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Molecular phylogeny of the beetle tribe Oxypodini (Coleoptera: Staphylinidae: Aleocharinae)

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Abstract. This is the first study to comprehensively address the phylogeny of the tribe Oxypodini Thomson and its phylogenetic relationships to other tribes within the staphylinid subfamily Aleocharinae. Using the hitherto largest molecular dataset of Aleocharinae comprising of 4599 bp for representatives of 22 tribes, the Oxypodini are recovered as non-monophyletic. Members of the tribe belong to three distantly related lineages within the Aleocharinae: (i) the *Amarochara* group as sister clade to the tribe Aleocharini, (ii) the subtribe Tachyusina within a clade that also includes the tribes Athetini and Hygronomini, (iii) all other Oxypodini in a clade that also includes the tribes Placusini, Hoplandriini and Liparocephalini. Based on the inferred phylogeny, five subtribes of the Oxypodini are recognized: Dinardina Mulsant & Rey, Meoticina Seevers, Microglottina Fenyes, Oxypodina Thomson and Phloeoporina Thomson. The following changes in the classification of the Aleocharinae are proposed: (i) *Amarochara* Thomson is removed from the Oxypodini and placed in the tribe Aleocharini; (ii) the subtribe Taxicerina Lohse of the Athetini is reinstated as tribe Taxicerini to include *Discerota* Mulsant & Rey, *Halobrecta* Thomson (both removed from the Oxypodini) and *Taxicera* Mulsant & Rey; (iii) the subtribe Tachyusina Thomson is excluded from the Oxypodini and provisionally treated as tribe Tachyusini; (iv) the oxypodine subtribe name Blepharhymenina Klimaszewski & Peck is placed in synonymy with the subtribe name Dinardina Mulsant & Rey.

Introduction

The staphylinid subfamily Aleocharinae contains approximately 12 000 described species classified into more than 50 tribes (Newton *et al*., 2000). This group of small beetles is distributed worldwide and occupies almost any terrestrial habitat (Thayer, 2005).

The monophyly of the Aleocharinae is well supported by morphological characters (Hammond, 1975; Ashe, 2005). In contrast, the relationships within the subfamily are poorly understood (Ashe, 2007). No phylogenetic study has comprehensively covered the aleocharine diversity at tribe and subtribe levels. The traditional tribal classification (e.g. Bernhauer & Scheerpeltz, 1926) is largely based on an intuitive assessment of easily observable characters, such as, for example, the tarsal formula or the number of segments in the maxillary and the labial palpi (Seevers, 1978). Recent phylogenetic studies revised the concepts of some tribes (e.g. Ahn & Ashe, 2004; Elven *et al*., 2010, 2012). However, establishing a new phylogeny-based classification of the Aleocharinae is difficult due to the high diversity of the group.

The aleocharine tribe Oxypodini Thomson includes approximately 2000 species and more than 150 genera (Newton & Thayer, 2005). As currently accepted (e.g. Seevers, 1978; Bouchard *et al*., 2011), the tribe can be defined only by a combination of characters, each shared with at least one other aleocharine tribe (Seevers, 1978). Within the Aleocharinae, most oxypodines can be recognized by the tarsal formula 5-5-5 (in some genera 4-5-5, or 4-4-4), antennae with 11 antennomeres, the maxillary palpus without a pseudosegment, and the aedeagus without an ‘athetine bridge’ (Seevers, 1978; Newton *et al*., 2000).

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The subtribe level classification of the Oxypodini varies from one author to another (Table 1). The most recent consensus classification recognized six subtribes: the Aphytopodina Bernhauer & Scheerpeltz that is endemic to New Zealand, and the five widespread subtribes, Blepharhymenina Klimaszewski & Peck, Dinardina Mulsant & Rey, Meoticina Seevers, Oxypodina Thomson and Tachyusina Thomson (Bouchard *et al*., 2011). The largest subtribe, Oxypodina, is only poorly characterized (Newton *et al*., 2000). Besides the type genus *Oxypoda* and closely related genera, it also includes several genera that cannot be placed in any other subtribe (Newton *et al*., 2000). Seevers (1978) further divided the Oxypodina into six informal groups, most of which lack a distinct diagnostic character.

The position of the subtribe Tachyusina has always been controversial. Based on a similar body shape, *Tachyusa* and closely related genera have been originally treated as members of the Falagriini (Lohse, 1974). Seevers (1978) demonstrated that they lack the important diagnostic characters of that tribe. Since then, the Tachyusina have been treated as members of either the Athetini (Sawada, 1987; Pace, 2006), Oxypodini (Seevers, 1978; Newton & Thayer, 1992; Newton *et al*., 2000), or as a separate tribe Tachyusini (Lohse, 1989; Paśnik, 2010). Paśnik (2010) studied the phylogeny of the Tachyusina (treated as tribe) based on morphological characters. The Tachyusini, represented by 28 genera, were recovered as sister clade to the six non-tachyusine Oxypodini, but with low support (Paśnik, 2010).

The phylogenetic relationships of the Oxypodini have never been studied comprehensively. In previous studies, the tribe has either been represented by the type genus *Oxypoda* only, or included one or two additional oxypodine genera (e.g. Steidle & Dettner, 1993; Maus *et al*., 2001; Ahn & Ashe, 2004; Thomas, 2009; Elven *et al*., 2010, 2012). The results of the phylogenetic analyses were largely dependent on the methods used in the respective studies, and in most of the studies including more than one oxypodine species the tribe appeared non-monophyletic (Steidle & Dettner, 1993; Maus *et al*., 2001; Thomas, 2009). However, in all the previous studies the oxypodine taxon sampling was inadequate to test the monophyly of the tribe. In a morphology-based study of Aleocharinae that included 41 genera and 12 aleocharine tribes, Muona (1997) found the Oxypodini to be polyphyletic. Unfortunately, no details were published and it is not clear which additional oxypodine genera besides *Oxypoda* were included.

The most comprehensive molecular phylogeny of aleocharine beetles so far was presented by Elven *et al*. (2012). The Oxypodini were represented by the genera *Oxypoda* and *Halobrecta*. *Oxypoda* was recovered as sister group of the Placusini, whereas *Halobrecta* was a sister group of the Taxicerina (Athetini). However, the relationships among these two clades and several other tribes remained unresolved (Elven *et al*., 2012).

In this study we present the first comprehensive molecular phylogeny of the Oxypodini. We test the monophyly of the tribe and infer its relationships to other aleocharine tribes. We also test hypotheses regarding the groups previously proposed within the Oxypodini and identify the main lineages of the tribe. Based on the phylogenetic analyses, we also revise the classification of the Oxypodini.

Material and methods

Taxon sampling

A total of 117 specimens belonging to 110 species from 87 genera were sampled for this study (Table 2). The tribe Oxypodini was represented by 56 species assigned to 39 genera, covering all but four previously proposed suprageneric groups, even those with invalid, unavailable or informal names (Table 1). The type genus *Oxypoda* was represented by four species, two of them from the nominotypical subgenus.

The outgroup included 54 species from 48 genera, among them 44 species from 21 other tribes of Aleocharinae, and two genera with uncertain tribal affiliation: *Stenectinobregma* and one unidentified aleocharine genus (labelled as Aleocharinae Genus 1). As more distant outgroup taxa, we included representatives of five other subfamilies of the Tachyporine group (Lawrence & Newton, 1982), i.e. Tachyporinae, Habrocerinae, Olisthaerinae, Phloeocharinae and Trichophyinae.

Molecular markers

A set of seven phylogenetically informative genes was targeted in this study. The nuclear 18S rRNA (*18S*) and 28S rRNA (*28S*) genes were included to infer the deeper phylogenies. We sequenced the internal part of *18S* (see Whiting *et al*., 1997) and the commonly used 5' region of *28S*. In addition, we included a partial sequence of the nuclear topoisomerase I (*TP*) gene. It was shown to be informative in Coleoptera from genus to family level (Wild & Maddison, 2008) and has been successfully applied to staphylinid beetle systematics (Chatzimanolis *et al*., 2010). Two mitochondrial regions yielding partial sequences of the mitochondrial 16S rRNA (*16S*), cytochromoxidase subunit I (*CO1*) and II (*CO2*), and NADH dehydrogenase subunit I (*ND1*) genes were selected to infer the more shallow nodes.

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from either the head, or the head and prothorax, following the protocol of the Qiagen DNeasy Blood & Tissue Kit (QIAGEN) with minor modifications as described by Elven *et al*. (2010). Most of the voucher specimens and all DNA extracts were deposited in the Natural History Museum, University of Oslo. Some voucher specimens are deposited in the Natural History Museum of Denmark, Copenhagen, and the Field Museum, Chicago. Full label information and depositories are listed in Table S1.

PCR was performed in a 25 μL reaction volume using 2.5 mM $MgCl_2$, 1X PCR buffer II (Applied Biosystems),

Table 1. List of suprageneric groups of the Oxypodini represented in this study and in recent classifications of the tribe.

Taxon name	Representation in this study		Recent classifications									
	At least one species	The type genus	Bernhauer & Scheerpeltz (1926)	Seevers (1978)	Muona (1979)	Lohse *et al*. (1990)	Newton & Thayer (1992)	Newton *et al*. (2000)	Navarrete-Heredia *et al*. (2002)	Smetana (2004)	Bouchard *et al*. (2011)	Classification proposed in this study
Aphytopodina Bernhauer & Scheerpeltz			+[9, 10]				+				+	+
Blepharhymenina Klimaszewski & Peck	+	+		+[14]			+	+		+	+	
Caloderina Mulsant & Rey	+	+	+[9, 11]									
Decusina Fenyes												
Dinardina Mulsant & Rey	+	+	+[9, 12]	+[12]	+		+	+	+	+	+	+
Homéusates Mulsant & Rey[1]												
Meoticina Seevers	+	+		+[15]	+		+	+	+	+	+	+
Microglottina Fenyes	+	+										+
Ocaleina Thomson	+	+										
Ocyusina Mulsant & Rey	+	+				+[9]	+					
Oxypodina Thomson	+	+	+[9, 13]	+[13]	+	+[9]	+	+	+	+	+	+
Acrimaea group	+	+[3]		+								
Amarochara group	+	+[4]		+								
Dexiogyia group	+	[5]		+								
Gnathusa group	+	+[6]		+								
Ocalea group	+	+[7]		+								+
Oxypoda group	+	+[8]		+								+
Phloeoporina Thomson[2]	+	+				+[9]	+					+
Saphoglossina Bernhauer & Scheerpeltz									+			
Tachyusina Thomson	+	+		+[16]	+		+	+	+	+	+	

[1] Unavailable name; [2] the junior name Phloeoporina Cameron, 1939 is based on the same type genus and therefore not listed; [3] *Tinotus* (= *Acrimaea*); [4] *Amarochara*; [5] *Crataraea*, *Thiasophila* and *Haploglossa*; [6] *Gnathusa*; [7] *Ocalea*; [8] *Oxypoda*; [9] treated as a subtribe of Aleocharini; [10] as Aphytopi; [11] as Caloderae; [12] as Dinardae; [13] as Oxypodae; [14] as Blepharhymeni; [15] as Meoticae; [16] as Tachyusae.

Table 2. List of specimens and GenBank accession numbers.

Subfamily/ tribes		Species name	ZMUN barcode	Collecting locality	GenBank Accession numbers				
					18S	28S	TP	16S + ND1	CO1 + CO2
Aleocharinae									
‡	Aleocharini	*Aleochara curtula* (Goeze)	10002704	Russia	KC132432	KC132516	KC132625	JX536396	KC132730
	Aleocharini	*Aleochara moerens* Gyllenhal	10002579	Norway	GQ981069*	KC132517	KC132626	GQ980970*	GQ980861*
	Aleocharini	*Aleochara obscurella* Gravenhorst	10008427	Norway	KC132433	KC132518	KC132627	JX536397	KC132731
	Aleocharini	*Tinotus morion* (Gravenhorst)	10008482	Greece	KC132434	KC132519	KC132628	JX536398	KC132732
‡	Athetini	*Atheta graminicola* (Gravenhorst)	10002561	Norway	GQ981133*	KC132520	KC132629	GQ981031*	GQ980926*
	Athetini	*Atheta kochi* Roubal	10008486	Austria	KC132435	KC132521	KC132630	JX536399	KC132733
	Athetini	*Hydrosmecta* sp.	10002650	U.S.A.	GQ981161*	KC132522	–	GQ981057*	GQ980955*
+	Athetini	*Meronera venustula* (Erichson)	10002576	U.S.A.	GQ981082*	KC132523	KC132631	GQ980983*	GQ980875*
+	Athetini	*Stethusa dichroa* (Gravenhorst)	10002567	U.S.A.	GQ981154*	KC132524	KC132632	GQ981051*	GQ980948*
+	Athetini	*Strigota ambigua* (Erichson)	10002571	U.S.A.	GQ981100*	KC132525	KC132633	GQ981000*	GQ980893*
	Athetini	*Taxicera* sp. cf. *perfoliata* Mulsant & Rey	10008503	Greece	KC132436	KC132526	KC132634	JX536400	KC132733
	Athetini	*Taxicera truncata* (Eppelsheim)	10008484	Austria	–	KC132527	KC132635	JX536401	KC132735
	Autaliini	*Autalia longicornis* Scheerpeltz	10030960	Germany	KC132437	KC132528	KC132636	JX536402	KC132736
	Deinopsini	*Deinopsis* sp.	10008437	U.S.A.	–	–	KC132637	JX536403	KC132737
‡	Diglottini	*Diglotta mersa* (Haliday)	10008426	Norway	–	KC132529	KC132638	JX536404	KC132738
+	Falagriini	*Cordalia obscura* (Gravenhorst)	10002651	Greece	GQ981071*	KC132530	KC132639	GQ980973*	GQ980864*
‡	Geostibini	*Geostiba circellaris* (Gravenhorst)	10002587	Norway	GQ981160*	KC132531	–	GQ981056*	GQ980954*
	Geostibini	*Geostiba* sp.	10029128	Greece	KC132438	KC132532	–	JX536405	KC132739
	Gymnusini	*Gymnusa variegata* Kiesenwetter	10002641	Romania	GQ981068*	KC132533	KC132640	GQ980969*	GQ980860*
	Himalusini	*Himalusa thailandensis* Klimaszewski, Pace & Center	10051228	Thailand	KC132439	KC132534	KC132641	JX536406	KC132740
	Homalotini	*Anommognathus cuspidatus* (Erichson)	10029211	Russia	KC132440	KC132535	KC132642	JX536407	KC132741
+	Homalotini	*Bolitochara pulchra* (Gravenhorst)	10002596	Norway	GQ981073*	KC132536	KC132643	GQ980974*	GQ980866*
	Homalotini	*Gyrophaena congrua* Erichson	10002584	Norway	GQ981074*	KC132537	KC132644	GQ980975*	GQ980867*
‡	Homalotini	*Homalota plana* (Gyllenhal)	10029184	Russia	KC132441	KC132538	KC132645	JX536408	KC132742
	Homalotini	*Silusa opaca* Fenyes	10051225	U.S.A.	KC132442	KC132539	KC132646	JX536409	KC132743
+	Homalotini	*Silusida marginella* (Casey)	10002625	U.S.A.	GQ981077*	KC132540	KC132647	GQ980978*	GQ980870*
‡	Hoplandriini	*Hoplandria lateralis* (Melsheimer)	10002550	U.S.A.	GQ981079*	KC132541	KC132648	GQ980980*	GQ980872*
‡	Hygronomini	*Hygronoma dimidiata* (Gravenhorst)	10030883	Germany	KC132443	KC132542	–	JX536410	KC132744
‡	Hypocyphtini	*Cypha longicornis* (Paykull)	10030896	Germany	KC132444	KC132543	–	JX536411	KC132745
	Hypocyphtini	*Oligota pumilio* Kiesenwetter	10030956	Germany	KC132445	KC132544	KC132649	JX536412	KC132746
	Liparocephalini	*Amblopusa magna* Zerche	10029212	Russia	KC132446	KC132545	KC132650	JX536413	KC132747
	Liparocephalini	*Amblopusa magna* Zerche	10029213	Russia	KC132447	KC132546	KC132651	JX536414	KC132748
+	Liparocephalini	*Diaulota densissima* Casey	10008421	U.S.A.	–	KC132547	KC132652	JX536415	KC132749
	Liparocephalini	*Liparocephalus cordicollis* LeConte	10008450	U.S.A.	KC132448	KC132548	KC132653	JX536416	KC132750
‡	Lomechusini	*Lomechusa emarginata* (Paykull)	10030941	Norway	JN581817*	KC132549	KC132654	JN581735*	JN581905*
	Lomechusini	*Pella caliginosa* (Casey)	10002617	U.S.A.	GQ981085*	KC132550	KC132655	GQ980986*	GQ980878*
	Myllaenini	*Myllaena audax* Casey	10030903	U.S.A.	JN581833*	KC132551	–	JN581749*	JN581918*
+	Oxypodini	*Acrostiba borealis* Thomson	10002729	Norway	KC132449	KC132552	KC132656	JX536417	KC132751
	Oxypodini	*Alisalia* sp.	10029195	U.S.A.	KC132450	KC132553	KC132657	JX536418	KC132752

Table 2. Continued.

	Subfamily/ tribes	Species name	ZMUN barcode	Collecting locality	GenBank Accession numbers				
					18S	28S	TP	16S + ND1	CO1 + CO2
	Oxypodini	*Amarochara brevios* Assing	10029139	U.S.A.	KC132451	KC132554	KC132658	JX536419	KC132753
	Oxypodini	*Amarochara* sp.	10029207	Laos	KC132452	KC132555	KC132659	JX536420	KC132754
	Oxypodini	*Apimela* sp. 1	10030869	U.S.A.	KC132453	KC132556	KC132660	JX536421	KC132755
	Oxypodini	*Apimela* sp. 2	10030861	Abkhasia	KC132454	KC132558	KC132662	JX536423	KC132757
	Oxypodini	*Apimela* sp. 3	10029190	Peru	–	KC132557	KC132661	JX536422	KC132756
	Oxypodini	*Bamona* sp.	10029121	U.S.A.	KC132455	KC132559	KC132663	JX536424	KC132758
	Oxypodini	*Blepharhymenus corsicus* (Mulsant & Rey)	10008454	France	KC132456	KC132560	KC132664	JX536425	KC132759
	Oxypodini	*Blepharhymenus* sp. 1	10029341	U.S.A.	KC132457	KC132561	KC132665	JX536426	KC132760
	Oxypodini	*Blepharhymenus* sp. 2	10008487	U.S.A.	KC132458	KC132562	KC132666	JX536427	KC132761
+	Oxypodini	*Brachyusa concolor* (Erichson)	10030880	Ukraine	KC132459	KC132563	KC132667	JX536428	KC132762
	Oxypodini	*Calodera aethiops* (Gravenhorst)	10002722	U.K.	KC132460	–	KC132668	JX536429	KC132763
+	Oxypodini	*Crataraea suturalis* (Mannerheim)	10030792	Germany	KC132461	KC132564	KC132669	JX536430	KC132764
+	Oxypodini	*Dacrila fallax* (Kraatz)	10030742	U.K.	KC132462	KC132565	KC132670	JX536431	KC132765
+	Oxypodini	*Devia prospera* (Erichson)	10002737	Russia	KC132463	KC132566	KC132671	JX536432	KC132766
	Oxypodini	*Dinarda hagensii* Wasmann	10051254	Germany	KC132464	KC132567	KC132672	JX536433	KC132767
	Oxypodini	*Dinarda maerkelii* Kiesenwetter	10002711	Norway	KC132465	KC132568	KC132673	JX536434	KC132768
	Oxypodini	*Dinarda maerkelii* Kiesenwetter	10002699	Norway	KC132466	KC132569	KC132674	JX536435	KC132769
	Oxypodini	*Gnathusa* sp.	10030932	Russia	KC132467	KC132570	KC132675	JX536436	KC132770
	Oxypodini	*Gnathusa* sp.	10030924	Russia	KC132468	KC132571	KC132676	JX536437	KC132771
	Oxypodini	*Gnypeta caerulea* (C.R.Sahlberg)	10029326	U.S.A.	KC132469	KC132572	KC132677	JX536438	KC132772
	Oxypodini	*Gnypeta* sp.	10029194	Peru	–	KC132573	KC132678	JX536439	KC132773
	Oxypodini	*Gnypeta* sp.	10029189	Peru	KC132470	KC132574	KC132679	–	KC132774
	Oxypodini	*Halobrecta algophila* (Fenyes)	10029224	U.S.A.	KC132471	KC132575	–	JX536440	KC132775
	Oxypodini	*Halobrecta* sp. cf. *halensis* Mulsant & Rey	10002647	Greece	GQ981172*	KC132576	KC132680	GQ981065*	KC132776
	Oxypodini	*Haploglossa villosula* (Stephens)	10008443	Belarus	KC132472	KC132577	KC132681	JX536441	KC132777
	Oxypodini	*Ilyobates bennetti* Donisthorpe	10030729	Germany	KC132473	KC132578	KC132682	JX536442	KC132778
+	Oxypodini	*Ilyobates nigricollis* (Paykull)	10030926	Russia	KC132474	KC132579	KC132683	JX536443	KC132779
+	Oxypodini	*Ischnopoderona gracilicornis* (Scheerpeltz)	10008434	South Africa	KC132475	KC132580	KC132684	JX536444	KC132780
	Oxypodini	*Isoglossa agnita* (Casey)	10029140	U.S.A.	KC132476	KC132581	KC132685	JX536445	KC132781
	Oxypodini	*Meotica filiformis* (Motschulsky)	10002706	Russia	KC132477	KC132582	KC132686	JX536446	KC132782
	Oxypodini	Meoticina Genus 1	10029210	Uganda	–	KC132583	KC132687	JX536447	KC132783
+	Oxypodini	*Mniusa incrassata* (Mulsant & Rey)	10002725	Norway	KC132478	KC132584	KC132688	JX536448	KC132784
+	Oxypodini	*Mniusa incrassata* (Mulsant & Rey)	10029205	Switzerland	–	KC132585	KC132689	JX536449	KC132785
	Oxypodini	*Myrmobiota* sp.	10029269	U.S.A.	KC132479	KC132586	KC132690	JX536450	KC132786
	Oxypodini	*Neothetalia canadiana* Klimaszewski	10008446	U.S.A.	KC132480	KC132587	KC132691	JX536451	KC132787
	Oxypodini	*Neothetalia nimia* (Casey)	10029172	U.S.A.	KC132481	KC132588	KC132692	JX536452	KC132788
	Oxypodini	*Ocalea badia* Erichson	10002740	Belarus	KC132482	KC132589	KC132693	JX536453	KC132789
	Oxypodini	*Ocalea corsicana* Fagel	10008453	France	KC132483	KC132590	KC132694	JX536454	KC132790
	Oxypodini	*Ocalea vancouveri* (Casey)	10029146	U.S.A.	KC132484	KC132591	KC132695	JX536455	KC132791
	Oxypodini	*Ocyusa picina* (Aubé)	10008444	Romania	KC132485	KC132592	KC132696	JX536456	KC132792
	Oxypodini	*Ocyustiba* sp.	10051226	U.S.A.	KC132486	KC132593	–	JX536457	KC132793

Table 2. Continued.

	Subfamily/ tribes	Species name	ZMUN barcode	Collecting locality	GenBank Accession numbers				
					18S	28S	TP	16S + ND1	CO1 + CO2
+	Oxypodini	*Oreuryalea watanabei* Assing & Maruyama	10002698	Russia	KC132487	KC132594	KC132697	JX536458	KC132794
	Oxypodini	*Oxypoda alternans* (Gravenhorst)	10008430	Germany	KC132488	KC132595	KC132698	JX536459	KC132795
	Oxypodini	*Oxypoda lentula* Erichson	10002707	U.K.	KC132489	KC132596	KC132699	JX536460	KC132796
	Oxypodini	*Oxypoda longipes* Mulsant & Rey	10002709	Germany	KC132490	KC132597	KC132700	JX536461	KC132797
	Oxypodini	*Oxypoda opaca* (Gravenhorst)	10002708	Germany	KC132491	KC132598	KC132701	JX536462	KC132798
	Oxypodini	Oxypodini Genus 1	10029199	Uganda	–	KC132599	KC132702	JX536463	KC132799
	Oxypodini	Oxypodini Genus 2	10029209	Laos	KC132492	KC132600	KC132703	JX536464	KC132800
+	Oxypodini	*Paradilacra densissima* (Bernhauer)	10029119	U.S.A.	KC132493	KC132601	KC132704	JX536465	KC132801
	Oxypodini	*Parocalea nearctica* Lohse	10029216	U.S.A.	–	–	KC132705	JX536466	KC132802
	Oxypodini	*Parocalea nearctica* Lohse	10029215	U.S.A.	KC132494	–	KC132706	JX536467	KC132803
	Oxypodini	*Phloeopora* sp.	10008442	Germany	KC132495	KC132602	KC132707	JX536468	KC132804
	Oxypodini	*Tachyusa gemma* Casey	10008433	South Africa	KC132496	KC132603	–	JX536469	KC132805
	Oxypodini	*Tachyusa objecta* Mulsant & Rey	10030757	Ukraine	KC132497	KC132604	KC132708	JX536470	KC132806
	Oxypodini	Tachyusina Genus 1	10029142	U.S.A.	KC132498	KC132605	KC132709	JX536471	KC132807
	Oxypodini	*Tetralaucopora longitarsis* (Erichson)	10008502	Greece	KC132499	KC132606	KC132710	JX536472	KC132808
	Oxypodini	*Tetralaucopora longitarsis* (Erichson)	10008475	Greece	KC132500	KC132607	KC132711	JX536473	KC132809
	Oxypodini	*Tetralaucopora rubicunda* (Erichson)	10008480	Greece	KC132501	KC132608	–	JX536474	-
+	Oxypodini	*Thiasophila angulata* (Erichson)	10030934	Norway	KC132502	KC132609	KC132712	JX536475	KC132810
+	Oxypodini	*Thinonoma atra* (Gravenhorst)	10002726	U.K.	KC132503	KC132610	KC132713	JX536476	KC132811
	Oxypodinini	*Thendelecrotona* sp.	10002612	South Africa	GQ981173*	KC132611	KC132714	GQ981066*	GQ980967*
	Paglini	*Pagla* sp.	10029237	U.S.A.	–	KC132612	KC132715	JX536477	KC132812
	Placusini	*Placusa* sp. prope *tachyporoides* (Waltl)	10002541	U.S.A.	GQ981090*	KC132613	–	GQ980990*	GQ980883*
	Pronomaeini	*Nopromaea* sp. 1	10030816	Uganda	KC132504	KC132614	KC132716	JX536478	KC132813
	Pronomaeini	*Nopromaea* sp. 2	10030841	Uganda	KC132505	KC132615	KC132717	JX536479	KC132814
	Pronomaeini	*Pronomaea korgei* Lohse	10008438	Greece	KC132506	KC132616	KC132718	JX536480	KC132815
	Pronomaeini	Pronomaeini Genus 1	10029218	Tanzania	–	KC132617	KC132719	JX536481	KC132816
	Pygostenini	*Typhloponemys* sp.	10029226	Tanzania	KC132507	KC132618	KC132720	JX536482	KC132817
	Tribe unknown	Aleocharinae Genus 1	10029193	Peru	KC132508	KC132619	KC132721	JX536483	KC132818
	Tribe unknown	*Stenectinobregma* sp.	10008435	South Africa	KC132509	KC132620	KC132722	JX536484	KC132819
Habrocerinae		*Habrocerus capillaricornis* (Gravenhorst)	10008441	Greece	KC132512	KC132623	KC132727	JX536488	KC132823
Olisthaerinae		*Olisthaerus megacephalus* (Zetterstedt)	10008447	Canada	KC132513	–	KC132728	JX536489	KC132824
Phloeocharinae		*Phloeocharis subtilissima* Mannerheim	10008508	Greece	KC132514	KC132624	KC132729	JX536490	KC132825
Tachyporinae									
	Deropini	*Derops uenoi* Watanabe	10029217	Russia	KC132510	KC132621	KC132723	JX536485	KC132820
+	Mycetoporini	*Lordithon thoracicus* (Fabricius)	10029203	Norway	–	KC132622	KC132724	JX536486	KC132821
	Tachyporini	*Tachinus proximus* Kraatz	10002542	Norway	GQ9810067*	–	KC132725	GQ980968*	GQ980859*
	Vatesini	*Vatesus* sp.	10008424	Ecuador	KC132511	–	KC132726	JX536487	KC132822
Trichophyinae		*Trichophya pilicornis* (Gyllenhal)	10008478	Greece	KC132515	–	KC261840	JX536491	KC132826

Sequences that were not newly generated are marked with an asterisk (*). Type species are marked with a plus (+), or double dagger (‡) if the respective genus is the type of its tribe. Additional label information is provided in Table S1. Classification follows traditional views prior to changes proposed in the present study.

0.8 mM GeneAmp dNTP Mix (Applied Biosystems), 0.5 μM of each primer, 1U of ABI AmpliTaq DNA Polymerase (Applied Biosystems) and 3 μL of the respective genomic DNA extract. If target genes were difficult to amplify, either 1.1 mg DMSO, or 0.4 μg BSA were added. For difficult amplifications of *16S,* concentrations of $MgCl_2$, PCR buffer II, and dNTP Mix were changed as described by Elven *et al*. (2010).

The general PCR profile consisted of an initial denaturation step at 94°C for 30 s, followed by 30 cycles at 94°C for 1 min, 45–67°C for 30 s, and 72°C for 2 min, and a final extension step of 10 min at 72°C. TP was amplified using the nested PCR approach described by Wild & Maddison (2008). The targeted regions of *28S*, *CO1* and *CO2* were amplified and sequenced in overlapping fragments. All primers used for amplification and amplification strategies are listed in Table S2. For 31 specimens, 1 or 2 of the targeted markers could not be amplified.

The PCR products were purified with ExoSAP-IT (Stratagene), and sequenced either externally by the ABI-Lab at the Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, or at the molecular lab of the Natural History Museum, University of Oslo using an ABI Prism 3130 Genetic Analyser (Applied Biosystems). All fragments were sequenced in both directions. The GenBank accession numbers of the sequences are provided in Table 2.

Sequence alignment

The obtained nucleotide sequences were edited and assembled into contigs in CodonCode Aligner v3.0 (CodonCode Corporation). Alignments were performed in MEGA v4.0 (Tamura *et al*., 2007). Alignment of the protein-coding sequences according to the amino acid translation was straightforward. Ribosomal sequence alignments were optimized by eye using published secondary structures as guide. Sequences of *28S* were aligned using secondary structure models of *Apis mellifera* (Gillespie *et al*., 2006) and *Diabrotica undecimpunctata howardi* (Gillespie *et al*., 2004). For the *18S* and *16S* sequences we followed the secondary structure models of *Apis mellifera* (Gillespie *et al*., 2006) with modifications for Staphylinidae suggested by Elven *et al*. (2010). The *leucine 1* and *leucine 2* tRNA genes were omitted from the alignment as they contribute only a very small number of parsimony informative characters. Ambiguously aligned regions were excluded from the downstream analyses.

Phylogenetic analyses

Two different datasets were used for the phylogenetic analyses. The first (= full dataset) included all seven genes and all 117 specimens, with 31 specimens missing 1 or 2 loci. The second (= reduced dataset) was restricted to the 86 specimens with complete sequence information and six genes (*ND1* was excluded as one important tribe represented by a single specimen was lacking its sequence). Maximum parsimony (MP), maximum likelihood (ML) and Bayesian (BI) analyses were performed on both datasets. Several ML analyses were also performed using alternative partitioning of the full dataset (see below), or with one of the seven genes excluded (except for the very short *ND1* sequences). MP analyses of the reduced dataset were also performed with third codon positions of the protein coding genes removed because of the high saturation at those positions as demonstrated by Elven *et al*. (2010) for a similar dataset.

MP analyses were performed in PAUP v4.0b10 (Swofford, 2002) using an heuristic search and 1000 initial addition sequences. All bases were weighted equally and gaps were treated as missing data. Bootstrap support (BS) was calculated with 1000 pseudoreplicates and 10 addition sequences per replicate.

Best-fit models for maximum likelihood (ML) and Bayesian (BI) analyses were calculated in MrModeltest2 (Nylander, 2004) using the Akaike information criterion (AIC). Due to ambiguous alignment and subsequent exclusion of most RNA loop regions, the remaining parts of RNA sequences were not partitioned in loop and stem regions. Both nuclear RNA sequences were included in a single partition. In ML and BI analyses, the following eight partitions were used (standard partitioning scheme): nuclear RNA (*18S* + *28S*), first, second, and third codon positions of the nuclear *TP* gene, mitochondrial RNA, and first, second, and third codon positions of the mitochondrial protein-coding genes (*CO1* + *CO2* + *ND1*). The GTR + G model was applied to the third codon positions of the mitochondrial protein-coding genes and the GTR + I + G model was applied to all other partitions. In addition, two alternative partitioning schemes were used in ML analyses of the full dataset: (i) the same as above, but with *18S* and *28S* in separate partitions; (ii) partitioning by the seven genes: *18S*, *28S*, *TP*, *16S*, *ND1*, *CO1* and *CO2*.

ML analyses were carried out in RAxML7.0,3 (Stamatakis, 2006) using the fast ML method under the GTR model. Bootstrap support was calculated using 1000 replicates with every fifth tree used as starting point for subsequent ML optimization on the original dataset.

BI analyses were performed in MrBayes 3.1 (MPI version) (Ronquist & Huelsenbeck, 2003) with four independent runs, each having three heated and one cold chain. Analyses were run for 43 million generations with trees sampled every 1000 generations. The first 25% of each run was discarded as burn-in. An average standard deviation of split frequencies < 0.05 was used as indication of convergence, and was reached between 4 and 5 million generations. Convergence among the runs was assessed using Tracer v1.5 (Rambaut and Drummond, 2007). All MP and BI analyses were performed on the Bioportal platform at the University of Oslo.

Results

Sequence data

The concatenated alignment consisted of 5446 bp, of which 847 ambiguous positions were excluded. Of the remaining

4599 bp, 2321 were constant and 402 variable, but parsimony uninformative. Details on the alignment are provided in Table S3.

There were no indels in the alignment of the protein-coding genes. Length variation was observed in almost all loop regions of the rDNA sequences, mainly among taxa representing different subtribes or tribes. These regions were thus excluded. The final sequence alignment is provided in the Supplement.

Phylogenetic analyses

The MP analysis of the full dataset yielded a bootstrap consensus tree with only the intra-subtribal relationships statistically well supported (Figure S1). The inter-subtribal and inter-tribal relationships remained unresolved. Excluding the specimens with incomplete sequence information did not improve the resolution at higher taxonomic levels (Figure S2). When the third codon positions of the protein-coding sequences of the reduced dataset were excluded, the MP analysis yielded a bootstrap consensus tree with a generally higher statistical support for both the intra-subtribal and inter-tribal relationships (Fig. 1).

The model-based analyses (BI and ML) of the full dataset yielded largely congruent trees with many inter-tribal relationships statistically well supported (Fig. 2). However, some of the nodes were well supported only in the BI analysis. Incongruence between the ML and BI trees was restricted to a few nodes weakly supported in both analyses.

ML analyses with one of the eight genes excluded yielded trees with the same well supported clades as obtained by the ML analysis of the full dataset. For some weakly supported nodes, the support did not improve or, depending on which gene was excluded became weaker (Figure S3). Standard and alternative partitioning schemes resulted in largely similar ML trees (Fig. 2 and Figures S4, S5). Except for one additional clade obtained with moderate support in the ML analysis partitioned by gene, the three trees differed only slightly in support values, and differed in topology only at some weakly supported nodes.

The BI analysis of the reduced dataset yielded a tree very similar to that obtained for the full dataset concerning the clades discussed below (Figure S6). Furthermore, reducing the dataset improved support for quite a few clades, while only slightly reducing support of others. Also, the ML tree for the reduced dataset was largely congruent with the BI tree. As in the analyses of the full dataset, incongruence was mostly restricted to a few nodes with low statistical support in both analyses.

Phylogenetic relationships of the Oxypodini

We refer in the following to the results of the BI and ML analyses of the full dataset (Fig. 2). Clades are labelled from the base of the tree towards the tips and in the order they are described below. We refer to the MP analyses only when their results support clades not recovered in the BI and ML analyses.

The 'higher' Aleocharinae are well supported in both the BI and the ML analyses (PP 1.00, BS 87). The tribe Oxypodini is recovered as non-monophyletic, as its members contribute to different lineages within the 'higher' Aleocharinae. *Amarochara* and two allied oxypodine genera (= *Amarochara* group; PP 1.00, BS 100) form the monophyletic clade A together with the tribe Aleocharini (PP 1.00, BS 99). The remaining lineages of the Oxypodini are scattered within the clades B and C. Clade B (PP 1.00) includes *Halobrecta*, all members of the oxypodine subtribe Tachyusina, and the tribes Athetini, Falagriini, Geostibini, Hygronomini, Lomechusini, Myllaenini, Oxypodinini, Paglini, Pronomaeini and Pygostenini, the subtribe Homalotina of the tribe Homalotini, and the genus *Stenectinobregma*. Within clade B, *Halobrecta* forms a monophyletic group together with the athetine genus *Taxicera* (clade D; PP 1.00, BS 100). More apically, the Tachyusina are nested within clade E (PP 1.00, BS 84) that also includes the tribes Athetini and Hygronomini. The basal relationships within clade E are unresolved. The Tachyusina are recovered as monophyletic (PP 1.00, BS 96) and most nodes within the clade are resolved and well supported.

The majority of oxypodine species included in this study form clade C together with the tribes Hoplandriini, Liparocephalini, and Placusini (PP 1.00). The basal relationships within clade C are unresolved. Clade C consists of five branches with a single terminal taxon [*Phloeopora*, *Myrmobiota* (both Oxypodini), *Hoplandria* (Hoplandriini), *Placusa* (Placusini), one aleocharine genus with unknown tribe assignment (Aleocharinae Genus 1)], and four well-supported subclades (F, G, H and I).

Subclade F (PP 1.00) includes most members of the subtribe Oxypodina. It further comprises two major lineages (clades J and K) and two branches with a single species each (*Oxypoda opaca*, *Neothetalia canadiana*). In MP analysis of the full dataset and in ML analysis partitioned by gene, *O. opaca* and *N. canadiana* are recovered as sister taxa (BS 84 and 68; Figures S1 and S5, respectively). Clade J (PP 1.00, BS 80) includes two sister clades, one consisting of *Ocalea, Neothetalia nimia* and *Isoglossa* (PP 1.00, BS 100), and the other of *Gnathusa* and *Mniusa* (PP 1.00, BS 100). Clade K (PP 1.00, BS 98) consists of *Oxypoda* (excluding *O. opaca*) and eight other genera. *Oxypoda* is recovered as non-monophyletic. *Oxypoda opaca* branched off prior to clade K, and within clade K, *Oxypoda lentula* is the sister of *Ocyusa* (PP 1.00, BS 69). The latter two contribute to clade L (PP 1.00, BS 65) that also includes the genera *Oreuryalea*, *Calodera*, *Devia*, and further a monophyletic lineage *Ilyobates* + *Tetralaucopora* (PP 1.00, BS 99).

The second well-supported subclade within clade C is the monophyletic subtribe Meoticina (clade G; PP 1.00, BS 100). Within clade G, *Meotica* is the sister to the remaining Meoticina (PP 1.00, BS 85), with *Apimela* as sister to the clade including *Alisalia*, and *Bamona* + one unidentified meoticine genus (labelled as Meoticina Genus 1). In the MP analysis of the full dataset, Meotica + Apimela (BS 64) is the sister

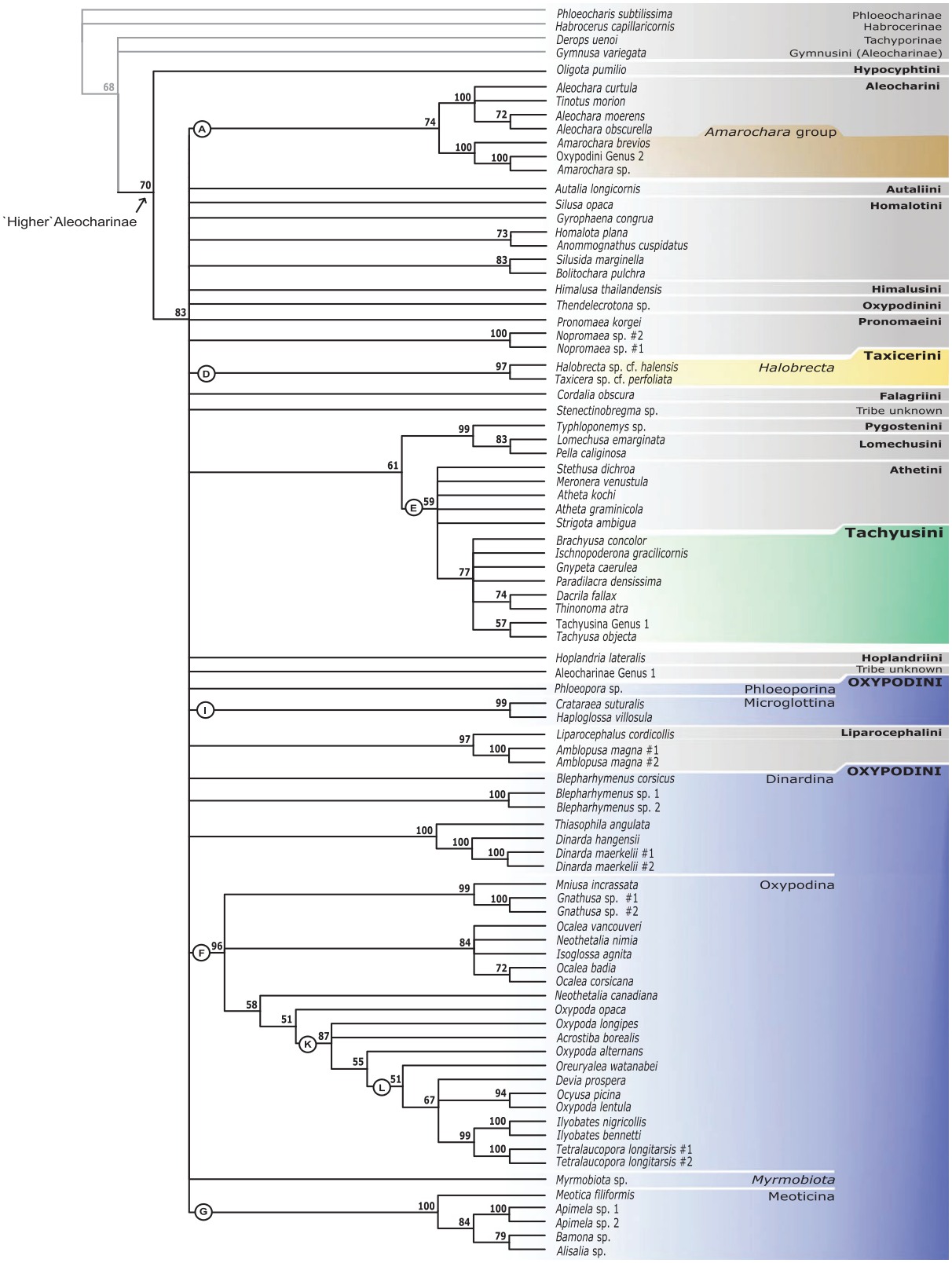

Fig. 1. Bootstrap consensus tree from the MP analysis of the reduced dataset with third codon positions excluded. Clade labels are in circles. Bootstrap support values ≥50 are indicated above branches. Clade names follow the newly proposed classification.

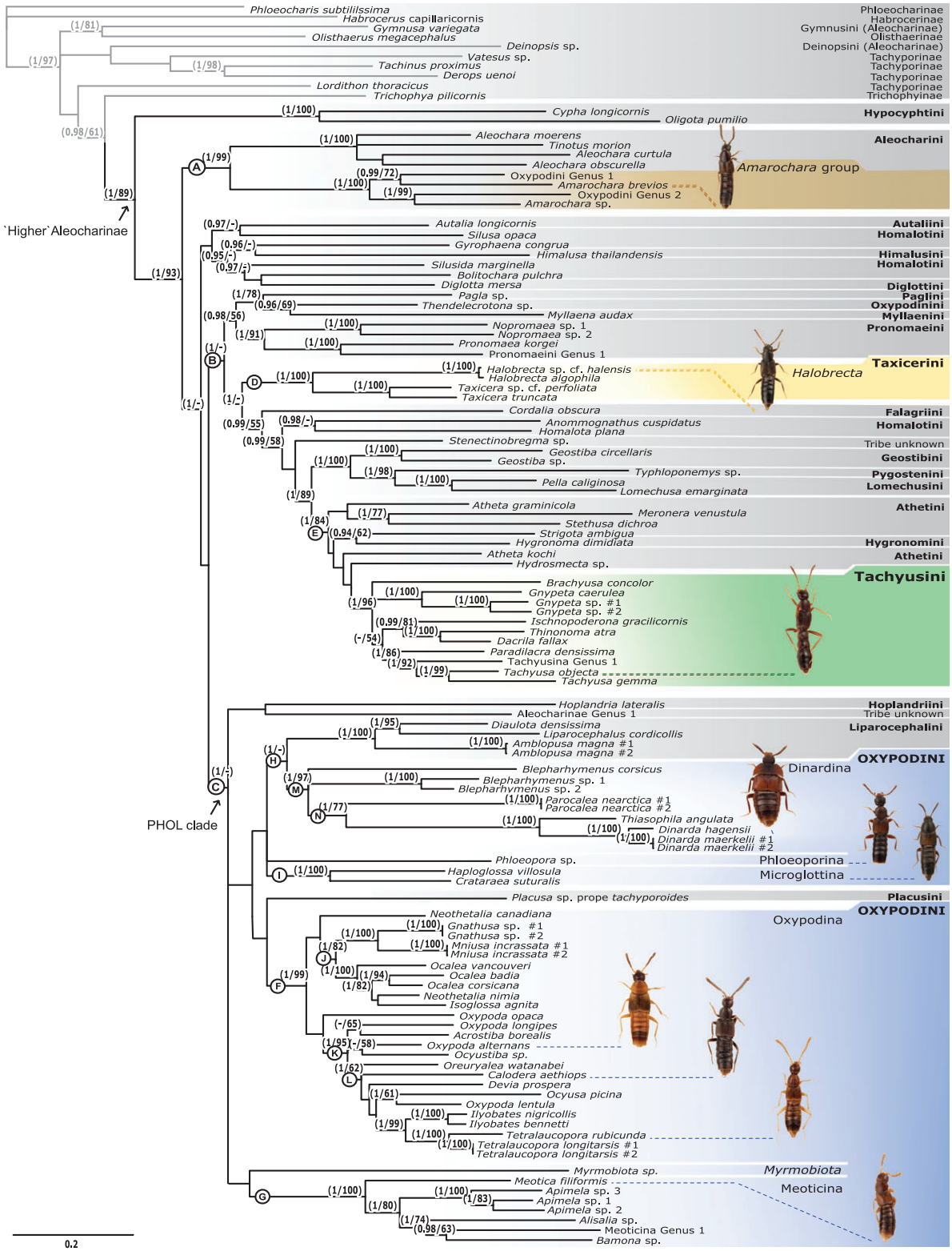

Fig. 2. Majority rule consensus tree from the BI analysis of the full dataset. Clade labels are in circles. Posterior probabilities ($PP \geq 0.94$) from the BI analysis and bootstrap support values ($BS \geq 50$) from the ML analysis are indicated above branches as PP/BS. Lower branch support ($PP < 0.94$ or $BS < 50$) is indicated with a dash. Clade names follow the newly proposed classification.

clade to *Alisalia* + *Bamona* + Meoticina Genus 1 (BS 56) (Figure S1).

The third well-supported subclade within clade C (clade H; PP 1.00) includes the monophyletic tribe Liparocephalini as sister to the clade that includes the oxypodine genera *Blepharhymenus*, *Parocalea*, *Thiasophila*, and *Dinarda* (clade M; PP 1.00, BS 95). Further, *Parocalea* + (*Thiasophila* + *Dinarda*) form the well-supported clade N (PP 1.00, BS 74). The relationships between *Blepharhymenus* and clade N are unresolved.

The fourth well-supported subclade within clade C includes the two oxypodine genera *Haploglossa* and *Crataraea* (clade I; PP 1.00, BS 100).

Discussion

Phylogeny of the Oxypodini

Using a DNA-based approach, the traditional concept of the tribe Oxypodini is firmly rejected. With 16 out of 20 formerly proposed suprageneric groups of the Oxypodini represented in the analyses (15 by their type genera; Table 1), this is the first comprehensive phylogenetic study that addresses the phylogeny of the tribe.

The phylogenetic analyses recovered members of the tribe in three different lineages of the Aleocharinae: (i) *Amarochara* and two related unidentified species: as a sister clade to the tribe Aleocharini (clade A); (ii) the oxypodine subtribe Tachyusina: as a member of clade E together with the tribes Athetini and Hygronomini; (iii) all remaining oxypodine genera, among them the type genus *Oxypoda*, in clade C also comprising the tribes Hoplandriini, Liparocephalini and Placusini.

Amarochara clade

Amarochara (represented by two species) and two related unidentified species (that may be congeneric with *Amarochara*) are recovered as a well-supported sister group to the tribe Aleocharini (clade A; Figs 1 and 2). Traditionally, the Aleocharini have been separated from the Oxypodini by the presence of a pseudosegment in both the maxillary and the labial palpi (Fenyes, 1918; Lohse, 1974; Seevers, 1978). However, Lohse (1974) also observed a pseudosegment in the maxillary palpi of some genera traditionally placed in the Oxypodini. A pseudosegment is also present in the tribes Hoplandriini (Fenyes, 1918; Newton *et al*., 2000) and Himalusini (Klimaszewski *et al*., 2010), both recovered as distantly related to the Aleocharini (Fig. 2). In contrast, *Amarochara* shares a strongly emarginate, sulcate apex of antennomere 1 with members of the Aleocharini, i.e. *Tetrasticta* and *Paraleochara* (Cameron, 1939). A similar apex of antennomere 1 is also present in two other oxypodine genera, *Porocallus* and *Paramarochara* (Cameron, 1952; Assing, 2001), indicating that they may be closely related to the Aleocharini, too. Future studies based on a wider sampling of genera traditionally placed in the Aleocharini may address this issue in more detail. For now, rather than establishing a separate tribe for *Amarochara* and further proliferating aleocharine tribes, we transfer *Amarochara* to the tribe Aleocharini.

Halobrecta

Halobrecta is recovered as the sister to *Taxicera* (clade D; Figs 1 and 2). *Taxicera* was recently placed, together with *Discerota*, in the subtribe Taxicerina of the Athetini (Lohse, 1989; Smetana, 2004; Kapp, 2005). Brundin (1943) and Kapp (2005) considered a close relationship between *Halobrecta* and *Taxicera*, but did not treat *Halobrecta* as a member of the Taxicerina. Elven *et al*. (2010) removed *Halobrecta* from the Athetini and provisionally assigned it to the Oxypodini. More recent analyses by Elven *et al*. (2012) recovered *Halobrecta* as sister to *Discerota* outside the clade that included, among others, the Athetini. However, the taxon sampling was insufficient for resolving the systematic position of *Halobrecta* and *Discerota* within the Aleocharinae. Corroborating the results of Elven *et al*. (2012), the present study rejects a close relationship of *Halobrecta* + *Taxicera* to either the Oxypodini or the Athetini. We raise the rank of Taxicerina to a tribe and expand it to include *Halobrecta*. Ádám & Hegyessy (2001) already used the family group name Taxicerini as tribe, but without providing any phylogenetic justification. The tribe Taxicerini can be recognized by the tarsal formula 4-5-5, the distinct shape of ligula (Gusarov, 2004), spermatheca (Gusarov, 2004; Kapp, 2005) and aedeagus (Gusarov, 2004; Kapp, 2005), the latter lacking the athetine bridge. The proposed tribe includes the three genera *Taxicera*, *Discerota* and *Halobrecta*.

Tachyusina clade

Most of the recent studies have treated the Tachyusina as subtribe of the Oxypodini (Seevers, 1978; Muona, 1979; Newton & Thayer, 1992; Newton *et al*., 2000; Navarrete-Heredia *et al*., 2002; Smetana, 2004; Bouchard *et al*., 2011). This study firmly rejects the hypothesis of a close relationship between the Tachyusina and any other group traditionally placed in the tribe. The Tachyusina form a monophyletic group within clade E that also includes the Athetini and the Hygronomini (Figs 1 and 2). This is in contrast to the morphology-based study of Paśnik (2010), that recovered the Tachyusina as a sister group to the Oxypodini. However, the latter relationship was not well supported and we consider the results of Paśnik (2010) an artifact of erroneous character coding [e.g. coding of the athetine bridge as missing in some taxa although it is present (*Meronera*, *Drusilla*, *Zyras* and *Amaurodera*), and coding of some highly correlated mouthpart characters as independent].

The athetine bridge of the aedeagus is present in the tribes Geostibini, Lomechusini and Athetini, supporting the close relationship recovered by Elven *et al*. (2012), and presented within this study. In the Tachyusina, the athetine bridge is considered absent (Seevers, 1978), at least in its typical

form. However, in some species of *Gnypeta* (Tachyusina) the sclerotized parameral side of the median lobe of the aedeagus has two short processes that could be interpreted as remains of the athetine bridge (V. Gusarov, unpublished observation). Besides, within several well-supported genera of the Athetini (e.g. *Philhygra*) there are also species with an incomplete athetine bridge (V. Gusarov, unpublished observation), providing an additional argument for a possible reduction of the athetine bridge within clade E and a close relationship between the Tachyusina and Athetini.

The present study provides sufficient taxon sampling and support for removing the Tachyusina from the Oxypodini. Because the basal relationships within clade E are not resolved, the Tachyusina are provisionally treated as separate tribe Tachyusini. Based on the present analyses, the tribe includes the genera *Brachyusa*, *Dacrila*, *Gnypeta*, *Ischnopoderona*, *Paradilacra*, *Tachyusa* and *Thinonoma*.

The PHOL clade

Comprising nine subclades, the PHOL clade (=Placusini–Hoplandriini–Oxypodini–Liparocephalini clade) makes up the main bulk of Oxypodini genera included in this study, as well as the tribes Hoplandriini, Liparocephalini and Placusini (clade C; Fig. 2). The relationships among the subclades, however, remain unresolved.

Subclade F largely corresponds to the subtribe Oxypodina *sensu* Seevers (1978). It includes, among others, the genera *Oxypoda*, *Ocalea*, *Calodera* and *Ocyusa*, which are the type genera of the family group names Oxypodina, Ocaleina, Caloderina and Ocyusina, respectively (Table 1). The names Oxypodina and Ocaleina have the same publication date. Newton & Thayer (1992), as the first revisers who listed the two names as synonyms, treated Oxypodina as the valid name and Ocaleina as invalid. For this reason subclade F is classified as the subtribe Oxypodina. However, no morphological apomorphy is known for the Oxypodina and the subtribe can only be defined by a combination of characters (Seevers, 1978; Newton *et al*., 2000).

Three of the six informal groups of the Oxypodina proposed by Seevers (1978) are not recovered as members of subclade F (i.e. *Acrimaea*, *Amarochara* and *Dexiogyia* groups). The other three – *Ocalea* (≈clade J), *Oxypoda* (≈clade K) and *Gnathusa* (within clade J) – together form subclade F.

The *Ocalea* group *sensu* Seevers included *Ocalea*, *Longipeltina* and *Ilyobates*, and was proposed without a diagnosis (Seevers, 1978). Klimaszewski & Pelletier (2004) revised the Nearctic species of the *Ocalea* group, based mostly on external characters and without analysing its phylogeny. Here, some of the hypotheses proposed by Seevers (1978) and Klimaszewski & Pelletier (2004) are rejected: (i) *Ilyobates* is closely related to *Oxypoda* (clade K) and not *Ocalea* (clade J); (ii) the genera *Ocalea sensu* Klimaszewski & Pelletier and *Neothetalia* are not monophyletic; (iii) *Parocalea* is closely related to *Dinarda* and *Thiasophila* (clade N) and not *Ocalea*. Corresponding to clade J, the *Ocalea* group is redefined and includes *Ocalea*, *Isoglossa*, *Neothetalia nimia*, *Mniusa* and *Gnathusa*, the latter placed by Seevers (1978) in the separate *Gnathusa* group. However, *Neothetalia canadiana* is not recovered within clade J. The sclerites of the internal sac of the aedeagus are very different in *N. canadiana* and *N. nimia* (V. Gusarov, unpublished observation), providing additional support for the hypothesis that the two species are not closely related, and should not be treated as congeneric.

The *Oxypoda* group was proposed by Seevers (1978) based on the presence of the frontal suture (= frontoclypeal; Beutel & Lawrence, 2005). However, depending on the sculpture and punctation of the head, in different species the suture may either appear well pronounced or almost indistinct (V. Gusarov, unpublished observation). Inside the head capsule, the suture corresponds to the frontoclypeal phragma connecting the anterior tentorial pits. The phragma is present in all genera of clade K except *Ilyobates*. In *Oxypoda opaca*, which does not belong to clade K, the phragma is absent (V. Gusarov, unpublished observation). We hypothesize that the presence of a frontoclypeal phragma is a synapomorphy of clade K (with reversal in *Ilyobates*). Future studies may address this issue in more details. Corresponding to clade K, the *Oxypoda* group is redefined and includes *Oxypoda* (but not *O. opaca*), *Acrostiba*, *Calodera*, *Devia*, *Ilyobates*, *Ocyusa*, *Ocyustiba*, *Oreuryalea* and *Tetralaucopora*.

Within clade K, the monophyly of two morphologically fairly uniform genera, *Ilyobates* and *Tetralaucopora*, is confirmed. In contrast, *Oxypoda*, represented by four species of three subgenera (*Oxypoda* s. str., *Mycetodrepa* and *Podoxya*), is recovered as non-monophyletic. As stated above, *Oxypoda* (s. str.) *opaca* is not even a member of clade K. However, with a total of 493 described species and 14 subgenera (Newton & Thayer, 2005), *Oxypoda* is a very large genus and a more extensive taxon sampling of *Oxypoda* and related genera is needed for more informative phylogenetic conclusions.

The second subclade (H) of the PHOL clade includes the members of the tribe Liparocephalini as sister to clade M, which consists of four genera traditionally placed in the Oxypodini. The Liparocephalini are a group of aleocharines restricted to marine coastal habitats. A phylogeny of the tribe was presented by Ahn & Ashe (1996) and Ahn *et al*. (2010), but in both studies the outgroup did not include any members of the Oxypodini. Clade M comprises the oxypodines *Blepharhymenus*, *Parocalea*, *Dinarda* and *Thiasophila*. A close relationship among these four genera has never been proposed. As discussed above, *Parocalea* was traditionally considered a member of the subtribe Oxypodina (Newton *et al*., 2000) closely related to *Ocalea* (Klimaszewski & Pelletier, 2004). *Blepharhymenus* was normally treated as single genus of the subtribe Blepharhymenina, erected based on the distinct body shape, particularly the very narrow neck (Seevers, 1978). *Thiasophila* was treated as member of the *Dexiogyia* group of the subtribe Oxypodina, together with *Dexiogyia*, *Crataraea* and *Haploglossa* (Seevers, 1978). As the latter two genera form the separate subclade I within the PHOL clade, the phylogenetic analysis rejects the hypothesis of a close relationship between *Thiasophila*

and *Haploglossa* or *Crataraea*. Instead, *Thiasophila* is found to be closely related to *Dinarda* of the oxypodine subtribe Dinardina. The Dinardina were defined based on a more or less limuloid body shape, with a broad and shield-like pronotum (Seevers, 1978). Besides *Dinarda*, the subtribe includes nine other myrmecophile genera, among them *Myrmobiota* (Seevers, 1978). As *Myrmobiota* is recovered as a separate lineage of the PHOL clade, distant from Dinarda, the Dinardina *sensu* Seevers (1978) are not monophyletic. Thus, the present study not only supports an independent origin of myrmecophily in *Dinarda* and *Myrmobiota*, but also suggests a single origin of myrmecophily in *Thiasophila* + *Dinarda*. However, myrmecophily is common in many groups of Aleocharinae (Seevers, 1965) and has evolved independently many times. The overall similarity in body shape among many myrmecophiles is likely correlated with a similar lifestyle (Maruyama, 2009). Because most branches of subclade M are very long, additional species of *Blepharhymenus* as well as other genera of Dinardina need to be included in future molecular studies to resolve the basal relationships.

The monophyly of the subtribe Meoticina (subclade G), as defined according to Muona (1991) and Seevers (1978), is confirmed. *Meotica* is recovered as the sister group to all the remaining Meoticina in BI and ML analyses (Fig. 2), whereas MP analysis yielded a sister group relationship between *Meotica* and *Apimela* (Figure S1). However, the presence of falcate claws (Seevers 1978) in all meoticine genera except *Meotica* supports the results of BI and ML analyses. Further, the clade *Alisalia* + (*Bamona* + Meoticina Genus 1) is supported by a derived tarsal formula, 4-4-4.

As discussed above, *Haploglossa* and *Crataraea* were placed by Seevers (1978) in the *Dexiogyia* group of the Oxypodina, together with *Dexiogyia* and *Thiasophila*. Within the present study, *Haploglossa* and *Crataraea* form the separate subclade I of the PHOL clade, distant from both the Oxypodina (subclade F) and *Thiasophila* (subclade N). There is an available family group name, Microglottina Fenyes, 1918 (Newton & Thayer, 1992), for subclade I and we reintroduce it as valid subtribe name.

Seevers (1978) placed the genus *Phloeopora* in the *Amarochara* group of the Oxypodina. The present study recovered *Phloeopora* as a separate lineage of the PHOL clade, with unresolved relationships to the other eight subclades. *Amarochara* is found not even to be a member of the tribe Oxypodini, refuting Seevers' (1978) hypothesis of the *Amarochara* group. Instead, based on the inferred phylogeny we treat *Phloeopora* as the only member of the subtribe Phloeoporina. Phloeoporina is an available family group name (Newton & Thayer, 1992) that was originally introduced for a subtribe that included *Phloeopora*, and three genera which are currently considered as members of the tribe Athetini (Benick & Lohse, 1974; Smetana, 2004).

The remaining three separate lineages of the PHOL clade are an unidentified genus from Peru (labelled as Aleocharinae Genus 1), and the tribes Placusini and Hoplandriini, both represented by their type genera. A close relationship of the Hoplandriini to either the Placusini or Oxypodini was not recovered by the analyses of Elven *et al*. (2010, 2012). In contrast, the close relationship of the Placusini and the Oxypodini as demonstrated by Elven *et al*. (2010, 2012) is confirmed. It is important to note that the *Hoplandria* branch is very long, which may have affected the results of the phylogenetic analyses. Additional genera of the Hoplandriini need to be included in the analyses in order to clarify the tribe's relationships to the Oxypodini and other aleocharines.

Updated classification of the Oxypodini

The present study reveals that *Amarochara, Halobrecta* and the Tachyusini do not belong to the tribe Oxypodini. Because the basal relationships in the PHOL clade remain unresolved, all genera of clade C traditionally classified as Oxypodini are still considered as members of the tribe. For the same reason, the Liparocephalini are not downgraded to a subtribe of the Oxypodini. The oxypodine subclades of clade C are recognized as subtribes, except for the *Myrmobiota* lineage, which has currently no available family group name. *Myrmobiota* is classified as Oxypodini *incertae sedis*.

Based on the present analyses, the following five subtribes are recognized: Oxypodina Thomson (clade F) (= Caloderina Mulsant & Rey; = Ocaleina Thomson; = Ocyusina Mulsant & Rey), Dinardina Mulsant & Rey (clade M) (= Blepharhymenina Klimaszewski & Peck, **syn.n**.), Meoticina Seevers (clade G), Microglottina Fenyes (clade I) and Phloeoporina Thomson (Tables 1, S4). An updated diagnosis for each subtribe is provided in Table S4.

The type genera of four oxypodine suprageneric groups were not available for the present study, namely Aphytopodina Bernhauer & Scheerpeltz, Decusina Fenyes, Homéusates Mulsant & Rey, and Saphoglossina Bernhauer & Scheerpeltz (Table 1). The Aphytopodina are considered a valid subtribe of the Oxypodini (Newton & Thayer, 1992; Bouchard *et al*., 2011). The family group names Decusina and Homéusates are currently treated as synonyms of the subtribe name Dinardina (Newton & Thayer, 1992; Bouchard *et al*., 2011). Regarding the Saphoglossina, we follow the traditional view (Newton & Thayer, 1992; Bouchard *et al*., 2011) and do not consider them as a member of the Oxypodini, in contrast to Navarrete-Heredia *et al*. (2002).

Aleocharine phylogeny

The present study relies on the most complete sampling of aleocharine tribes. A comprehensive phylogeny of the subfamily with 12 000 described species classified into more than 50 tribes (Newton & Thayer, 2005) is beyond the scope of this study, but the results allow for new insights into the phylogenetic relationships within the Aleocharinae.

Tribe Aleocharini

The tribe Aleocharini (clade A) is the sister group to the remaining 'higher' aleocharines except the Hypocyphtini.

Recently, the Aleocharini were considered as closely related to the Hoplandriini (Seevers, 1978; Ashe, 2007). However, morphology-based analyses have never provided unequivocal evidence for the sister group relationship between the Aleocharini and the Hoplandriini (Maus *et al*., 2001; Ahn & Ashe, 2004; Ashe, 2005; Paśnik, 2010). The present study does not support a close relationship between the two tribes.

Tribe Hygronomini

The tribe Hygronomini, represented by the single species *Hygronoma dimidiata*, is firmly placed in clade E together with the Athetini and the Tachyusini. The athetine bridge of the aedeagus is present in *H. dimidiata* (V. Gusarov, unpublished observation). This further supports a close relationship between *H. dimidiata* and the Athetini. Thirty-eight genera have been assigned to the Hygronomini based on the tarsal formula 4-4-4 (Bernhauer & Scheerpeltz, 1926), which is considered rare within the Aleocharinae. Some of these genera have already been moved to other tribes (e.g. Seevers, 1957, 1965, 1978). However, no study has yet addressed the phylogeny of the Hygronomini and their relationships to other tribes.

Additional aleocharine clades

Five further conclusions on the phylogeny of the 'higher' Aleocharinae seem justified, as many intertribal relationships were recovered with high statistical support.

1 Corroborating the results of Ahn & Ashe (2004) the tribe Hypocyphtini is confirmed as sister group to all other tribes of 'higher' aleocharines.
2 In contrast to the traditional classification of the Homalotini (Newton & Thayer, 1992), the subtribe Homalotina is not closely related to the subtribes Gyrophaenina and Bolitocharina of the Homalotini.
3 Contrary to the recent hypothesis of Klimaszewski *et al*. (2010), a close relationship of the tribe Himalusini to any of the tribes Aleocharini, Hoplandriini, Placusini, or the subtribe Homalotina is not supported.
4 The tribe Pygostenini is recovered as the sister clade to the Lomechusini. An extended taxon sampling may clarify the relationship between the two tribes.
5 *Stenectinobregma* is not closely related to either the Tachyusini or Pronomaeini. The genus was described by Scheerpeltz (1974) twice, as a member of the tribe Pronomaeini, and under the name *Gnypetoidea* as a member of the Tachyusini. Paśnik (2007) synonymized *Gnypetoidea* with *Stenectinobregma*, but did not explicitly assign it to a tribe.

Proposed changes in classification

Based on the present study, the following changes in the classification of the Aleocharinae are proposed:

1 The genus *Amarochara* Thomson is transferred from the tribe Oxypodini Thomson to the tribe Aleocharini Fleming.
2 The subtribe Tachyusina Thomson is removed from the tribe Oxypodini Thomson and provisionally treated as the valid tribe Tachyusini.
3 The tribe Oxypodini Thomson is divided into six subtribes: Aphytopodina Bernhauer & Scheerpeltz, Oxypodina Thomson (= Caloderina Mulsant & Rey; = Ocaleina Thomson; = Ocyusina Mulsant & Rey), Dinardina Mulsant & Rey (= Blepharhymenina Klimaszewski & Peck, **syn.n**.), Meoticina Seevers, Microglottina Fenyes and Phloeoporina Thomson (Table 1).
4 The subtribe Taxicerina Lohse is reinstated as tribe Taxicerini. The tribe includes *Halobrecta* Thomson, *Discerota* Mulsant & Rey and *Taxicera* Mulsant & Rey.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12011

Figure S1. Bootstrap consensus tree from the MP analysis of the full dataset. Clade labels are in circles. Bootstrap support values ≥ 50 are indicated above branches. Clade names follow the newly proposed classification.

Figure S2. Bootstrap consensus tree from the MP analysis of the reduced dataset. Clade labels are in circles. Bootstrap support values ≥ 50 are indicated above branches. Clade names follow the newly proposed classification.

Figure S3. Best tree from the ML analysis of the full dataset with *28S* sequences excluded. Clade labels are in circles. Bootstrap support values ≥ 50 are indicated above branches. Clade names are based on the newly proposed classification.

Figure S4. Best tree from the ML analysis of the full dataset based on a modified partitioning scheme (*18S* and *28S* one partition each). Clade labels are in circles. Bootstrap support values ≥ 50 are indicated above branches. Clade names are based on the newly proposed classification.

Figure S5. Best tree from the ML analysis of the full dataset based on a modified partitioning scheme (partitioned by gene). Clade labels are in circles. Bootstrap support values ≥ 50 are indicated above branches. Clade names are based on the newly proposed classification.

Figure S6. Majority rule consensus tree from the BI analysis of the reduced dataset. Clade labels are in circles. Posterior probabilities ≥ 0.94 are indicated above branches. Clade names are based on the newly proposed classification.

Table S1. Label information for the specimens included in this study. The specimens marked with asterisk (*) and dagger (†) are deposited in the Natural History Museum of Denmark (ZMUC) and the Field Museum of Natural

History (FMNH), respectively. The remaining specimens are deposited in the Natural History Museum, University of Oslo (ZMUN).

Table S2. List of primers and amplification strategies with annealing temperatures (Ta) used in this study.

Table S3. Characteristics of the sequence data.

Table S4. Diagnoses of the subtribes of Oxypodini.

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