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Author(s): Xi Zhang and Hong-Zhang Zhou
Source: Zoological Science, 30(6):490-501. 2013.
Published By: Zoological Society of Japan
DOI: http://dx.doi.org/10.2108/zsj.30.490
URL: http://www.bioone.org/doi/full/10.2108/zsj.30.490

ZOOLOGICAL SCIENCE **30**: 490–501 (2013)

How Old Are the Rove Beetles (Insecta: Coleoptera: Staphylinidae) and Their Lineages? Seeking an Answer with DNA

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The phylogeny and related evolutionary history of rove beetles (Coleoptera, Staphylinidae) remain unclear. This study provides phylogenetic analyses for the family based on three genes (mitochondrial COI, nuclear protein-coding wingless and a portion of the ribosomal 28S rDNA) including 2413 bp for 104 taxa representing most major staphylinid lineages. The subfamilies Oxyporinae, Paederinae, Steninae, and Proteininae are all well-supported clades, as evidenced by all three inference methods, namely maximum parsimony, Bayesian inference, and maximum likelihood. From fossils available for calibration, the divergence time of the main lineages in the family is estimated based on an uncorrelated lognormal relaxed molecular clock analysis method. The molecular clock analysis suggests that the family Staphylinidae dates from approximately the Early Triassic epoch and the most lineages of the family started to radiate from the Late Jurassic to the Early Paleogene.

Key words: Staphylinidae, Staphylininae, maximum parsimony, Bayesian inference, maximum likelihood, molecular dating, relaxed molecular clock

INTRODUCTION

The family Staphylinidae Latreille, 1802 (Insecta: Coleoptera: Staphylinoidea), commonly known as rove beetles, is one of the largest beetle families, with high biological diversity on global scale and very complex evolutionary history over a very long geological time (Crowson, 1955; Newton and Thayer, 1992; Hansen, 1997; Grimaldi and Engel, 2005; Lefebvre et al., 2005; Clarke and Chatzimanolis, 2009; Engel and Chatzimanolis, 2009; Grebennikov and Newton, 2009). This group is considered one of the most successful groups of insects, and is well adapted to most heterogeneous habitats (Thayer, 2005; Grebennikov and Newton, 2009). Phylogenetic studies to such a species-rich beetle group are therefore of great significance to biological evolution and speciation as well as to biodiversity conservation (Zhou, 2000; Thayer, 2005). Since Erichson (1840), the high-level classification system of the Staphylinidae, discussed and improved by a many of the later taxonomists, has experienced dramatic modifications (cf. Paulian, 1941; Jeannel and Jarrige, 1949; Lawrence and Newton, 1982; Naomi, 1985; Newton and Thayer, 1992; Herman, 2001a; Zhou, 2005). Some studies focused on the phylogenetic relationships within the Staphylinidae, such as those between the subfamilies Staphylininae, Scydmaeninae, Euaesthetinae, Steninae, and Leptotyphlinae (Leschen and Newton, 2003; Solodovnikov and Newton, 2005; Grebennikov and Newton, 2008; Clarke and Grebennikov, 2009). However, the modern taxonomic system of the Staphylinidae, in part or in whole, was not phylogenetically evaluated and thus was constructed on a poorly-established phylogenetic basis (Solodovnikov and Newton, 2005; Zhou, 2005; Chatzimanolis et al., 2010). Conflict hypotheses were frequently found in studies with different analysis methods, for example, the monophyly of Staphylinidae and its genealogical affinity to other related taxa was very ambiguous (Ashe and Newton, 1993; Newton and Thayer, 1995; Korte et al., 2004; Ashe, 2005; Caterino et al., 2005; Hunt et al., 2007; Grebennikov and Newton, 2009); Naomi (1985) proposed that the family Staphylinidae *auct*. should be divided into three families: Oxytelidae, Staphylinidae, and Oxyporidae, whereas most other taxonomists preferred a four-grouped system: omaliine-group, oxyteline-group, staphylinine-group and tachyporine-group (Newton and Thayer, 1988, 1992, 1995; Ashe and Newton, 1993; Herman, 2001b). Therefore, there is a pressing requirement to reconstruct a more reliable phylogeny, so that the rove beetle taxonomy can be established on a more stable, or a natural, classification system.

Molecular phylogenetics has become a well-established approach over the past decade, and has played an important role in studies on modern animal evolution and phylogenetics. High-level systematic problems have been analyzed and their complex phylogenetic patterns unraveled using this approach; some remarkable advances have been made in many different high-level taxa, including Metazoa,

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Supplemental material for this article is available online.
doi:10.2108/zsj.30.490

Arthropoda, Hexapoda or Insecta, Coleoptera etc. (Nielsen, 1989; Hedges and Kumar, 1998; Nardi et al., 2003; Hunt et al., 2007; Budd and Telford, 2009). From these studies, especially those focusing on the macroevolution and high level phylogeny of Coleoptera, Polyphaga, or Staphyliniformia, we were also able to obtain valuable, but fragmentary, cues to the phylogeny of the rove beetles themselves (Caterino et al., 2002, 2005; Korte et al., 2004; Hunt et al., 2007). Using molecular approaches, some pioneering scientists concentrated their studies on the phylogeny of the Staphylinidae *per se*. Ballard et al. (1998) conducted a phylogenetic analysis of Staphylinidae using mitochondrial markers; Maus et al. (2001), Thomas (2009) and Elven et al. (2010) presented some molecular phylogenetic patterns in the subfamily Aleocharinae. Chatzimanolis et al. (2010) made a profound molecular analysis to the phylogeny of the tribe Staphylinini; Jeon et al. (2012) focused on the genus *Cafius* of the subfamily Staphylininae.

In this study, we designed our analysis based on the above-mentioned previous works and thus sampled an even larger number of terminal species of Staphylinidae, including 15 of the extant 32 subfamilies of the entire family, especially species-rich subfamilies such as Staphylininae, Paederinae, Oxytelinae, Osoriinae, Aleocharinae, and Tachyporinae. In addition to increasing the total number of representative species, we also use one mitochondrial marker cytochrome *c* oxidase subunit I (COI) gene and two nuclear markers, wingless (Wg) and partial 28S rRNA (28S) genes, so that we are able to investigate both deeper and shallower divergences (Hedges and Kumar, 1998).

As one of the major objectives of evolutionary studies, the dating of radiation events is greatly helpful for us to understand the evolutionary history of one certain group (Gaunt and Miles, 2002). Using the molecular clock analysis method and the available fossil records, we can make assumptions about the divergence times among lineages and the dating of branching events on phylogenetic trees. Many advances have been made in estimating phylogenetic timescales of beetles by the molecular clock hypothesis approach (Farrell, 1998; Prüser and Mossakowski, 1998; Gómez-Zurita et al., 2000, 2007; Hunt et al., 2007; Ruiz et al., 2009). In contrast, no divergence time estimation had been performed either for the family Staphylinidae as a whole or for any subfamily therein. In the present study, we conducted a phylogenetic timescale analysis for rove beetles using relaxed-clock method. The following questions were addressed: (1) the time of the origin of the family Staphylinidae and the divergence times of its sub-lineages with multiple calibrations; and (2) a preliminary investigation of the phylogenetic patterns of the main subfamilies within the family Staphylinidae.

MATERIALS AND METHODS

Taxon selection and sampling

A total of 102 species belonging to 77 genera representing all the four, traditionally-accepted subgroups in the family Staphylinidae were included in this study. The omaliine-group was represented by four genera from the three subfamilies, Omaliinae, Proteininae, and Pselaphinae. The oxyteline-group was represented by 12 genera from the four subfamilies Oxytelinae, Osoriinae, Piestinae, and Scaphidiinae. The staphylinine-group was represented by 57 genera from the six subfamilies Euaesthetinae, Oxyporinae, Paederinae, Scydmaeninae, Staphylininae and Steninae. The tachyporine-group was represented by four genera from the two subfamilies Aleocharinae and Tachyporinae. The family Silphidae, a supposed sister family to Staphylinidae (Newton and Thayer, 1992; Hansen, 1997), was included as the outgroup taxa to root the resulting trees. Most sequences of the tribe Staphylinini of the subfamily Staphylininae and two sequences of the subfamily Paederinae were obtained from GenBank submitted by Chatzimanolis et al. (2010); the other sequences were newly generated in this study, and can be found in the supplementary material, Table S1.

DNA extraction, amplification and sequencing

DNA was extracted from the head and prothorax of beetles using the Tiangen DNeasy Blood and Tissue Kit (Tiangen, China) following the manufacturer's protocol. Three target genes, viz. COI, Wg and 28S, were amplified by PCR using the primer combinations listed in Table 1. PCR amplification was carried out following the protocols as described in Chatzimanolis et al. (2010). PCR products were purified using the High Pure PCR Product Purification Kit (TAKARA BIO INC., China) and sequenced in both directions using an automated sequencer (ABI Prism 3730 XL DNA Analyzer; ABI Prism, Foster City, CA) at the Beijing Genomics Institute.

Sequence alignment

The sequences for COI and Wg were initially aligned using the default settings in Clustal X version 2.0 (Higgins et al., 2007) and adjusted in Se-Al v2.0a11 (Rambaut, 2002). Alignment of the COI sequences was straightforward. The 5′ and 3′ ends of wingless were easy to align, but a central region of about 50 nucleotides was more challenging to align. That region of Wg is consistently hard to align in beetles (Wild and Maddison, 2008; Maddison et al., 2009; Chatzimanolis et al., 2010). For the 28S sequences, secondary structure was inferred through comparison with published secondary structures of *Tenebrio* sp. (Gillespie et al., 2004) and used as a guide for manual sequence alignment in MEGA 5.0 (Tamura et al., 2011).

Table 1. Primers used to amplify the sequences studied.

Gene	Primer name	Dir.	Sequence (5′–3′)	References
mtDNA				
COI	C1-J-2183 (Jerry)	F	CAACATTTATTTTGATTTTTTGG	Simon et al. (1994)
	L2-N-3014 (Pat)	R	TCCAATGCACTAATCTGCCATATTA	Simon et al. (1994)
Nuclear				
Wingless	Wg550	F	ATGCGTCAGGARTGYAARTGYCAYGGYATGTC	Wild and Maddison (2008)
	Wg578	F	TGCCANGTGAARACYTGCTGGATG	Ward and Downie (2005)
	WgABR	R	ACYTCGCAGCACCARTGGAA	Abouheif and Wray (2002)
	WgABRZ	R	CACTTNACYTCRCARCACCARTG	Wild and Maddison (2008)
28S	NFL184-21	F	ACCCGCTGAAYTTAAGCATAT	Van der Auwera et al. (1994)
	LS1041	R	TACGGACRTCCATCAGGGTTTCCCCTGACTTC	Maddison (2008)

Sequence saturation

Nucleotide saturation was analyzed by plotting number of transitions (Ti) and transversions (Tv) against corrected genetic distance values in DAMBE version 5.2 (Xia and Lemey, 2009). Separate plots were made for all the three genes, and also for the 1st, 2nd, and 3rd codon positions of the pooled protein coding genes. A second order polynomial regression line was fitted to the saturation plots. The data was considered saturated if the slope of this regression line was zero or negative for comparisons within the ingroup taxa.

Phylogenetic analysis

The concatenated data set was analyzed using maximum parsimony (MP), Bayesian inference (BI) and maximum likelihood (ML). All the MP, ML and BI analyses were performed both with and without the saturated 3rd codon positions included. MP analyses were performed in PAUP*4b10 (Swofford, 2003) using heuristic searches with TBR branch swapping and 10,000 random addition sequences. Confidence in each node was assessed by bootstrapping (2000 pseudo-replicates, heuristic search of 20 random addition replicates with TBR option). ML analyses were performed in PhyML v3.0 (Guindon and Gascuel, 2003) using the sequence evolution model selected by Modeltest 3.7 (Posada and Crandall, 1998) under the Akaike information criterion. The equilibrium frequencies were optimised. The Ts/Tv ratio, proportion of invariable sites and gamma distribution parameter were estimated by the software. The support of the data for each internal branch of the phylogeny was estimated using non-parametric bootstrap (1000 replicates). BI analyses were performed in MrBayes v3.1 (Ronquist and Huelsenbeck, 2003) with 25,000,000 generations, sampling trees every 100 generations. Sequence evolution models were selected by Modeltest 3.7 (Posada and Crandall, 1998). Likelihood values were observed with Tracer v1.5 (Rambaut and Drummond, 2007). Stationarity was also reassessed using a convergence diagnostic. An average standard deviation of the split frequencies (ASDSF) < 0.03 were used as criteria of convergence between both runs. The data used in Bayesian analyses were partitioned under two schemes: partitioned among genes (three partitions, COI, Wg and 28S) and partitioned by gene and 1st, 2nd and 3rd codon position of protein coding genes (seven partitions, COI_1st, COI_2nd, COI_3rd, Wg_1st, Wg_2nd, Wg_3rd and 28S).

Bayesian estimation of divergence times

The concatenated sequence alignment was analyzed using a relaxed molecular-clock model in the Bayesian phylogenetic software BEAST 1.6.1 (Drummond and Rambaut, 2007). Sequence

Table 2. Details on the concatenated alignment of the three target regions used in this study.

	COI_1st	COI_2nd	COI_3rd	Wg_1st	Wg _2nd	Wg _3rd	28S
Excluded positions	3[a]	3[a]	3[a]	10[b]	10[b]	10[b]	53[c]
Final length	275	275	275	136	136	136	1180
Constant sites	133	180	5	71	82	3	270
Uninformative sites	18	27	3	5	2	1	209
Informative sites	124	68	267	60	52	132	701
Mean base frequency (%)							
A	30.7	19.7	45	32.5	36	12.3	20.3
C	15.1	23.5	10.1	25.2	19.6	44.5	28.2
G	24.3	14.9	2.3	25	25.3	27.2	32.4

[a] Three codons at the 5′ end of COI excluded due to gene length polymorphism.
[b] Thirty positions of Wingless excluded due to ambiguous alignment.
[c] Positions excluded due to ambiguous alignment.

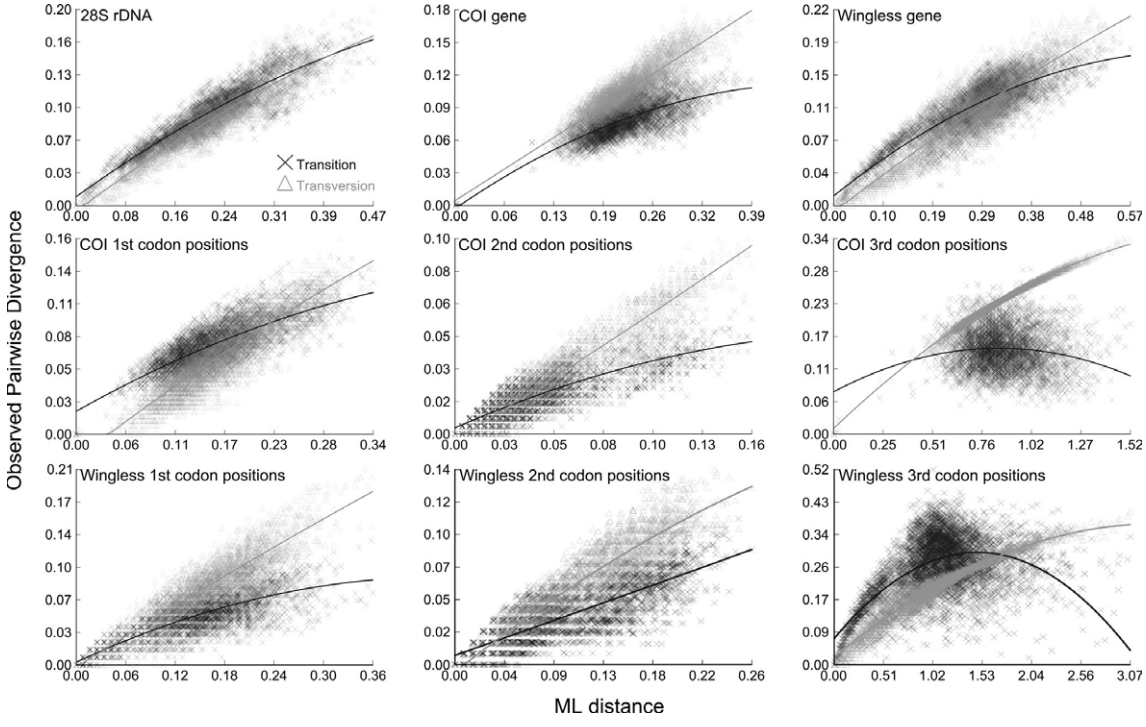


Fig. 1. Saturation analyses of transitions and transversions at the 28S gene, the COI gene, the Wg gene and 1st, 2nd, and 3rd codon positions of protein coding genes. The x-axis represents pairwise distance estimated by maximum likelihood, the y-axis is the absolute number of transitions and transversions. Transitions are shown as multiplication signs and transversions as triangles. The trend line is a best-fit 2nd degree polynomial.

variation was partitioned into three subsets according to different genes. Gene-specific nucleotide substitution model parameters were used, with each gene allowed to evolve at a different rate. The substitution models were GTR+Γ+I for COI and Wg, HKY+Γ+I for 28S following model selection by Modeltest 3.7. Rate variation among branches was modeled using uncorrelated lognormal relaxed clocks (Drummond et al., 2006). A Yule process was used for the tree prior. Posterior distributions of the parameters, including the tree, were estimated via Markov chain Monte Carlo (MCMC) sampling. Two replicate MCMC runs were performed, with the tree and parameter values sampled every 1000 steps over a total of 100 million steps. Independent runs were combined using LogCombiner1.5.4 (Rambaut and Drummond, 2010), with the first 25% of the generations from each run discarded as 'burn in'. Convergence of the chains was checked using Tracer 1.5 (Rambaut and Drummond, 2007). The searches achieved adequate mixing as assessed by the high effective sampling size (ESS) values for all parameters of 100 or greater. Node ages and upper and lower bounds of the 95% highest posterior density interval for divergence times were calculated using TreeAnnotator 1.5.4 (Drummond and Rambaut, 2007) and visualized using FigTree 1.3.1 (Rambaut, 2009).

The minimal known ages of subfamilies Euastheninae, Omaliinae, Oxyporinae, Oxytelinae, Steninae, and Tachyporinae based on fossils, were used as prior to estimate the divergence time of representative nodes. A normal distribution was used to provide for uncertainties of fossil of all calibration points (Ho, 2007). More specifically, the following six calibration points were used.

(1) The subfamily Euastheninae: we used a normally distributed estimate prior with a mean value of 130 million years ago (Mya) and a standard deviation (SD) of 5.0 (95% interval: 120.2–139.8 Mya) based on the Early Cretaceous (Neocomian) amber fossil *Libanoeuaesthetus pentatarsus* from Mdeyrij-Hammana, Caza Baabda, Mouhafazit Jabal Loubnan, Central Lebanon (Lefebvre et al., 2005).

(2) The subfamily Omaliinae: we used a normally distributed estimate prior of 165 Mya, SD 5.0 (95% interval: 155.2–174.8 Mya) based on the fossil *Prostaphylinus mirus* in the Middle Jurassic Haifanggou Formation from the Haifanggou Village, Beipiao, Liaoning Province, north-east China (Cai and Huang, 2010). According to Cai and Huang (2010), the general morphology (e.g., antenna, pronotum and small body size) of *Prostaphylinus mirus* is closely related to *Globoides* species, and the genus *Globoides* has been assigned into the Recent subfamily Omaliinae (Herman, 2001b). Therefore, the fossil *Prostaphylinus mirus* is most likely an Omaliinae species.

(3) The clade Oxyporinae: we used a normally distributed estimate prior with mean value being 127.5 Mya, and SD 5.0 (95% interval: 117.7–137.3 Mya) based on the fossil *Oxyporus yixianus* in the Early Cretaceous Yixian Formation from Chaomidian Village, Beipiao City, Liaoning Province, northeast China (Yue et al., 2011).

(4) The clade *Oxytelus* belonging to the subfamily Oxytelinae was calibrated to 127.5 Mya with SD 5.0 (95% interval: 117.7–137.3 Mya) based on the fossil *Sinoxytelus euglypheus* which is also from the Yixian Formation in northeastern China (Yue et al., 2010); based on abdominal segments with seven visible, complete sternites, and mesocoxae moderately separated by mesosternal process, Yue et al. (2010) suggested that the genus *Sinoxytelus* can be assigned to the tribe Oxytelini. Among the taxa used in this study, only the genus *Oxytelus* is the member of the tribe Oxytelini, accordingly, the fossil *Sinoxytelus euglypheus* is more closely related to *Oxytelus* species than other species.

(5) The subfamily Steninae: we used a normally distributed estimate prior with mean value 80 Mya, SD 5.0 (95% interval: 70.2–89.8 Mya) based on the Late Cretaceous fossil *Stenus imputribilis* from Russia (Ryvkin, 1988).

(6) The subfamily Tachyporinae: we used a normally distributed estimate prior with mean value 150 Mya, SD 5.0 (95% interval: 140.2–159.8 Mya) based on the fossil *Mesotachinus major* in the Late Jurassic Karatau Formation from Kazakhstan (Tikhomirova, 1968).

Table 3. Best fitting models determined by the Akaike information criterion (AIC) for the data partitions used in this study.

Partition	Model (AIC)	*P*-Inv.	G-shape
COI 1st codon position	GTR+Γ+I	0.48	0.91
COI 2nd codon position	GTR+Γ+I	0.57	0.56
COI 3rd codon position	TN93+Γ+I	0.02	1.27
COI 1st+2nd	GTR+Γ+I	0.42	0.35
COI total	GTR+Γ+I	0.39	0.9
Wg 1st codon position	TN93+Γ	–	0.21
Wg 2nd codon position	JC+Γ	–	0.11
Wg 3rd codon position	T92+Γ+I	0.02	2.45
Wg 1st+2nd	TN93+Γ+I	0.6	1.56
Wg total	GTR+Γ+I	0.43	1.35
28S total	K2+Γ+I	0.3	0.39
COI+Wg+28S	GTR+Γ+I	0.4	1.02

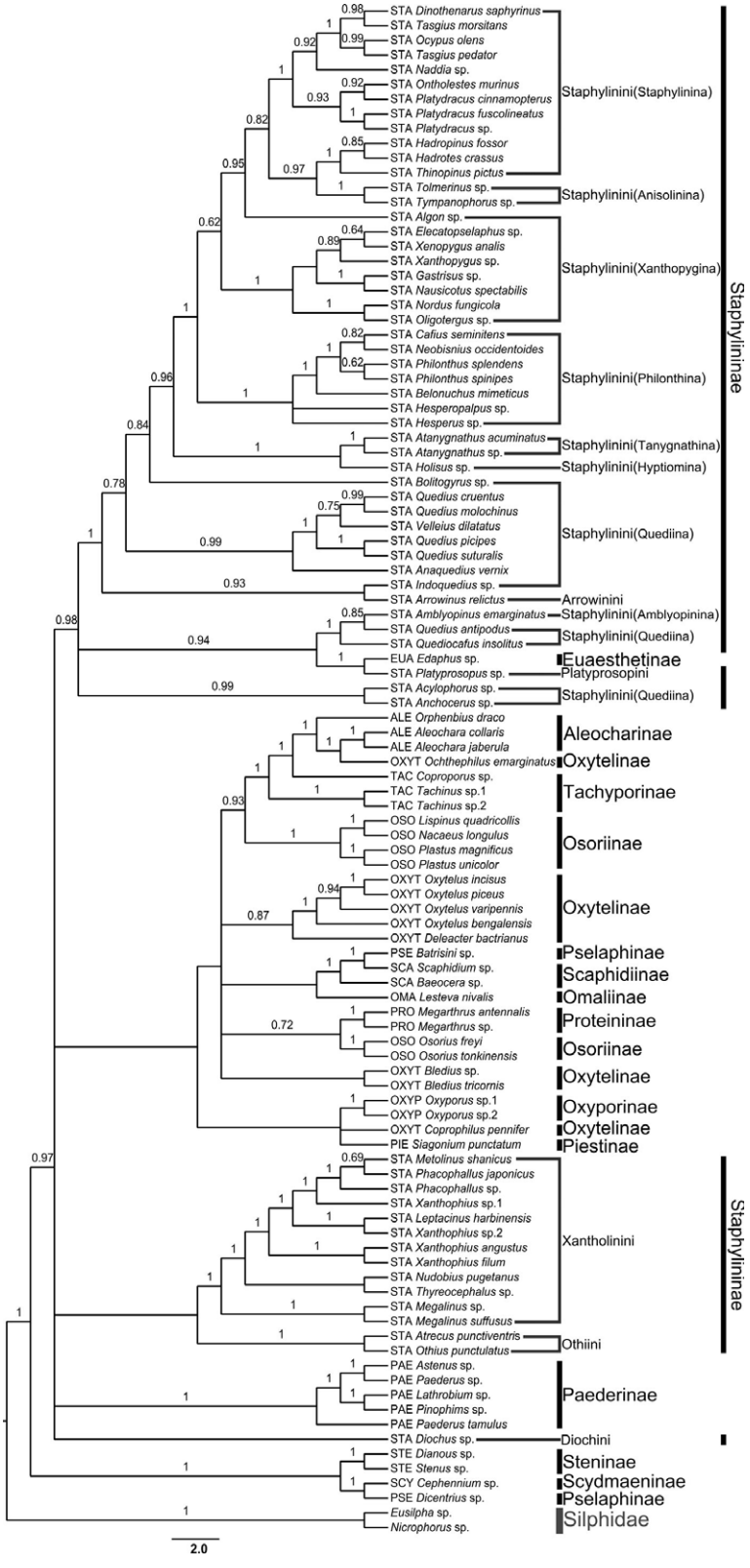
Table 4. Support values of focal clades under seven analyses. 'N' indicates the clade is unsupported by the corresponding analysis.

Clade	BI (pp)			MP (bootstrap)		ML (bootstrap)	
	3 partitions	7 partitions	Without 3rd	With 3rd	Without 3rd	With 3rd	Without 3rd
Oxyporinae	1	1	1	100	100	100	100
Paederinae	1	1	1	99	99	99	99
Steninae	1	1	1	100	100	100	100
Proteininae	1	1	1	100	100	100	100
Euaesthetinae + Platyprosopini	1	0.92	0.55	N	N	N	5
Aleocharinae + *Ochthephilus*	1	0.94	1	N	51	51	16
Tachyporinae + Aleocharinae + *Ochthephilus*	1	0.94	N	N	N	48	N
Scydmaeninae + *Dicentrius* + Steninae	1	0.94	0.88	19	43	34	30
Othiini	1	1	1	90	99	99	99
Anisolinina	1	1	0.89	58	34	79	57
Staphylinina + Anisolinina + *Algon*	0.95	0.97	N	13	N	44	N
Xanthopygina (without *Algon*)	1	1	1	95	90	98	94
Philonthina	1	1	1	31	46	72	67
Hyptiomina + Tanygnathina	1	1	1	93	85	98	92
Oxytelus	1	1	1	100	100	100	100

RESULTS

Sequence alignment and saturation

All amplifications were successful, with fragments ranging from 792 bp (*Lesteva nivalis*) to 834 bp (*Tachinus* sp.1) for COI, from 366 bp (*Paederus tamulus*) to 438 bp (*Edaphus* sp.) for Wg and from 899 bp (*Phacophallus japonicus*) to 1,132 bp (*Platydracus fuscolineatus*) for 28S. The concatenated sequence alignment contained 104 sequences and 2413 positions after trimming. A total of 92 positions were excluded from all downstream analyses due to ambiguous sequence alignment (Table 2). Plots of the number of substitutions against GTR distances revealed only 3rd codon positions of protein coding genes showed high levels of saturation in our dataset and this partition was excluded in another MP, BI and ML analyses based on the evidence of substitutional saturation (Fig. 1). Transitions of all other process partitions were in disagreement with our saturation criteria.



Model selection and analyses statistics

Model test suggested the general time reversible model (GTR+Γ+I) for six of the included partitions, and less parameter rich models for the remaining six (Table 3). For the BI analyses, the first 62,500 trees were discarded as 'burn in', and the ASDSF (average standard deviation of the split frequencies) values of BI analyses with three data partitions, seven data partitions and excluding the saturated 3rd codon positions were 0.028, 0.026 and 0.019, respectively. The MP analysis with and without the saturated positions included yielded five and 49 equally parsimonious trees with tree length = 18,241 and 9,712, CI = 0.1925 and 0.2665, RI = 0.4189 and 0.4929, respectively. The log-likelihood values of the ML analysis with and without saturated positions were −76,486.76109 and −44,472.55622, respectively.

Tree topology

A total of seven analyses by three genes with and without the saturated data under the three phylogenetic inference methods, namely MP, BI and ML, were completed in this study. The clades Oxyporinae, Paederinae, Steninae, Proteininae, Scydmaeninae + *Dicentrius* + Steninae, Othiini, Anisolinina, Xanthopygina (with-

Fig. 2. Bayesian phylogenetic tree of the family Staphylinidae, based on the combined data set of COI+Wg+28S (three data partitions). This tree is a majority rule consensus of 187,500 trees (all trees obtained following 6,250,000 burn-in generations). Only posterior probabilities above 0.60 are shown. Names of selected subfamilies are abbreviated as follows: EUA, Euaesthetinae; STA, Staphylininae; PAE, Paederinae; OXYP, Oxyporinae; STE, Steninae; SCY, Scydmaeninae; OMA, Omaliinae; PRO, Proteininae; PSE, Pselaphinae; OXYT, Oxytelinae; OSO, Osoriinae; PIE, Piestinae; SCA, Scaphidiinae; ALE, Aleocharinae; TAC, Tachyporinae. Black bar represents related subfamily; thin grey bar represents related tribes/subtribe of the main subfamily Staphylininae; thick grey bar represents the outgroup.

out *Algon*), Philonthina, Hyptiomina + Tanygnathina and *Oxytelus* were supported by all the analyses, and the clades Euaesthetinae + Platyprosopini, Aleocharinae + *Ochthephilus*, Tachyporinae + Aleocharinae + *Ochthephilus* and Staphylinina + Anisolinina + *Algon* were supported by most of the analyses. The support values of those clades under various analyses were compared and shown in Table 4. Generally, the overall resolution and support value were reduced with exclusion of the saturated 3rd codon positions. The resolution between the BI analysis with three data partitions and the BI analysis with seven data partitions were similar overall with respect to the focal clades, but the support values of focal clades in the BI analysis with seven data partitions were a little lower than that in the BI analysis with three data partitions. Therefore, the tree generated by BI analysis with three data partitions was the best among all seven trees, and we performed the following BEAST analysis based on this analysis.

In the BI analysis with three data partitions (Fig. 2), the clade including the subfamily Aleocharinae and the genus *Ochthephilus* of the subfamily Oxytelinae was well-supported, with posterior probability (pp) = 1.0. Excluding the genus *Osorius*, the remaining Osoriinae was recognized as a monophyletic group with high support value (pp = 1.0). The monophyly of the genus *Oxytelus* within the subfamily Oxytelinae was well-supported with high support value (pp = 1.0). The clades Oxyporinae, Paederinae, Steninae and Proteininae were also well-supported and all with 1.0 pp support value. The subfamily Scydmaeninae and one Pselaphinae genus *Dicentrius* formed a single clade, which was a sister group to the subfamily Steninae. The main subfamily Staphylininae was not recovered as a monophyletic group. Six of total eight subtribes (Amblyopinina, Anisolinina, Hyptiomina, Philonthina, Quediina, Staphylinina, Tanygnathina and Xanthopygina) of the tribe Staphylinini and their relationships proposed by Chatzimanolis et al. (2010) were also supported in this BI analysis. Taxonomic positions of the other two subtribes (Amblyopinina and Quediina) were confused in both analyses. The tribe Xantholinini was shown to be a well-recognized monophyletic group with high support value (pp = 1.0). The tree generated by the BI analysis with seven data partitions and the tree generated by the BI analysis with three data partitions were similar overall with respect to the focal nodes (Fig. 3). When the third codon positions of protein coding genes were excluded, the tribe Staphylinini of the subfamily Staphylininae was resolved as a well-supported group (Supplementary Fig. S1). The sister-group relationship between tribes Arrowinini and Diochini was revealed with high support value (pp = 1.0). However, the monophyly of the tribe Xantholinini was not recovered, with the subfamily Piestinae nested among it.

The MP analysis with the saturated 3rd codon

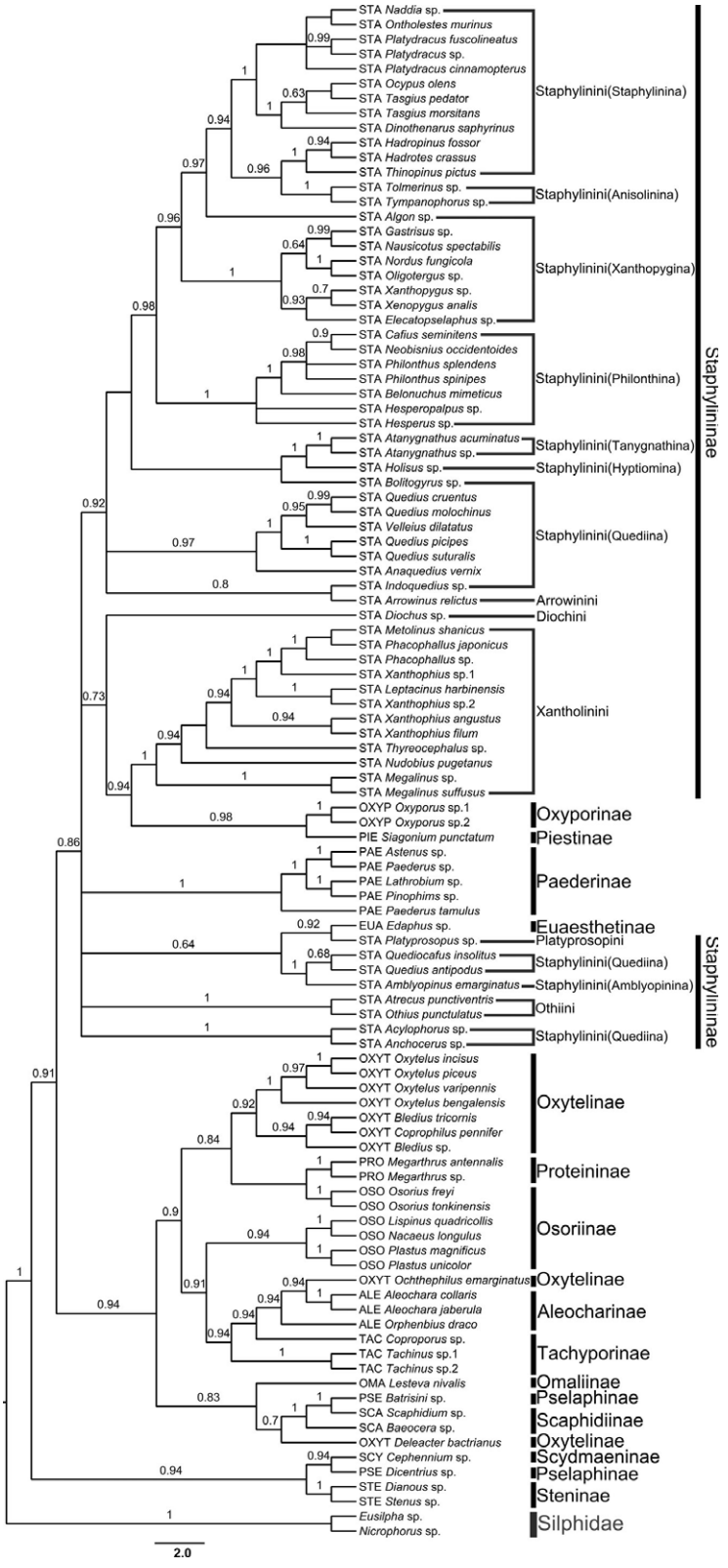


Fig. 3. Bayesian phylogenetic tree of the family Staphylinidae, based on the combined data set of COI_1st+COI_2nd+COI_3rd+Wg_1st+Wg_2nd+Wg_3rd+28S (seven data partitions). This tree is a majority rule consensus of 187,500 trees (all trees obtained following 6,250,000 burn-in generations). Only posterior probabilities above 0.60 are shown. Abbreviation of subfamily names and bars are as in Fig. 2.

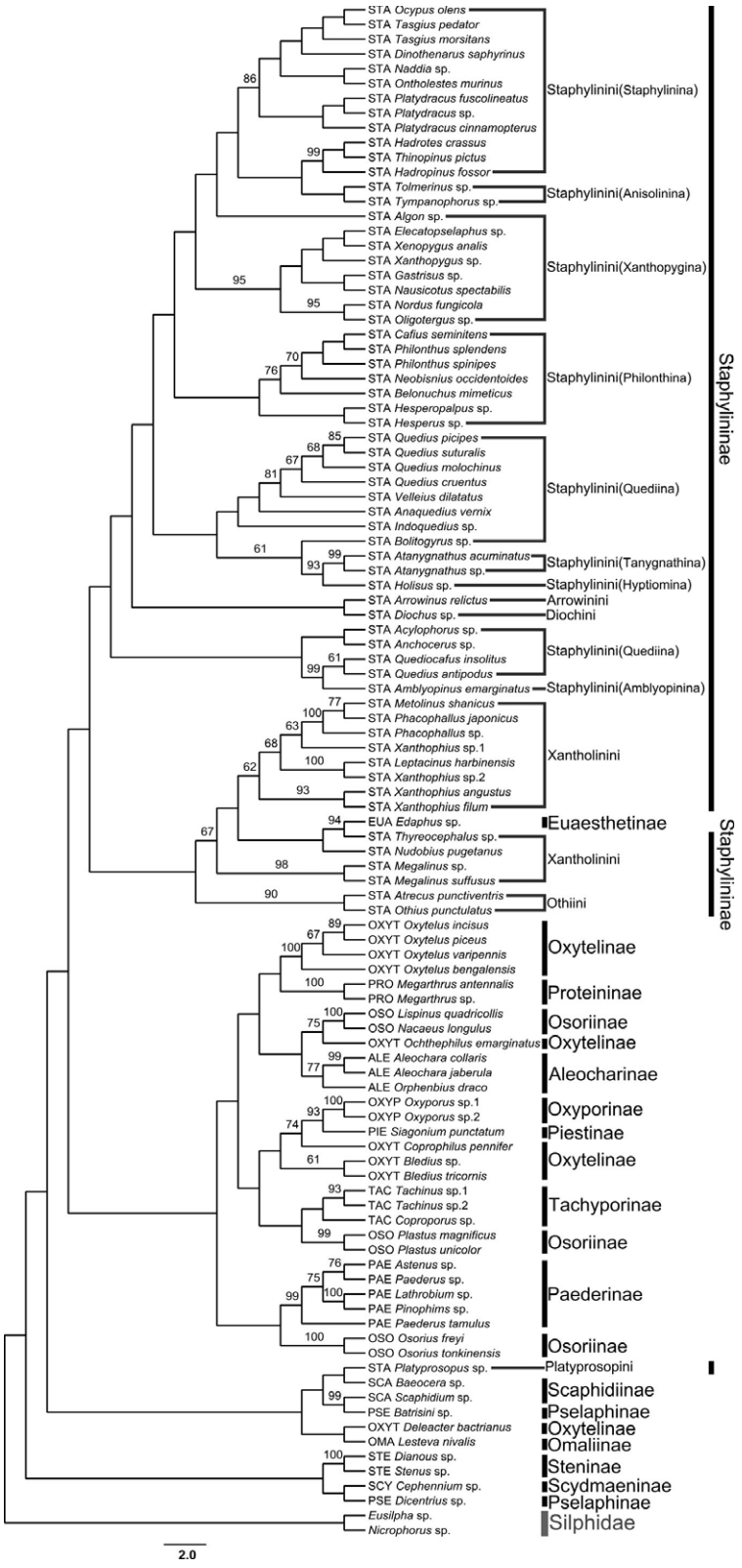


Fig. 4. Maximum parsimony phylogenetic tree of the family Staphylinidae, based on the concatenated sequence of three genes. This tree is a strict consensus tree of five equally parsimonious trees. Tree length = 18,241 steps. Only bootstrap values above 60 are shown. Abbreviation of subfamily names and bars are as in Fig. 2.

positions included resolved 12 of 15 focal clades (Fig. 4). The clades Euaesthetinae + Platyprosopini, Aleocharinae + *Ochthephilus* and Tachyporinae + Aleocharinae + *Ochthephilus* were unsupported. And the clades Scydmaenina + *Dicentrius* + Steninae, Anisolinina, Staphylinina + Anisolinina + *Algon* and Philonthina were supported with low bootstrap values (below 60). The resolution was not increased when the 3rd codon positions of protein coding genes were excluded (Supplementary Fig. S2).

The tree of the ML analysis with the saturated positions included and the tree of the BI analysis with three data partitions were congruent with respect to the focal clades, except for the clade Euaesthetinae + Platyprosopini (Fig. 5). The subfamily Euaesthetinae inserted into the tribe Xantholinini and the tribe Platyprosopini as the sister-group to the clade *Quediocafus insolitus* + *Quedius antipodus* + *Amblyopinus emarginatus* in the ML analysis. When the saturated 3rd codon positions were excluded, the ML analysis resolved 13 of 15 focal clades (Supplementary Fig. S3). The clades Tachyporinae + Aleocharinae + *Ochthephilus* and Staphylinina + Anisolinina + *Algon* were unsupported; the close relationship between tribes Arrowinini and Diochini was poorly supported (with bootstrap support value = 68).

Divergence-time estimation

The ESS values for all parameters were above 100 in both independent BEAST runs, for example, the ESS values for posterior, prior, likelihood, yule.birthRate, meanRate and speciation in the first run were 780.111, 404.751, 1419.348, 2292.628, 145.482 and 200.396, and these values in the second run were 794.851, 437.018, 1962.407, 2621.891, 175.942 and 194.322, respectively. The tree topologies generated by two BEAST runs were congruent, except for the position of the clade Xantholinini. The BEAST chronogram generated from two combined independent runs is shown in Fig. 6, and the analysis for the age of calibrated nodes is summarized in Table 5.

According to the relaxed molecular clock analysis of the concatenated data, the family Staphylinidae started radiating in the Early Triassic epoch (243.35 Mya). The earliest divergence of the subfamily Paederinae was estimated at about 176.74 Mya with a 95% highest posterior density (HPD) of 136.27–212.8 Mya. The early branching of the clade Aleocharinae + *Ochthephilus* started at about 111.46 Mya with a 95% HPD of 93.11–129.46 Mya. The earliest divergence of the subfamily Osoriinae (excluding the genus *Osorius*) was estimated at about 146.86 Mya with a 95% HPD of 108.58–182.06 Mya, and the genus *Osorius* was dated to around 90.24 Mya (95% HPD: 42.97–136.86). Within the main subfamily Staphylininae, the earliest divergence of the tribe Xantholinini

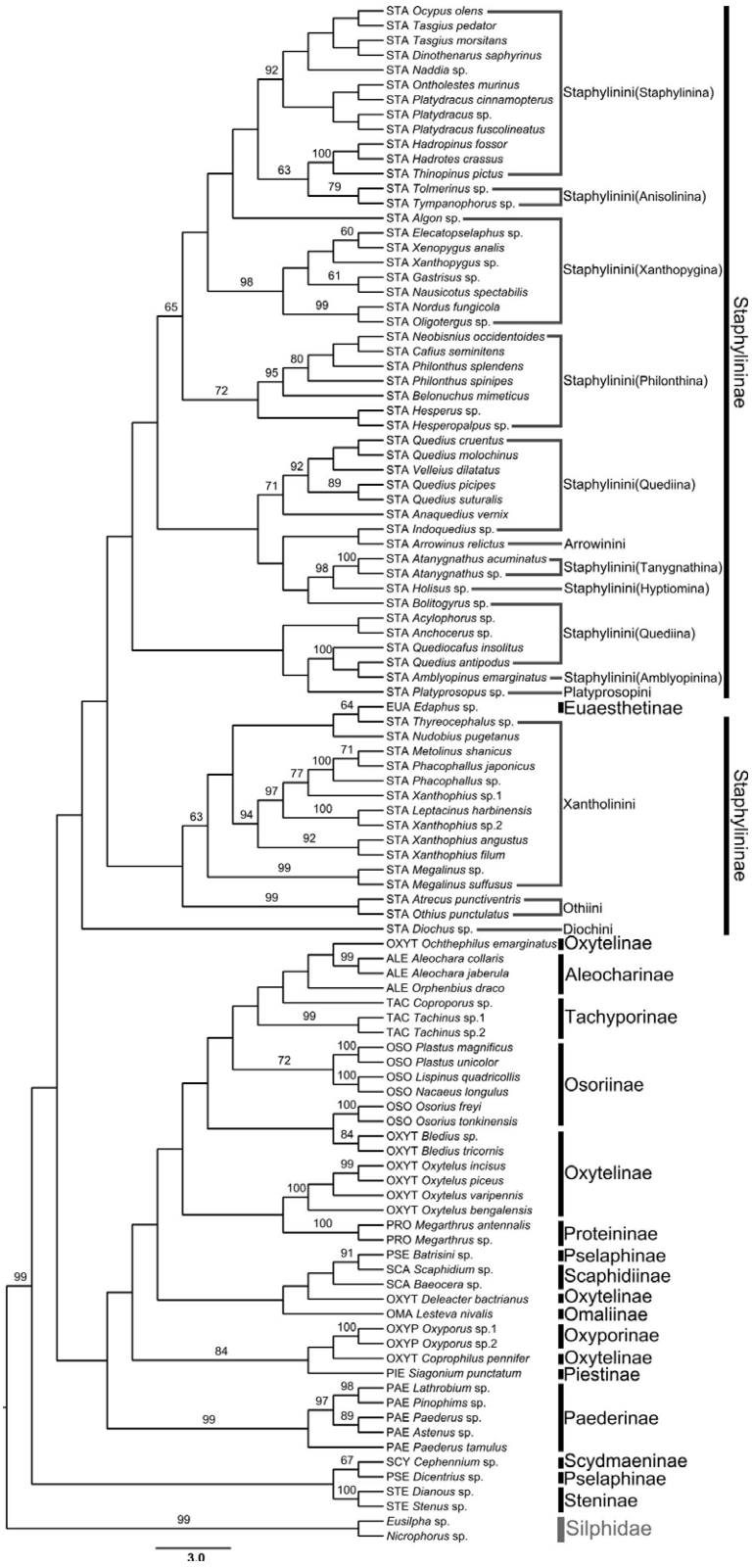


Fig. 5. Maximum likelihood phylogenetic tree of the family Staphylinidae, based on the concatenated sequence of three genes. Log-likelihood = –76,486.76109. Only bootstrap values above 60 are shown. Abbreviation of subfamily names and bars are as in Fig. 2.

was estimated to 176.03 Mya with a 95% highest posterior density of 147.99–201.88 Mya. The clade Othiini was dated to 105.14 Mya (95% HPD: 45.24–166.73). Most subtribes of the tribe Staphylinini started radiating from the Early Cretaceous to the Late Cretaceous: the early radiation of the subtribe Xanthopygina (except *Algon*) was estimated at about 110.05 Mya (Early Cretaceous, 95% HPD: 78.21–143.55); the earliest divergence of the subtribe Anisolinina was estimated at about 104.12 Mya (Middle Cretaceous, 95% HPD: 57.73–143.98); the subtribe Tanygnathina came into existence in the Late Cretaceous (66.76 Mya, with a 95% HPD of 32.01–108.14 Mya). The early branching of the clade Hyptiomina + Tanygnathina started at about 122.11 Mya (95% HPD: 81.94–158.79 Mya).

DISCUSSION

The clades of the subfamilies Oxyporinae, Paederinae, Steninae, and Proteininae were well supported under all the three phylogenetic inference methods (MP, BI and ML), but it is difficult to determine the monophyly of the subfamilies with the present dataset given the limited number of terminal taxa used in this study. Some recent studies have supported the monophyly of the subfamily Staphylininae and considered it as the sister group of the subfamily Paederinae (Solodovnikov and Newton, 2005; Chatzimanolis et al., 2010); however, the monophyletic Staphylininae never appeared in all of our analyses, nor did its close relationship to the subfamily Paederinae (Figs. 2–5 and Supplementary Figs. S1–S3). Grebennikov and Newton (2009) downgraded the family Scydmaenidae as the 32nd recent subfamily within the megadiverse Staphylinidae *sensu latissimo*, and as the sister group of the clade containing subfamilies Steninae and Euaesthetinae. Whereas, the subfamily Scydmaeninae plus a genus *Dicentrius* (Pselaphinae) form a sister group to Steninae, and Euastheninae nests in a different part of all the seven phylogenetic trees.

According to Newton and Thayer (1992) and Herman (2001b), the subfamily Staphylininae includes seven tribes: Arrowinini, Diochini, Maorothiini, Othiini, Platyprosopini, Staphylinini and Xantholinini. Solodovnikov and Newton (2005) grouped these tribes in two lineages: Xantholinine-lineage (tribes Xantholinini, Othiini, Maorothiini, Diochini and Platyprosopini) and Staphylininae-lineage (tribes Staphylinini and Arrowinini). The monophyly of the traditionally recognized subfamily Staphylininae was not resolved by our analyses. Similar to the conclusion of Chatzimanolis et al. (2010), the monophyly of the tribe Othiini and subtribes Anisolinina, Philonthina, Tanygnathina, Xanthopygina (excluding the genus *Algon*), and clades Hyptiomina +

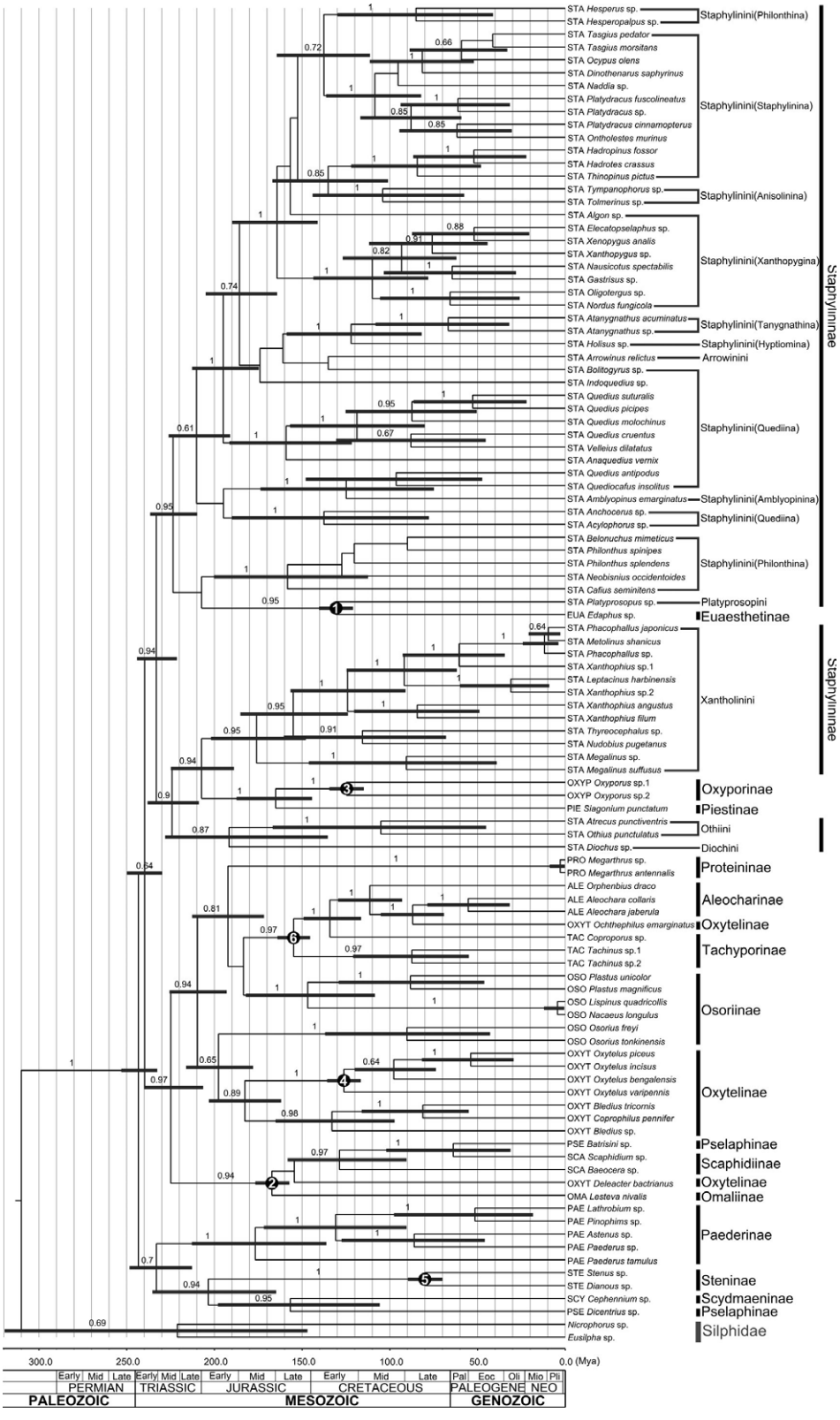


Fig. 6. BEAST chronogram of the family Staphylinidae, based on the combined analysis of COI+Wg+28S (three data partitions). Branch lengths have been scaled according to time, with nodal ages representing median posterior estimates. Nodes are labeled with posterior probabilities and only probabilities values above 0.60 are shown. Horizontal blue bars represent the 95% credibility intervals of the age estimates. Abbreviation of subfamily names and vertical bars are as in Fig. 2. Circled numbers represent calibration points. The 'NEO' in the geological age bar represents the 'Neogene' era.

Tanygnathina, Anisolinina + Staphylinina + *Algon* were also supported by the BI and ML analyses in our study. However, there are also several differences: (1) the clade Arrowinini + Diochini was supported by the analysis of Chatzimanolis et al. (2010). But in our results, the tribe Arrowinini was always the sister group of the genus *Indoquedius* (Quediina) in the BI and ML analyses when using the whole genes, although the Arrowinini + Diochini sibling relationship stood when the 3rd codon positions of protein coding genes were excluded in all the three phylogenetic inference methods (Supplementary Figs. S1–S3). Moreover, Solodovnikov and Newton (2005) considered the tribe Arrowinini as a sister-group to the tribe Staphylinini based on morphological characters. The phylogenetic position of the tribe Diochini was confused in our analyses (Figs. 2–5). Traditional classification based on morphological data also did not offer a commonly accepted treatment to the tribe Diochini (Blackwelder, 1943; Smetana, 1982; Assing, 2000), so its systematic position is still questionable. (2) Chatzimanolis et al. (2010) upheld the sister-group relationship between the tribe Xantholinini and the tribe Othiini, where only one terminal species of Xantholinini was sampled. We expanded this to a total of 12 terminal species this time, but our results remain inconclusive. The BI analysis with three data partitions poorly supported the sister-group relationship between Xantholinini and Othiini (pp = 0.56), but their close relationship was not supported by the BI analysis with seven data partitions (Fig. 2 and Fig. 3). Although the sister-group relationship between Xantholinini and Othiini was supported by other analyses, the monophyly of Xantholinini was destroyed by inserting members of other subfamilies. For instance, the subfamily

Table 5. Summary of the BEAST analysis for the age of calibrated nodes.

	Euaesthetinae + Platyprosopini	Omaliinae + Scaphidiinae + *Batrisini* + *Deleacter*	Oxyporinae
Mean	131.0593	168.1546	124.9712
Stderv of mean	2.82E-01	0.2568	6.47E-02
Median	130.9414	168.0688	124.9862
Geometric mean	130.9514	168.0734	124.8706
95% HPD lower	120.6769	157.9503	115.1741
95% HPD upper	141.2963	178.4219	134.6435
Auto-correlation time (ACT)	3.00E+05	2.59E+05	17,787.0063
Effective sample size (ESS)	360.4382	417.153	6071.9043
	Oxytelus	Tachyporinae + Aleocharinae + *Ochthephilus*	Steninae
Mean	126.1601	154.0843	79.888
Stderv of mean	1.63E-01	0.3104	6.44E-02
Median	126.1788	153.9297	79.882
Geometric mean	126.0651	153.9958	79.7305
95% HPD lower	116.6917	143.8745	70.1675
95% HPD upper	135.6676	164.1057	89.4985
Auto-correlation time (ACT)	1.20E+05	3.76E+05	17,556.4265
Effective sample size (ESS)	903.5438	287.0421	6151.6505

Euaesthetinae was inserted into the Xantholinini in the MP and ML analyses (Figs. 4, 5). When the saturated data were excluded, the tribe Xantholinini and the subfamily Piestinae grouped into a single clade in the MP, BI and ML analyses (Supplementary Figs. S1–S3). (3) Both in Chatzimanolis et al. (2010) and in our study, the Quediina genera did not have a unifying phylogenetic relationship, nor did they cluster together. More attention should thus be paid to the phylogeny of the subtribe Quediina in the future; it may form a focus in rove beetle phylogenetic studies. Despite the taxon sampling, a possible reason for the differentiation between the two studies is that our analysis only employed three of the four genetic markers (without the nuclear gene topoisomerase I) used in Chatzimanolis et al. (2010). Anyway, the branching pattern of the tribe Staphylinini in most of this analysis is basically the same as Chatzimanolis et al. (2010).

The broad range (ca. ± 20 Mya) of estimated dates on the origin and radiation of the family Staphylinidae reflects the uncertainty of fossil identification and time calibration usually mentioned in previous studies (Gómez-Zurita et al., 2000; Ruiz et al., 2009). As shown in Table 5, the estimated ages of nodes used for calibration are basically consistent with the corresponding fossil records (Tikhomirova, 1968; Ryvkin, 1988; Lefebvre et al., 2005; Cai and Huang, 2010; Yue et al., 2010; Yue et al., 2011). The estimated age of Staphylinidae suggests that the rove beetles began radiating in the Early Triassic. The radiation time is a little earlier than the oldest known fossil records (220–230 Mya) of rove beetles (Gore, 1988; Fraser et al., 1996). The divergence time of the subfamily Paederinae, estimated to the Middle Jurassic epoch, is earlier than the Paederinae fossil *Mesostaphylinus laiyangensis* in the Late Jurassic Laiyang Formation from Laiyang City, Shandong province of China (Zhang, 1988). But the subfamily affinity of the fossil record is unclear, and it might belong to either Paederinae or Staphylininae (Schomann and Solodovnikov, 2012). The early branching of the clade *Oxytelus* + *Bledius* + *Coprophilus* was estimated to the Middle Jurassic (182.63 Mya) in our BEAST analysis, which indicates that the taxa in the subfamily Oxytelinae had diverged at least in the Middle Jurassic. This branching time is slightly earlier than the oldest known fossil records of the subfamily Oxytelinae. According to Tichomirova (1968), the oldest known fossil records of the subfamily are *Mesoxytelus parvus* and *M. mandibularis* from the Late Jurassic Karatau Formation in Kazakhstan; however, the systematic position of these fossils are ambiguous, thus we did not use them as a calibration point in this study. The subfamily Staphylininae are known from the Jurassic (e.g., Tikhomirova, 1968; Zhang, 1988), Cretaceous (e.g., Schlüter, 1978; Ryvkin, 1988), and throughout the Cenozoic (e.g., Scudder, 1900). The estimated age of Staphylininae suggests that the taxa in this subfamily came into existence in the Late Triassic, and most subtribes within the subfamily with their divergence time during the Cretaceous era (Fig. 6). In summary, according to the molecular clock calculation on the Bayesian hypothesis of rove-beetle phylogeny, most genera of the family Staphylinidae originated from the Late Jurassic to the Early Paleogene, this origin period is consistent with the timescale estimation of other beetle groups based on molecular clock approach (Farrell, 1998; Gómez-Zurita et al., 2007; Hunt et al., 2007; Ge et al., 2011).

ACKNOWLEDGMENTS

We are grateful to Alexey Solodovnikov (Natural History Museum, Copenhagen, Denmark) for helpful comments and valuable suggestions on earlier manuscripts, thank Mr. L. Lü, Ms. Y. L. Z. Zhou, Drs. L. Li, X. Y. Li and Z. Yang (IZ-CAS) for collecting and identifying specimens used in this study, and thank two anonymous reviewers for critical comments on the manuscript. This study was supported by the National Natural Science Foundation of China (NSFC-31071909), National Science Foundation for Fostering Talents in Basic Research (NSFC-J0930004), CAS Innovation Program (KSCX2-EW-Z-5), and a grant from the Key Laboratory of the Zoological Systematics and Evolution of CAS (No. O529YX5105).

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(Received August 16, 2012 / Accepted December 14, 2012)