Molecular Phylogenetics and Evolution 94 (2016) 358–364

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

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

Kazunori Yoshizawa [a,*], Izumi Yao [a], Charles Lienhard [b]

[a] Systematic Entomology, Graduate School of Agriculture, Hokkaido University, Sapporo 060-8589, Japan
[b] Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Switzerland

ARTICLE INFO

Article history:
Received 7 May 2015
Revised 18 August 2015
Accepted 18 September 2015
Available online 3 October 2015

Keywords:
Morphology
Parsimonious reconstruction
Homoplasy
Taxonomy
Old World species
Species groups

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.

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 and Johnson, 2006). The genus consists of more than 200 species distributed in all zoogeographical regions (summarized in Lienhard and Smithers, 2002; Lienhard, 2011, 2015; Yoshizawa and Lienhard, 2015) except for the Australian Region, where only one introduced species is known (Yoshizawa and 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 and 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 and 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 and Johnson, 2006; Song and 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

☆ This paper was edited by the Associate Editor S.L. Cameron.

* Corresponding author. Tel.: +81 11 706 2424.
E-mail address: psocid@res.agr.hokudai.ac.jp (K. Yoshizawa).

http://dx.doi.org/10.1016/j.ympev.2015.09.018
1055-7903/

the genital structures (Arnqvist and 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 and Smithers, 2002; Lienhard, 2011, 2015; Yoshizawa and 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 and 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 and Lienhard, 2015).

Table 1
Taxa included in this study; – indicates missing data.

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	LC051915	LC051972	LC052088
Trichadenotecnum sabahense	Sabah	KY461	LC052031	LC052127	LC051916	LC051973	LC052089
Trichadenotecnum sp.*Nepal10*	Nepal	KY378	LC052032	LC052128	LC051917	LC051974	LC052090
Trichadenotecnum sp.*Sabah2*	Sabah	KY462	LC052033	LC052129	LC051918	LC051975	–
Trichadenotecnum sp.*Tiger6*	Thailand	KY438	LC052034	LC052130	LC051919	LC051976	–
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	LC051921	LC051978	LC052092
Trichadenotecnum sclerotum	Nepal	KY364	LC052037	LC052134	LC051922	LC051979	LC052093
Trichadenotecnum sp.*Nepal2*	Nepal	KY340	LC052038	LC052135	LC051923	LC051980	–
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	LC051925	LC051982	LC052095
Trichadenotecnum sp.*Tiger27*	Thailand	KY443	LC052041	LC052139	LC051926	LC051983	–
Trichadenotecnum sp.*Tiger36*	Thailand	KY458	LC052042	LC052140	LC051927	LC051984	–
Trichadenotecnum sp.*Tiger43*	Thailand	KY460	LC052043	LC052141	LC051928	LC051985	LC052096
Trichadenotecnum sp.*Tiger30*	Thailand	KY457	LC052044	LC052142	LC051929	LC051986	–
Trichadenotecnum sp.*Tiger37*	Thailand	KY459	LC052045	LC052143	LC051930	LC051987	LC052097
Trichadenotecnum sp.*Tiger38*	Thailand	KY450	LC052046	–	LC051931	LC051988	–
Trichadenotecnum sp.*Tiger26*	Thailand	KY442	LC052047	LC052144	LC051932	LC051989	LC052098
Trichadenotecnum sp.*Ghana*	Ghana	KY363	LC052048	LC052145	LC051933	LC051990	LC052099
Trichadenotecnum malayense	Malaysia	KY334	LC052049	LC052146	LC051934	LC051991	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	LC051936	LC051993	LC052102
Trichadenotecnum sp.*Tiger44*	Thailand	KY451	LC052052	LC052150	LC051937	LC051994	LC052103
Trichadenotecnum sp.*Tiger29*	Thailand	KY448	LC052053	–	LC051938	LC051995	–
Trichadenotecnum yatai	Malaysia	KY187	LC052054	LC052151	LC051939	LC051996	–
Trichadenotecnum fuscipenne	Japan	KY159	AY374596	LC052152	AY374629	AY374579	AY374563

(*continued on next page*)