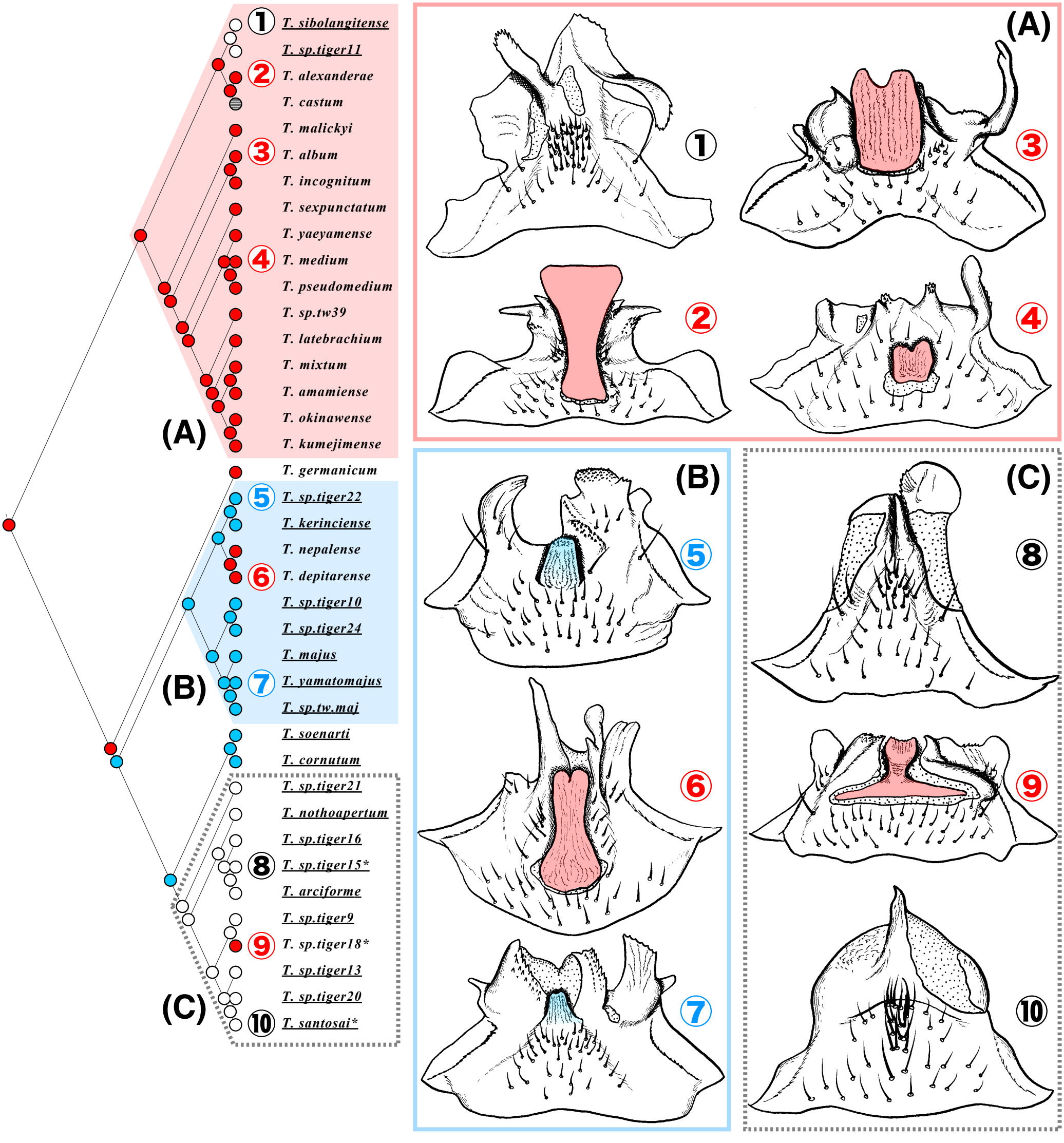
Kaindipsocus sp.283
Amphigerontia jezoensis.213
Blaste sp.293
Blastopsocus lithinus.8.31.2001.11
Atrichadenotecnum quadripunctatum.164
Indiopsocus bisignatus.289
Indiopsocus sp.305
Steleops sp.309
Podopterocus kakisayap.240
Longivalvus nubilus.218
Cerastipsocus trifasciatus.301
Loensia variegata.179
Hyalopsocus floridanus.287
Psocus crosbyi.316
Atropsocus atratus.284
Psocus bipunctatus.225
Loensia conspersa.292
Symbiopsocus hastatus.180
Oreopsocus buholzeri.291
Atlantopsocus personatus.294
Copostigma sp.288
Ptycta johnsoni.235
Trichadenotecnum
circularoides group
marginatum group
corniculum group
longimucronatum group
spiniserrulum group
Trichadenotecnum s.str.
krucilense group
majus group I
alexanderae group
digitatum group
"sexpunctatum group" +
medium group
Subtree shown in Fig. 2
medium group
"majus group II" +
two other groups
distinctum group
vaughani group
Trichadenotecnum circularoides.178
Trichadenotecnum sabahense.461
Trichadenotecnum tigrinum.M.436
Trichadenotecnum tigrinum.F.474
Trichadenotecnum corniculum.160
Trichadenotecnum cinnamonum.My13.347
Trichadenotecnum sp.tiger6.438
Trichadenotecnum sp.nep10.378
Trichadenotecnum sp.sabah2.462
Trichadenotecnum isseii.nep1.349
Trichadenotecnum falx.174
Trichadenotecnum dobhanense.nep.8.355
Trichadenotecnum sp.tiger44.451
Trichadenotecnum suwai.nep4.353
Trichadenotecnum fuscipenne.159
Trichadenotecnum sp.tiger29.448
Trichadenotecnum yatai.My1.187
Trichadenotecnum furcalingum.176
Trichadenotecnum malayense.My9.334
Trichadenotecnum danieli.nep1.339
Trichadenotecnum sp.tiger43.460
Trichadenotecnum sp.tiger36.458
Trichadenotecnum sp.tiger35.449
Trichadenotecnum sp.tiger27.443
Trichadenotecnum sp.nep2.340
Trichadenotecnum sp.tw.344
Trichadenotecnum sclerotum.nep.6.364
Trichadenotecnum sp.tiger26.442
Trichadenotecnum sp.ghana.363
Trichadenotecnum sp.tiger38.450
Trichadenotecnum sp.tiger30.457
Trichadenotecnum sp.tiger37.459
Trichadenotecnum krucilense.My11m.346
Trichadenotecnum sp.tiger17.445
Trichadenotecnum sibolangitense.My3.345
Trichadenotecnum sp.tiger11.444
Trichadenotecnum alexanderae.USA.161
Trichadenotecnum castum.172
Trichadenotecnum malickyi.374
Trichadenotecnum album.163
Trichadenotecnum incognitum.168
Trichadenotecnum sexpunctatum.357
Trichadenotecnum yaeyamense.405
Trichadenotecnum medium.tw.362
Trichadenotecnum pseudomedium.384
Trichadenotecnum sp.tw.365
Trichadenotecnum latebrachium.170
Trichadenotecnum mixtum.169
Trichadenotecnum amamiense.381
Trichadenotecnum okinawense.388
Trichadenotecnum kumejimense.412
Trichadenotecnum germanicum.375
Trichadenotecnum sp.tiger22.456
Trichadenotecnum kerinciense.My12.191
Trichadenotecnum nepalense.nep3.341
Trichadenotecnum depitarense.nep4.342
Trichadenotecnum sp.tiger10.439
Trichadenotecnum sp.tiger24.447
Trichadenotecnum majus.359
Trichadenotecnum yamatomajus.162
Trichadenotecnum sp.tw.343
Trichadenotecnum soenarti.My2.188
Trichadenotecnum cornutum.My4.189
Trichadenotecnum sp.tiger21.441
Trichadenotecnum nothoapertum.173
Trichadenotecnum sp.tiger16.455
Trichadenotecnum sp.tiger15.454
Trichadenotecnum arciforme.337
Trichadenotecnum sp.tiger9.437
Trichadenotecnum sp.tiger18.440
Trichadenotecnum sp.tiger13.453
Trichadenotecnum sp.tiger20.446
Trichadenotecnum santosai.My7.333
0.05

Figure


(A)
(B)
(C)
1
T. sibolangitense
T. sp.tiger11
2
T. alexanderae
T. castum
T. malickyi
3
T. album
T. incognitum
T. sexpunctatum
T. yaeyamense
4
T. medium
T. pseudomedium
T. sp.tw39
T. latebrachium
T. mixtum
T. amamiense
T. okinawense
T. kumejimense
T. germanicum
5
T. sp.tiger22
T. kerinciense
T. nepalense
6
T. depitarense
T. sp.tiger10
T. sp.tiger24
T. majus
7
T. yamatomajus
T. sp.tw.maj
T. soenarti
T. cornutum
T. sp.tiger21
T. nothoapertum
T. sp.tiger16
8
T. sp.tiger15*
T. arciforme
T. sp.tiger9
9
T. sp.tiger18*
T. sp.tiger13
T. sp.tiger20
10
T. santosai*

Tables

Sample	Locality	Voucher ID	18S	Histone 3	12S	16S	COI
Outgroups (Psocidae excl. *Trichadenotecnum*)							
Kaindipsocus splendidus	Vietnam	KY283	EF662270	EF662149	EF662236	EF662109	EF662072
Clematostigma sp.KY418	Australia	KY418	JF820388	JF820387	JF820377	JF820380	–
Amphigerontia jezoensis	Japan	KY213	AY630546	EF662143	EF662233	EF662104	EF662067
Blaste sp.KY293	USA	KY293	EF662267	EF662146	EF662235	EF662107	EF662070
Blastopsocus lithinus	USA	8.31.2001.11	AY630548	EF662147	AY275313	AY275363	AY275288
Longivalvus nubilus	Japan	KY218	AY630559	EF662152	AY139905	AY139952	EF662075
Cerastipsocus trifasciatus	USA	KY301	EF662271	EF662150	EF662237	EF662110	EF662073
Podopterocus kakisayap	Malaysia	KY240	AY630557	–	EF662239	EF662112	EF662076
Atrichadenotecnum quadripunctatum	Japan	KY164	AY630551	EF662157	AY374622	AY374572	AY374555
Hyalopsocus floridanus	USA	KY287	EF662277	EF662160	EF662246	EF662119	EF662082
Atropsocus atratus	USA	KY284	EF662275	EF662158	EF662244	EF662117	EF662080
Psocus bipunctatus	Japan	KY225	AY630555	EF662162	EF662248	EF662121	EF662084
Psocus crosbyi	USA	KY316	EF662279	EF662163	EF662219	EF662122	EF662085
Steleops sp.KY309	USA	KY309	EF662291	EF662176	EF662259	EF662133	EF662095
Loensia variegata	France	KY179	AY630549	EF662170	AY139906	AY139953	AY374556
Loensia conspersa	USA	KY292	EF662285	EF662171	EF662254	EF662128	EF662090
Copostigma sp.KY288	Fiji	KY288	EF662282	EF662166	EF662251	EF662125	EF662089
Ptycta johnsoni	Japan	KY235	AY630553	EF662175	AY139907	AY139954	EF662093
Symbiopsocus hastatus	Japan	KY180	AY630552	EF662178	AY374625	AY374575	AY374559
Atlantopsocus personatus	Italy	KY294	EF662280	EF662164	EF662250	EF662123	–
Oreopsocus buholzeri	Israel	KY291	EF662286	EF662172	EF662255	EF662129	–
Indiopsocus bisignatus	USA	KY289	EF662283	EF662167	EF662252	EF662126	EF662087
Indiopsocus sp.KY305	USA	KY305	EF662284	EF662168	EF662253	EF662127	EF662088
Ingroups							
Trichadenotecnum circularoides	Australia	KY178	EF662294-5	EF662180	AY374623	AY374573	AY374557
Trichadenotecnum tigrinum Male	Thailand	KY436	LC052029	LC052125	LC051914	LC051971	–
Trichadenotecnum tigrinum Female	Thailand	KY474	LC052030	LC052126	LC51915	LC51972	LC052088
Trichadenotecnum sabahense	Sabah	KY461	LC052031	LC052127	LC51916	LC51973	LC052089
Trichadenotecnum sp.Nepal10	Nepal	KY378	LC052032	LC052128	LC51917	LC51974	LC052090
Trichadenotecnum sp.Sabah2	Sabah	KY462	LC052033	LC052129	LC51918	LC51975	–
Trichadenotecnum sp.Tiger6	Thailand	KY438	LC052034	LC052130	LC51919	LC51976	–
Trichadenotecnum corniculum	Japan	KY160	AY374593	LC052131	AY374626	AY374576	AY374560
Trichadenotecnum cinnamonum	Malaysia	KY347	LC052035	LC052132	LC051920	LC051977	LC052091
Trichadenotecnum sp.Taiwan.spi	Taiwan	KY344	LC052036	LC052133	LC51921	LC51978	LC052092
Trichadenotecnum sclerotum	Nepal	KY364	LC052037	LC052134	LC51922	LC51979	LC052093
Trichadenotecnum sp.Nepal2	Nepal	KY340	LC052038	LC052135	LC51923	LC51980	–
Trichadenotecnum furcalingum	Japan	KY176	AY374594	LC052136	AY374627	AY374577	AY374561
Trichadenotecnum isseii	Nepal	KY349	LC052039	LC052137	LC051924	LC051981	LC052094
Trichadenotecnum sp.Tiger35	Thailand	KY449	LC052040	LC052138	LC51925	LC51982	LC052095
Trichadenotecnum sp.Tiger27	Thailand	KY443	LC052041	LC052139	LC51926	LC51983	–
Trichadenotecnum sp.Tiger36	Thailand	KY458	LC052042	LC052140	LC51927	LC51984	–
Trichadenotecnum sp.Tiger43	Thailand	KY460	LC052043	LC052141	LC51928	LC51985	LC052096
Trichadenotecnum sp.Tiger30	Thailand	KY457	LC052044	LC052142	LC51929	LC51986	–
Trichadenotecnum sp.Tiger37	Thailand	KY459	LC052045	LC052143	LC51930	LC51987	LC052097
Trichadenotecnum sp.Tiger38	Thailand	KY450	LC052046	–	LC51931	LC51988	–
Trichadenotecnum sp.Tiger26	Thailand	KY442	LC052047	LC052144	LC51932	LC51989	LC052098
Trichadenotecnum sp.Ghana	Ghana	KY363	LC052048	LC052145	LC51933	LC51990	LC052099
Trichadenotecnum malayense	Malaysia	KY334	LC052049	LC052146	LC51934	LC51991	LC052100
Trichadenotecnum falx	Japan	KY174	AY374595	LC052147	AY374628	AY374578	AY374562
Trichadenotecnum danieli	Nepal	KY339	LC052050	LC052148	LC051935	LC051992	LC052101
Trichadenotecnum dobhanense	Nepal	KY355	LC052051	LC052149	LC51936	LC51993	LC052102
Trichadenotecnum sp.Tiger44	Thailand	KY451	LC052052	LC052150	LC51937	LC51994	LC052103
Trichadenotecnum sp.Tiger29	Thailand	KY448	LC052053	–	LC51938	LC51995	–
Trichadenotecnum yatai	Malaysia	KY187	LC052054	LC052151	LC51939	LC51996	–
Trichadenotecnum fuscipenne	Japan	KY159	AY374596	LC052152	AY374629	AY374579	AY374563
Trichadenotecnum suwai	Nepal	KY353	LC052055	LC052153	LC051940	LC051997	LC052104
Trichadenotecnum krucilense	Malaysia	KY346	LC052056	LC052154	LC51941	LC51998	LC052105
Trichadenotecnum sp.Tiger17	Thailand	KY445	LC052057	LC052155	LC51942	LC51999	–
Trichadenotecnum sibolangitense	Malaysia	KY345	LC052058	LC052156	LC51943	LC052000	LC052106
Trichadenotecnum sp.Tiger11	Thailand	KY444	LC052059	LC052157	LC51944	LC052001	LC052107
Trichadenotecnum malickyi	Nepal	KY374	LC052060	LC052158	LC51945	LC052002	LC052108
Trichadenotecnum mixtum	Japan	KY169	AY374600	LC052159	AY374633	AY374583	AY374567
Trichadenotecnum amamiense	Japan	KY381	LC052061	LC052160	LC051946	LC052003	LC052109
Trichadenotecnum okinawense	Japan	KY388	LC052062	LC052161	LC51947	LC052004	LC052110
Trichadenotecnum kumejimense	Japan	KY412	LC052063	LC052162	LC51948	LC052005	LC052111
Trichadenotecnum latebrachium	Japan	KY170	AY374601	LC052163	AY374634	AY374584	AY374568
Trichadenotecnum sp.Taiwan.med1	Taiwan	KY365	AY374602	LC052164	AY374635	AY374585	AY374569
Trichadenotecnum medium	Taiwan	KY362	LC052064	LC052165	LC051949	LC052006	–
Trichadenotecnum pseudomedium	Japan	KY384	LC052065	LC052166	LC51950	LC052007	LC052112
Trichadenotecnum yaeyamense	Japan	KY405	LC052066	LC052167	–	–	LC052113
Trichadenotecnum sexpunctatum	Switzerland	KY357	LC052067	LC052168	LC051951	LC052008	LC052114
Trichadenotecnum album	Japan	KY163	AY374604	LC052169	AY374637	AY374587	AY374571
Trichadenotecnum incognitum	Japan	KY168	AY374603	LC052170	AY374636	AY374586	AY374570
Trichadenotecnum alexanderae	USA	KY161	AY630554	LC052171	AY275312	AY275362	AY275287
Trichadenotecnum castum	Japan	KY172	AY374591	LC052172	AY374624	AY374574	AY374558
Trichadenotecnum germanicum	Finland	KY375	LC052068	LC052173	LC051952	LC052009	LC052115
Trichadenotecnum arciforme	Hong Kong	KY337	LC052069	LC052174	–	LC052010	–
Trichadenotecnum sp.Tiger15	Thailand	KY454	LC052070	LC052175	LC051953	LC052011	–
Trichadenotecnum sp.Tiger16	Thailand	KY455	LC052071	LC052176	LC51954	LC052012	LC052116
Trichadenotecnum nothoapertum	Japan	KY173	AY374599	LC052177	AY374632	AY374582	AY374566
Trichadenotecnum sp.Tiger9	Thailand	KY437	LC052072	LC052178	LC051955	LC052013	–
Trichadenotecnum sp.Tiger18	Thailand	KY440	LC052073	LC052179	LC51956	LC052014	–
Trichadenotecnum sp.Tiger20	Thailand	KY446	LC052074	LC052180	LC51957	LC052015	–
Trichadenotecnum santosai	Malaysia	KY333	LC052075	LC052181	LC51958	LC052016	LC052117
Trichadenotecnum sp.Tiger13	Thailand	KY453	LC052076	LC052182	LC51959	LC052017	–
Trichadenotecnum sp.Tiger21	Thailand	KY441	LC052077	LC052183	LC51960	LC052018	–
Trichadenotecnum soenarti	Malaysia	KY188	LC052078	LC052184	LC51961	LC052019	LC052118
Trichadenotecnum cornutum	Malaysia	KY189	LC052079	LC052185	LC51962	LC052020	LC052119
Trichadenotecnum sp.Tiger10	Thailand	KY439	LC052080	–	LC51963	LC052021	–
Trichadenotecnum sp.Tiger24	Thailand	KY447	LC052081	LC052186	LC51964	LC052022	–
Trichadenotecnum yamatomajus	Japan	KY162	AY374598	LC052187	AY374631	AY374581	AY374565
Trichadenotecnum sp.Taiwan.maj	Taiwan	KY343	LC052082	LC052188	LC051965	LC052023	LC052120
Trichadenotecnum majus	Switzerland	KY359	LC052083	LC052189	LC51966	LC052024	LC052121
Trichadenotecnum kerinciense	Malaysia	KY191	LC052084	LC052190	LC51967	LC052025	LC052122
Trichadenotecnum sp.Tiger22	Thailand	KY456	LC052085	–	LC51968	LC052026	–
Trichadenotecnum depitarense	Nepal	KY342	LC052086	LC052191	LC51969	LC052027	LC052123
Trichadenotecnum nepalense	Nepal	KY341	LC052087	LC052192	LC51970	LC052028	LC052124