

ON THE DIVERGENCE OF PSOCIDAE (PSOCODEA, PSOCOMORPHA): FOSSILS OR BIOGEOGRAPHY?

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RESUMEN

Con más de 900 especies válidas, Psocidae es la familia más diversa de psocideos. A pesar de que la información molecular disponible ha permitido hipotetizar sobre las relaciones filogenéticas entre los diferentes linajes, el contexto temporal ha sido hasta ahora poco discutido, y la influencia de factores intrínsecos y extrínsecos en su diversificación es aun desconocido. En este artículo probamos la congruencia de tres evidencias de divergencia (i.e. dos fósiles y una biogeográfica), y discutimos la correlación entre la edad de los clados y otros mayores eventos (e.g. geológicos, ecológicos). Encontramos que la familia Psocidae probablemente divergió durante la transición Mesozoico-Paleozoico. Además, las subsecuentes ramificaciones de los sub-linajes mayores ocurrió en un corto tiempo entre 68 y 77 My. Estas fechas también corresponden con los cambios de diversificación en múltiples linajes de angiospermas y el incremento en la temperatura global.

Palabras clave: Reloj molecular, Psócidos, Biogeografía, Tiempo, Fósiles.

ABSTRACT

With more than 900 valid species, Psocidae is the most diverse family of psocodeans. Even though the availability of molecular data has allowed hypothesizing on the phylogenetic relations for the different lineages, the evolutionary timing is still poorly discussed and the influence of intrinsic and extrinsic factors on their diversification is hitherto unknown. In this paper, we aim to test the temporal congruence of three evidences (i.e., two fossils and one biogeographical constraint), and discuss the correlation between clade's age and other major events (e.g., geological, ecological). We found that family Psocidae likely diverged during the Mesozoic – Paleozoic transition. Moreover, the subsequent splits of the major sub-lineages occurred in a short time interval between 68 to 77 Mya. These dates also correspond to diversification shifts in multiple angiosperm lineages and the increase in global temperature.

Key words: Molecular clock, Psocids, Biogeography, Timing, Fossils.

INTRODUCTION

Psocidae is the largest family within the psocodean Suborder Psocomorpha. To date, more

than 900 species have been described in ca. 80 Genera (Yoshizawa & Johnson 2008). As consequence of the high species richness and relative few studies restricted to specific lo-

cations and/or scientific disciplines, there is still a lack of knowledge about their ethology, physiology, morphology, biogeography, natural history and evolution (Liu *et al.* 2013; Slifer & Sekhon 1977). This family has several biological features that allows being considered as an interesting study group: (i) extensive within-and-among-species morphological variation, (ii) cosmopolitan distribution, (ii) elevated richness, among others (Yoshizawa 2004; Yoshizawa *et al.* 2011).

The monophyly of family Psocidae is supported by both morphological and molecular data (Johnson & Mockford 2003; Yoshizawa & Johnson 2008). Even though the higher-level relations have been discussed before, the temporal context has not been discussed in deep. Psocopterans appeared during the Permian-Carboniferous transition in the fossil record (300 Mya). This suggests two aspects: (i) the occurrence of a shift in diversity during the late Jurassic, and (ii) that this lineage reached its maximum diversity during the Cenozoic Oligocene (Labandeira & Eble 2000). Paleontological information has indicated a general pattern about the psocopteran diversity extrapolated from different fossil deposits (i.e., Lagerstätte). Yet, the family Psocidae has not been explicitly analyzed. In particular, two major papers have attempted to give a temporal framework to the evolution of the Psocidae. Misof *et al.* (2014) set the minimum bound for the divergence of Psocodea in 200 Mya, and Bess *et al.* (2014) published a molecular clock for the Hawaiian species of *Ptycta* (Psocinae: Ptyctini). In this paper, we intend to provide the first discussion on the evolutionary timing for the family Psocidae based on two fossils and a single biogeographic evidence.

MATERIAL AND METHODS

TAXON SAMPLING AND SEQUENCE ALIGNMENT

We sampled 120 species from 27 psocid genera. Outgroups were selected from families Myopsocidae, Psilopsocidae, and Hemipsocidae. We sampled four mitochondrial genes (12s, 16s, Cytochrome Oxidase subunit 1, and NADH dehydrogenase, subunit 5) and two nuclear genes (18s, and Histone 3; see Appendix 1; Benson

et al. 2006). Protein coding genes were aligned using MAFFT (Katoh & Standley 2013) with default parameters. The applied algorithm varied between loci depending on its biological functions and number of taxa included (E-ins-i for Wg and COI; L-ins-i applied to H3; G-ins-i used in ND5). Non-protein-coding genes (16s, 18s, and 12s) were analyzed using webPRANK (Löytynoja & Goldman 2010) with default parameters and based on their secondary structure.

ABSOLUTE DATING

Molecular dating was performed using the multi-coalescent approach implemented in BEAST 2 (Bouckaert *et al.* 2014). This method estimates the different genealogies included in the species reconstruction tree taking into account the stochasticity and incongruence between gene /species trees (Heled & Drummond, 2010). BEAUTi 2.2.3 was used to create the input file for BEAST runs. An uncorrelated molecular clock was set with a lognormal distribution to model substitution rates across branches in the tree. We selected a Birth-Death speciation process for tree building that accounts for extinction and speciation events. We constrained several nodes across the phylogeny based on three shreds of evidence of divergence related to fossils (two) and biogeography (one). The dating parameters and an background information for each of the applied constraints are shown in Table 1.

We used two independent Markov chain Monte Carlo (MCMC) that ran in the CIPRES portal (Miller *et al.* 2011). BEAGLE library was used for our analyses (Ayres *et al.* 2011). Each MCMC consisted of 50 million generations logged every 50,000 samples. Convergence was assessed in Tracer 1.6 based on the estimated sample size (ESS >200) of the parameters of interest. Nodes with support values (pp) higher than 0.95 (Condamine *et al.* 2015) are considered as well supported. Bayes factors were used for comparing the relative fit of the different models (e.g. fossil 1, fossil 2 and biogeography). Significant support of one hypothesis concerning the other was confirmed by BF>5 (Condamine *et al.* 2015).

RESULTS

Molecular dating reconstructions indicated congruent topologies despite the dating evidence. All the major lineages were recovered and highly supported (Fig. 1). However, discrepancies are clear when fossil- and biogeography-based chronograms are compared. Both Fossil 2 (F2) and Biogeographic evidences (BG) indicated the older divergence of the lineage, contradicting Fossil 1 (F1). Overall, the different chronograms suggest that the family divergence predates the Pangaea fragmentation.

Fossil dataset 1 (F1) sets the youngest divergence times for all nodes in Psocidae. Moreover, this chronogram recovered the narrowest temporal intervals across the tree (95% HPD; i.e. low uncertainty and high confidence). This evidence places the divergence of the family during upper Cretaceous and Early Paleocene (54 - 91 Mya). The crown ages of major lineages occurred within 48 to 64 Mya. Kaindipsocinae is here the least derived and younger lineage (28.08-71.84 Mya HPD). The crown age of Amphigerontiinae and Psocinae may have occurred 61 and 64 Mya respectively (41.67-80.81 Mya HPD; 49.38-79.44 Mya HPD). This evidence places the divergence of the major lineages of Psocidae during a recent and short time interval. Fossil 2 (F2) suggests an ancient divergence of the family. The crown age of Psocidae was placed during the Upper Jurassic (153.04 Mya; 152.02-155.02 Mya HPD) and the divergence of the major lineages in a narrow interval within 68.69-77.32 Mya. subfamily Kaindipsocinae (68.69 Mya) was recovered as the youngest, followed by Psocinae (72.26 Mya) and Amphigerontiinae (77.32 Mya). Biogeographic evidence (BG) places the crown age of Psocidae near 260 Mya (212.59-310.14 Mya HPD). The estimated dates corresponded to the younger estimates among the utilized evidence. Kaindipsocinae probably diverged in a wide time interval during the Cretaceous

and the Triassic (197 Mya; 129.22-262.95 Mya HPD), Amphigerontiinae 208 Mya (147.15-274.21 Mya HPD) and finally Psocinae 293 Mya (200.38-282.26 Mya HPD).

The three hypotheses of the Psocidae evolutionary timing suggest both ancient (F2 and BG) and recent (F1) divergences. Comparative analyses of relative fit of each model approached from Bayes factors (Table 2), favored biogeographic evidence (BF>5 for all pairwise comparisons). This statistical support indicates the biogeographic evidence is statistically, a better explanation for the divergence of Psocidae than the dates recovered using F1 and F2 evidence.

DISCUSSION

All analyses recovered the high-level phylogenetic relations proposed by Yoshizawa & Johnson (2008). Our results suggest a pre-Pangaea divergence of Psocidae in congruence with several ordinal-level dated phylogenies (Misof *et al.* 2014). The following discussion involves some remarks on different key aspects of the family evolutionary timing.

METHODOLOGICAL ARTIFACTS AND FOSSILIZATION PROBABILITY

Fossils described in *Trichadenotecnum* and *Psocidus* (F1 evidence) may represent a substantial gap between the time of the cladogenetic events and their recovery. These fossils perhaps do not represent an accurate measure of the family diversity and underestimate the divergence times across the tree. Although the molecular dating strategy used for the analyses takes into account the uncertainty in the node-ancestor (i.e., statistical distribution), the recent dating of the fossils might pull nodes towards younger ages (Jablonski *et al.* 2003).

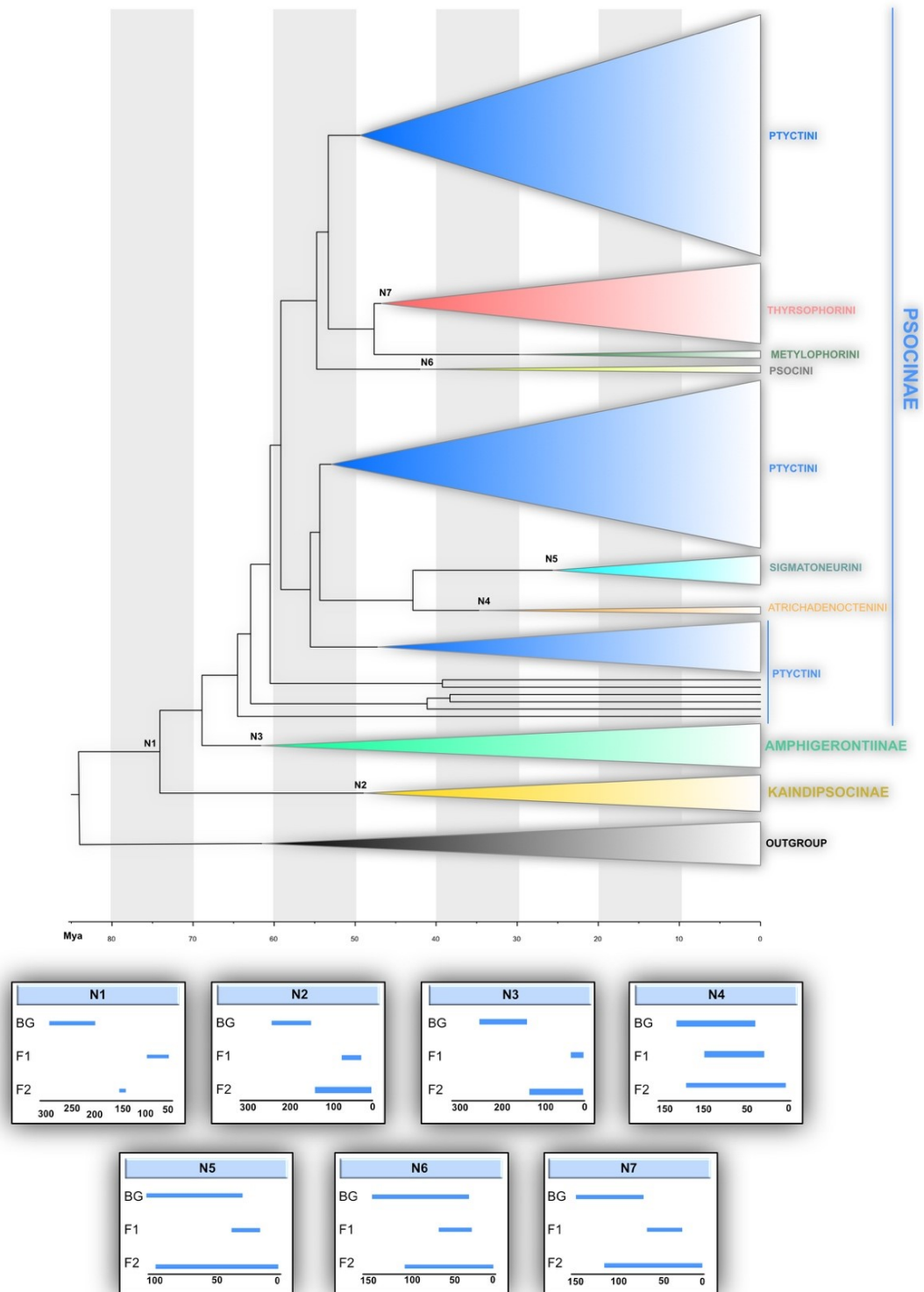


Figure 1. Differences in age across the phylogeny between psocid chronograms (i.e., fossils and biogeography; Table 1). Backbone phylogeny corresponds to the F1-based chronogram. Boxes at the bottom summarize the 95 % Highest Posterior Density intervals in selected nodes for the three used

evidence. Nodes labeled as N1-7 are indicated also in the phylogeny. See also Table 1..

Table 1. Dating evidence evaluated for calibrating the barklouse phylogeny.

Evidence	Abbreviators	Parameters	95% HPD (prior)	Description	Reference
Fossil dataset 1	F1	Lognormal	35.1-39.3 Ma	Five fossils have been reported and described in modern Psocidae lineages. These fossils correspond to two dating points of the genera <i>Trichadenotecnum</i> and <i>Psocidus</i> . All fossils were recovered from Tertiary amber, mainly from the European region.	Lienhard & Smithers (2002)
		$\mu=1$ $\sigma=1$ Offset=35			
Fossil dataset 2	F2	Lognormal	152-156 Ma	The fossil record of Psocoptera begins from the Permian. A fossil with Psocidae venation-type imprinted over mineral surfaces have been described.	"Grimaldi & Engel (2005 page 270)"
		$\mu=1$ $\sigma=1$ Offset=152			
Biogeography	BF	Normal	173-177 Ma	The historical biogeography of Thyrso-phorini psocids is most likely explained through vicariance (i.e., continental fragmentation).	Román-P et al. (2016)
		$\mu=1$ $\sigma=1$ Offset=175			

Table 2. Pairwise comparison of Bayes factors between the dating hypotheses employed. Dating strategy as indicated in Table 2. A positive value indicates better relative fit of row compared to columns. The favored hypothesis is highlighted.

Dating strategy	Ln p(data—model)	SE	F1	F2	BG
F1	-63937.097	+/- 0.201	-	-134.455	-251.23
F2	-63802.642	+/- 0.083	134.455	-	-116.775
BG	-63685.867	+/- 0.051	251.23	116.775	-

It is important to highlight that the fossils of *Psocidus* and *Trichadenotecnum* were recorded in the same time interval. A recurrent pattern in other groups such as Coleoptera suggest an amber threshold near 50 to 25 Mya (Smith & Marcot, 2015). Most of the modern lineages are thus well represented in the shallower deposits, but not in the deeper ones (see dates indicated by the biogeographic evidence). Fossilization probabilities increase as a function of plant-insect interactions (i.e. amber). In this sense, even if both *Trichadenotecnum* and *Psocidus* fossils we used for dating the crown age of each clade, neither give insights of the real divergence times for the entire family. The temporal biases in these fossils imply the underestimation of the whole dates. The objectivity of the fossil presented by Grimaldi & Engel (2005, Page 270), Fossil 2 (F2), is questionable

regarding of usefulness for molecular dating analyses (e.g., Joyce, 2012; Parham *et al.* 2011). F2 fails to meet most criteria for an objective dating.

Lastly, the biogeographic evidence is based on the hypothesized pattern for Thyrso-phorini psocids. Initially, Mockford (2004) proposed that the divergence of this tribe and Cycetini happened during Pangaea. Recently, Román-P. *et al.* (2016) supported the ancestral vicariance hypothesis using likelihood-based and parsimony methods. Therefore, a vicariance-driven biogeographic pattern in the evolution of Thyrso-phorini was found, mostly recurring to shifts on the current continental configurations. This scenario could only be favored and reconstructed by considering a pre-Pangaea occurrence of the lineage.

PSOCIDAE DIVERGENCE: FOSSILS OR BIOGEOGRAPHY?

The temporal context of Psocidae has been poorly addressed before. The only insights are currently based on the description of a few fossils psocids and the only molecular clock that was applied to the Hawaiian species of *Ptycta* (Smithers 1972; Bess *et al.* 2014). Analyses that are here presented, allow a wider discussion of the evolutionary timing for the Psocidae. The reconstruction based on Fossil 1 indicates that most of the cladogenetic events of the supra-generic lineages were concentrated in a narrow interval between 25 and 50 Ma. This suggests a probable major radiation of the modern lineages during the Paleocene. Biogeographic evidence and Fossil 2 indicated an older divergence for the family. The former, which was also the most statistically favored, suggest a crown age between 200-300 Ma. Despite the significant differences found with other evidence, none of the results contradict previous proposals, such as those presented by Misof *et al.* (2014), Rainford *et al.* (2014) and Wiens *et al.* (2015) that resulted in a maximum divergence for Psocodea within 300-400 Mya.

PREVIOUS ABSOLUTE DATINGS

The Hawaiian *Ptycta* are particularly interesting the intrinsic biological importance of island-endemic lineages (Bess *et al.* 2014). All dating schemes used here contrast significantly with the results presented by Bess *et al.* (2014) for the same lineage. Fossil dataset 1 indicated the younger ages for the *Ptycta* clade, with reconstructing dating crown age of the monophyletic clade as occurring 17 Mya (6-21 Mya HPD) that differs in at least 7 Mya with the biogeographical dating made by the same authors.

THE THYRSOPHORINI TIMING OF EVOLUTION

Tribe Thyrsophorini was erected by Yoshizawa & Johnson (2008) after including species contained in subfamilies Cerastipsocinae and Thyrsophorinae from other taxonomic classifications. The temporal context here presented allows us to discuss its timing of evolution. Fossil dataset 1 suggests its occurrence during

the Cenozoic (24 Mya; 16.56-32.66 Mya HPD), which contradicts with Mockford's (2004) hypothesis of divergence by continental drift. This new scenario proposes the influence of the Amazonian dynamism as preponderant during the diversification of the tribe in the Neotropical region (Hoorn *et al.* 2010). An older divergence was better supported in our paper (i.e., Fossil dataset 2 and Biogeography), and thus the current distribution of Thyrsophorini-like psocids as Cycetini and Sigmatoneurini may be better explained by fragmentation of the present continental configurations (Mockford 2004).

TIMING OF PSOCIDAE EVOLUTION

In sum, the favored biogeographic evidence (BG) proposes that the divergence of Psocidae took place near the crown Psocodea (260 Mya; 212.59-310.14 Mya HPD). This suggests that family Psocidae is among the oldest psocopterans. This family is an ancient lineage that diverged during the Mesozoic – Paleozoic transition. Moreover, the major sublineages split in a short time interval after their divergence. Even though this trend should be reviewed with caution, this clade shows a similar pattern to that of many herbivore insects (i.e., increased diversification since the Paleocene; 52-59 Mya; Wiens *et al.* 2015). This was analyzed by Currano (2008) who concluded on the existence of release of multiple physiological constraints, in addition to increasing environmental and ecological opportunity (e.g., temperature, plant diversity, leaf mass/area).

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Appendix 1. GenBank accession numbers for the sequences analyzed in this paper.

Taxa	12s	16s	18s	COI	H3	ND5	WG
<i>Amphigerontia jezoensis</i>	EF662233	EF662104	AY630546	EF662067	EF662143	-	EF662189
<i>Amphigerontia sp.</i>	KF651948	KF499262	EF662266	EF662068	EF662144	-	EF662190
	EF662234	EF662105		KF651829			KF651710
<i>Atlantopsocus personatus</i>	EF662250	EF662123	EF662279	-	-	-	-
<i>Atrichadenotecnum quadripunctatum</i>	AY374622	AY374572	AY374588	AY374555	EF662157	AY374605	EF662203
<i>Atrichadenotecnum sp.</i>		EF662116	EF662273	EF662079	EF662156	-	EF662202
			AY630551				GU569370
<i>Atropsocus atratus</i>	EF662244	EF662117	EF662274	EF662080	EF662158	-	EF662204
<i>Blaste cf. lunulata</i>	JF820378	JF820381	-	JF820373	-	-	JF820383
<i>Blaste quieta</i>	-	EF662106	AY630547	EF662069	EF662145	-	-
<i>Blaste sp.</i>	EF662235	EF662107	EF662267	EF662070	EF662146	-	EF662191
<i>Blastopsocus lithinus</i>	AY275313	AY275363	AY275338	AY275288	EF662147	-	EF662192
<i>Blastopsocus sp.</i>	-	EF662108	EF662268	EF662071	EF662148	-	EF662193
<i>Camelopsocus monticolus</i>	-	EF662124	EF662280	EF662086	EF662165	-	EF662210
<i>Camelopsocus sp.</i>	KF651832	KF499146	JN797294	KF651713	-	-	KF651594
<i>Cerastipsocus sp.</i>	-	-	-	JN797359	JN797375	-	JN797328
<i>Cerastipsocus trifasciatus</i>	EF662237	EF662110	EF662270	EF662073	EF662150	-	EF662195
<i>Cerastipsocus venosus</i>	-	-	AY252141	-	-	-	-
<i>Clematoscena sp.</i>	EF662238	EF662111	AY630560	EF662074	EF662151	-	EF662196
	JF820377	JF820380	JF820388		JF820387		
<i>Clematostigma sp.</i>	-	-	-	-	-	-	-
<i>Copostigma sp.</i>	-	-	EF662281	-	EF662166	-	-
<i>Copostigma collinum</i>	KF651897	KF499211	-	KF651778	-	-	KF651659
<i>Copostigma dispersum</i>	KF651898	KF499212	-	KF651779	-	-	KF651660
<i>Copostigma marosticum</i>	KF651833	KF499147	-	KF651714	-	-	KF651595
<i>Copostigma natewa</i>	KF651834	KF499148	-	KF651715	-	-	KF651596
<i>Copostigma sp.</i>	EF662251	EF662125	-	EF662089	-	-	EF662213
<i>Hemipsocus chloroticus</i>	AY139910	AY139957	AY630545	AY275290	AB919140	-	-
<i>Hemipsocus sp.</i>	EF662229	EF662100	AY630544	AB919141-	AB919055	-	GU569366
		DQ104765		GU569252	EF662139		EF662184
				EF662063	DQ104792		EF662185
<i>Hyalopsocus floridanus</i>	EF662246	EF662119	EF662276	EF662082	EF662160	-	EF662206
<i>Hyalopsocus morio</i>	EF662245	EF662118	EF662275	EF662081	EF662159	-	EF662205
<i>Hyalopsocus sp.</i>	EF662247	EF662120	EF662277	EF662083	EF662161	-	EF662207
<i>Indiopsocus bisignatus</i>	EF662252	EF662126	EF662282	EF662087	EF662167	-	EF662211
<i>Indiopsocus sp.</i>	KF651946	KF499260	EF662283	EF662088	EF662168	-	EF662212
	EF662253	EF662127	-	KF651827	-	-	KF651708
<i>Kaindipsocus sp.</i>	EF662236-	KF499264	EF662269	EF662072	EF662149	-	EF662194
	JF820376			KF651831			KF651712
	KF651950						
<i>Kimupsocus takumai</i>	GQ231536	GQ231535	GQ231538	GQ231537	-	-	-
<i>Lichenomima muscosa</i>	AY139908	AY139955	-	-	-	-	-
<i>Lichenomima sp.</i>	AY275314	EF662103	AY275339	AY275289	EF662142	-	EF662188
	EF662232	AY275364		EF662066			
<i>Loensia conspersa</i>	EF662254	EF662128	EF662284	EF662090	EF662171	-	EF662216
<i>Loensia moesta</i>	AY275310	AY275360	AY275335	AY275285	EF662169	-	EF662214
<i>Loensia variegata</i>	AY139906	AY139953	AY374589	AY374556	EF662170	AY374606	EF662215
<i>Longivalvus nubilus</i>	-	-	-	EF662075	EF662152	-	EF662197
<i>Longivalvus hyalospilus</i>	JQ910986	-	-	-	-	-	-
<i>Metylophorus novaescotiae</i>	AY275311	AY275361	AY275336	AY275286	EF662154	-	-
<i>Metylophorus purus</i>	EF662241	EF662114	EF662272	-	EF662155	-	EF662200
<i>Myopsocus sp.</i>	EF662231	EF662102	EF662265	EF662065	EF662141	-	EF662187
<i>Oreopsocus buhalzeri</i>	EF662255	EF662129	EF662285	-	EF662172	-	-
<i>Psocidus sp.</i>	EF662256	KF499168	EF662286	EF662091	EF662173	-	EF662217
	KF651854	KF499204		KF651735			
	KF651890	KF499258-		KF651771			
	KF651944	EF662130		KF651825			
<i>Psococerastis nubila</i>	AY139905	AY139952	AY630559	-	-	-	-
<i>Psococerastis sp.</i>	KF651836	EF662113-	EF662271-	KF651717	EF662153	-	KF651598
	EF662240	KF499150	EF662287	EF662077	EF662174		EF662199
	EF662257	EF662131		EF662092			EF662218
<i>Psocus bipunctatus</i>	EF662248	EF662121	-	EF662084	EF662162	-	EF662208
<i>Psocus crosbyi</i>	EF662249	EF662122	EF662278	EF662085	EF662163	-	EF662209
<i>Psocus sp.</i>	-	-	AY630555	-	-	-	GU569371
<i>Ptycta aaroni</i>	KF651837	KF499151	-	KF651718	-	-	KF651599
<i>Ptycta apicantha</i>	KF651858	KF499172	-	KF651739	-	-	KF651620

Taxa	12s	16s	18s	COI	H3	ND5	WG
<i>Ptycta diadela</i>	KF651853	KF499167	-	KF651734	-	-	KF651615
<i>Ptycta diastema</i>	KF651845	KF499159	-	KF651726	-	-	KF651607
<i>Ptycta distinguenda</i>	KF651861	KF499175	-	KF651742	-	-	KF651623
<i>Ptycta frogneri</i>	KF651913	KF499227	-	KF651794	-	-	KF651675
<i>Ptycta giffardi</i>	KF651846	KF499160	-	KF651727	-	-	KF651608
<i>Ptycta haleakalae</i>	KF651884	KF499198	-	KF651765	-	-	KF651646
<i>Ptycta hardyi</i>	KF651863	KF499177	-	KF651744	-	-	KF651625
<i>Ptycta johnsoni</i>	KF651899	KF499213	-	EF662093	EF662175	-	EF662219
<i>Ptycta kauaiensis</i>	KF651891	KF499205	-	KF651772	-	-	KF651653
<i>Ptycta leucothorax</i>	KF651872	KF499186	-	KF651753	-	-	KF651634
<i>Ptycta lobophora</i>	KF651876	KF499190	-	KF651757	-	-	KF651638
<i>Ptycta maculifrons</i>	KF651860	KF499174	-	KF651741	-	-	KF651622
<i>Ptycta microglena</i>	KF651883	-	-	KF651764	-	-	KF651645
<i>Ptycta molokaiensis</i>	KF651851	KF499165	-	KF651732	-	-	KF651613
<i>Ptycta monticola</i>	KF651892	KF499201	-	KF651768	-	-	KF651649
<i>Ptycta palikea</i>	KF651895	KF499209	-	KF651776	-	-	KF651657
<i>Ptycta pikeloi</i>	KF651849	KF499163	-	KF651730	-	-	KF651611
<i>Ptycta placophora</i>	KF651840	KF499153	-	KF651720	-	-	KF651601
<i>Ptycta sp.</i>	-	EF662132	-	-	-	-	-
		AY139954					
		KF499149					
<i>Ptycta simulator</i>	KF651843	KF499178	-	KF651724	-	-	KF651605
<i>Ptycta stenomedia</i>	KF651902	KF499216	-	KF651783	-	-	KF651664
<i>Ptycta telma</i>	KF651893	KF499207	-	KF651774	-	-	KF651655
<i>Ptycta zimmermani</i>	KF651925	KF499239	-	KF651806	-	-	KF651687
<i>Sigmatoneura kakisayap</i>	EF662239	EF662112	-	EF662076	-	-	EF662198
							GU569372
<i>Sigmatoneura kolbei</i>	EF662242	EF662115	AY630556	EF662078	-	-	EF662201
<i>Steleops elegans</i>	EF662259	EF662133	EF662290	EF662095	EF662176	-	EF662221
<i>Steleops sp.</i>	EF662260	EF662134	EF662291	EF662096	EF662177	-	EF662222
<i>Symbiopsocus hastatus</i>	-	-	EF662292	-	EF662178	-	EF662223
<i>Tanystigma sp.</i>	JF820379	JF820382	-	JF820374	-	-	JF820384
				JF820375			JF820385
<i>Thyrsothorus sp.</i>	EF662264	EF662138	EF662298	-	EF662183	-	EF662228
<i>Trichadenotecnum album</i>	AY374637	AY374587	AY374604	AY374571	-	AY374621	-
<i>Trichadenotecnum castum</i>	AY374624	AY374574	AY374591	AY374558	-	AY374608	-
<i>Trichadenotecnum circularoides</i>	AY374623	AY374573	AY374590	AY374557	-	AY374607	EF662224
<i>Trichadenotecnum corniculum</i>	AY374626	AY374576	AY374593	AY374560	-	AY374610	-
<i>Trichadenotecnum desolatum</i>	EF662263	EF662137	EF662297	EF662099	-	AY374612	EF662227
<i>Trichadenotecnum falx</i>	AY374628	AY374578	AY374595	AY374562	-	AY374611	-
<i>Trichadenotecnum furcilingum</i>	AY374627	AY374577	AY374594	AY374561	-	AY374613	-
<i>Trichadenotecnum fuscipenne</i>	AY374629	AY374579	AY374596	AY374563	-	AY374620	-
<i>Trichadenotecnum incognitum</i>	AY374636	AY374586	AY374603	AY374570	-	AY374618	-
<i>Trichadenotecnum latebrachium</i>	AY374634	AY374584	AY374601	AY374568	-	-	-
<i>Trichadenotecnum mixtum</i>	AY374633	AY374583	AY374600	AY374567	-	AY374617	-
<i>Trichadenotecnum nothoapertum</i>	AY374632	AY374582	AY374599	AY374566	-	AY374616	-
<i>Trichadenotecnum quaesitum</i>	EF662262	EF662136	EF662296	EF662098	EF662181	-	EF662226
<i>Trichadenotecnum yamatomajus</i>	AY374631	AY374581	AY374598	AY374565	-	AY374615	-