

OPINION

The peril of dating beetles

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Introduction

Recently, McKenna *et al.*, 2015 (MCK15 hereafter) investigated the higher level phylogenetic relationships of beetles (Insecta, Coleoptera) using the most comprehensive molecular dataset to date, and inferred the absolute ages of major groups using multiple fossil calibrations across the beetle tree of life. Based on the result of their dating analysis, beetles diverged from Strepsiptera in the Early Permian *c.* 278.33 Ma with a 95% credibility interval (95% CI) of 288.28 to 271.89 Ma, and the crown age of Coleoptera was estimated for the Late Permian *c.* 252.89 Ma (95% CI: 267.68 to 238.78 Ma), supporting the view that beetles originated before and survived through the End-Permian Mass Extinction that occurred *c.* 252 Ma (Shen *et al.*, 2011). However, some of the age estimates found in MCK15 are in conflict with current knowledge of the beetle fossil record (e.g. Nikolajev & Ren, 2010; Pan *et al.*, 2011; Prokin & Ren, 2011; Fikáček *et al.*, 2012a; Wang *et al.*, 2013, 2014; Cai *et al.*, 2014b, 2015a; Kirejtshuk *et al.*, 2014; Boucher *et al.*, 2016) and with other recently published molecular age estimates for some major beetle clades (e.g. Zhang & Zhou, 2013; Ahrens *et al.*, 2014; Bloom *et al.*, 2014; Kergoat *et al.*, 2014; Kim & Farrell, 2015; Bocák *et al.*, 2016; Gunter *et al.*, 2016). In some cases, the difference in age estimates is significant and might change our understanding of the mode and tempo of diversification dynamics of these groups.

Based on a careful examination of the data and analyses performed in MCK15, we propose that the divergence time estimates which they found are likely to underestimate clade ages. We believe this is due to the subset of fossil Coleoptera that MCK15 selected as calibration points, as well as the methodological approach used in their analyses. To explore the impact of fossil selection on the age of Coleoptera, we derived an alternative set of fossil calibration points based on best-practice recommendations (e.g. Parham *et al.*, 2012),

and performed new molecular dating analyses to investigate the effect of fossil selection and maximum ages, on posterior estimates of divergence times.

Materials and methods

Analyses based on the original set of fossils

We first replicated the results of MCK15 using the same dataset (File S2 in MCK15) and settings. To do so, we recovered the molecular matrix from MCK15 comprising eight gene fragments for a total of ~9000 bp (see MCK15 for more details). We then specified the same fossil constraints as in MCK15 following the procedure described in the original paper. Calibrated nodes as well as some suprafamilial nodes were constrained to be monophyletic. The Tree Model was set to a Yule: speciation prior in BEAUTI 1.8.2 (Drummond *et al.*, 2012). All fossil calibrations were specified using a lognormal prior (mean = 30, log-SD = 0.75) on the stem of the targeted clades except for the root that received a normal prior density (mean = 302, SD = 30). The prior distribution of the root was then truncated to the interval 270–396 Ma as in MCK15. The partitions (one partition for the ribosomal gene fragments, one partition for first and second positions of protein-coding gene fragment codons, and one partition for third positions of protein-coding gene fragment codons) and substitution models (GTR + Γ + I for all partitions) were the same as in MCK15. Preliminary analyses revealed that most parameters were critically undersampled and their associated ESS values <100 when using only a 100 million generations sampled every 1000 generations, as described in MCK15. Therefore, we ran two independent analyses with a Markov chain Monte Carlo (MCMC) running for 300 million generations and a parameter sampling every 3000 generations. The posterior trees and log files were resampled at a frequency of 30 000 then combined in LOGCOMBINER 1.8.2 (Drummond *et al.*, 2012) before applying a conservative burn-in of 50%.

Second, we replicated these analyses but instead of using monophyletic constraints, we used a fixed topology the same

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as the time tree of MCK15 (provided by Duane McKenna) as a starting tree, and unchecked the parameters allowing topology changes in BEAUTI 1.8.2. The objective of this analysis was to show that by enforcing a fixed topology we would recover similar ages as in the analysis using monophyletic constraints.

We found very similar ages between the original chronogram from MCK15 and our analyses with or without fixing the tree topology (see Files S1 and S2). Therefore, we conducted the rest of the analyses with a fixed topology.

Analyses based on the new set of fossils

In order to calibrate the tree from MCK15, we carefully checked the fossil record of Coleoptera. We selected beetle fossils known as the most ancient representatives of clades recovered in MCK15. We checked fossils for the presence of synapomorphies or relevant diagnostic characters, based partly on consultations with specialists on particular groups (see File S3 and Acknowledgements). The selection was not solely based on published data because in some instances, original descriptions had incomplete or even lacked reliable justification for the systematic placement of the fossils. Fossils were selected on the basis of shared apomorphies with a specific clade of the tree to allow their confident placement on the stem of each focal clade. Our search targeted all beetle clades and selected all available oldest representatives that we could possibly fit in the tree using the same stringent criteria. Our final fossil set consisted of 34 fossils listed in detail in Table 1. Justification for their placement in the tree is provided following the recommendation of Parham *et al.* (2012) when possible. It is noteworthy that Table 1 lists only the specimens that were ultimately retained to provide a minimum age; however, in many cases additional fossils of nearly the same age were available and reliably assigned to the same or sister clades, thereby providing even more evidence for the calibration of particular stems (see File S3 for more details).

We chose not to use the fossil calibrations used to enforce minimum ages for Hymenoptera and Neuroptera in MCK15 for several reasons. First, the taxon sampling in these two clades is extremely reduced and most major branching events are missing. Second, multiple orders of insects closely related to Coleoptera were not included in the dataset. In order to use such fossil calibrations, it would have been advisable to sample representatives of the other megadiverse orders Diptera and Lepidoptera that are representatives of the sister group of beetles and their closest relatives (e.g. Misof *et al.*, 2014). Third, the fact that all fossil calibrations from MCK15 were originally enforced at the stem of focal clades means that the fossil calibration used to constrain Hymenoptera actually enforced a minimum age on the root of the tree. This is problematic because it means that the root has in fact two different constraints that are not enforcing the same age prior. If the root was constrained with the Hymenoptera fossil calibration, then 95% of the age distribution would be found between 240 and 330 Ma. These ages are far younger than the original root calibration in MCK15 where the truncated normal distribution encompassed

an older interval (270–396 Ma). A similar issue was found for the Chrysomeloidea and Curculionoidea calibrations where the stems of both clades were constrained with different fossil taxa. However, because both calibrations were on the stem of sister lineages, the only node being constrained was the crown of Chrysomeloidea + Curculionoidea (=Phytophaga). Fortunately, in that case, both calibrations encapsulate the same information because the chrysomeloid and curculionoid fossils are from the same geological stratum in Kazakhstan. Nonetheless, these imprecisions lowered the number of informative fossil calibrations from 15 to 13 in MCK15.

Although MCK15 would not have been able to know at the time of their analyses, the root calibration they used (270–396 Ma) has proven to be problematic in light of contemporary studies. The minimum bound of the root prior in MCK15 conflicts with the most recent reviews of the beetle fossil record (e.g. Kirejtshuk *et al.*, 2014) and also with the most recent phylogenomic studies of insect evolution. In Misof *et al.* (2014) and Tong *et al.* (2015), the lower bound of the age credibility interval for the Holometabola node was estimated at 320 and 350 Ma, respectively. For future studies, a more justifiable way to place an interval on the age of the root is to use the age estimates of the recent dating studies of Misof *et al.* (2014) and Tong *et al.* (2015) in which the age of the crown Holometabola was found to be ~345 Ma (CI: ~320–370 Ma) and ~370 Ma (CI: ~350–400 Ma), respectively. These studies are based on the same phylogenomic dataset. Tong *et al.* (2015) only revisited the ages of Misof *et al.* (2014) using additional fossil evidence and different parametrisation of the Bayesian molecular dating analyses. We therefore chose to use an interval encompassing both estimates (320–400 Ma).

The new fossil calibrations were enforced in BEAUTI 1.8.2 (Drummond *et al.*, 2012) using the same priors used in MCK15, a lognormal density with mean = 30 and log (SD) = 0.75 was assigned to every fossil calibration. All other settings were left identical as in MCK15. As for the previous runs, we conducted two independent analyses of 300 million generations with a sampling every 3000 cycles. The .xml file generated in BEAUTI to perform this analysis is provided in File S4. The resulting log and tree files were then resampled at a lower frequency (30 000) and combined in LOGCOMBINER 1.8.2 with a conservative burn-in of 50% (Drummond *et al.*, 2012).

Results

All BEAST analyses performed with 300 million generations converged, with all parameters properly sampled as indicated by ESS values >200. The chronograms recovered in the preliminary tests (monophyletic constraints vs fixed topology) are presented in Files S1 and S2. Using the same settings as specified in MCK15, we recovered very similar age estimates, as indicated in File S1. Likewise, when constraining the topology to the time tree of MCK15 as presented in File S4 of the original paper, we did not recover major differences in divergence time estimates in comparison to the unconstrained analysis (File S2). The median age estimates from these two analyses are very similar to the ones of MCK15 presented in Table 2.

Table 1. List of the fossil calibrations used in the present study to infer beetle absolute divergence times.

FC	Taxon	Node (stem)	Deposit	Age	Ref.	CR1	CR2	CR3	CR4	CR5
1	<i>Coleopsis archaica</i>	Coleoptera	Grügelborn, Germany	295.5	1	✓	✓	✓	✓	✓
2	<i>Omma liassicum</i>	Ommatidae	Hasfield, United Kingdom	201.3	2	✓	✓	✓	✓	✓
3	<i>Priacma tuberculosa</i>	Priacminae	Huangbanjigou, Yixian Formation, China	125.5	3	✓	✓	✓	✓	✓
4	<i>Haplochelus georissoides</i>	Lepiceridae	Burmese amber, Myanmar	93.5	4,5	✓	✓	✓	✓	✓
5	<i>Protonectes germanicus</i>	Hydradephaga	Schönbachsmühle, Hassberge Formation, Germany	221.5	6	✓	✓	✓	✓	✓
6	<i>Oxycheilopsis cretacicus</i>	Cicindelinae	Crato Formation, Brazil	112.0	7	✓	✓	✓	✓	✓
7	<i>Juropeltastica sinica</i>	Derodontidae	Daohugou, Nei Mongol, China	157.3	8	✓	✓	✓	✓	✓
8	Undescribed species	Silphidae	Daohugou, Nei Mongol, China	157.3	9	✓	✓	✓	✓	✓
9	Undescribed species	Nicrophorinae	Hunagbanjigou, Yixian Formation, China	125.5	9	✓	✓	✓	✓	✓
10	<i>Protochares brevipalpis</i>	Hydrophilidae	Talbragar Fossil Fish Beds, Australia	152.1	10	✓	✓	✓	✓	✓
11	<i>Mesochodaeus daohugouensis</i>	Ochodaecidae	Daohugou, Nei Mongol, China	157.3	11	✓	✓	✓	✓	✓
12	<i>Sinaesalus longipes</i>	Lucanidae	Yangshuwanzi, Yixian Formation, China	122.5	12	✓	✓	✓	✓	✓
13	<i>Glaresis tridentata</i>	Glaresidae	Chaomidian, Yixian Formation, China	125.5	13	✓	✓	✓	✓	✓
14	<i>Cretodascillus sinensis</i>	Dascillidae	Liutiaogou, Yixian Formation, China	122.5	14	✓	✓	✓	✓	✓
15	<i>Sinoparathyrea bimaculata</i>	Schizopodidae	Daohugou, Nei Mongol, China	157.3	15, 16	✓	✓	✓	✓	✓
16	<i>Elmadulescens rugosus</i>	Elmidae	El Soplao amber, Las Peñasas Formation, Spain	109.0	17	✓	✓	✓	✓	✓
17	<i>Heterocerites magnus</i>	Heteroceridae	Chaomidian, Yixian Formation, China	125.5	18	✓	✓	✓	✓	✓
18	<i>Sinobrevipogon jurassicus</i>	Artematopodidae	Daohugou, Nei Mongol, China	157.3	19	✓	✓	✓	✓	✓
19	<i>Stephanopachys vetus</i>	Dinoderinae	Font-de-Benon Quarry, Charentese amber, France	99.6	20	✓	✓	✓	✓	✓
20	<i>Actenobius magneoculus</i>	Anobiinae	San Just amber, Spain	105.3	21	✓	✓	✓	✓	✓
21	<i>Rhyzobius antiquus</i>	Coccidulinae	Oise amber, France	47.8	22	✓	✓	✓	✓	✓
22	<i>Archelatrus marinae</i>	Latridiinae	Lebanese amber, Lebanon	122.5	23	✓	✓	?	✓	✓
23	<i>Paleoripiphorus deploegi</i>	Ripidiinae	Archingeay/Les Nouillers amber, France	99.6	24, 25, 26	✓	✓	✓	✓	✓
24	<i>Vetuprostomis consimilis</i>	Prostomidae	Burmese amber, Myanmar	93.5	27	✓	✓	✓	✓	✓
25	<i>Mirimordella gracilicruralis</i>	Mordellidae	Huangbanjigou, Yixian Formation, China	125.5	28	✓	✓	✓	✓	✓
26	Undescribed species	Aderidae	Lebanese amber, Lebanon	122.5	29	✓	✓	✓	✓	✓
27	<i>Alphitopsis initialis</i>	Tenebrioninae	Beipiao City, Yixian Formation, China	125.5	30	✓	✓	✓	✓	✓
28	<i>Idgiaites jurassicus</i>	Prionoceridae	Daohugou, Nei Mongol, China	157.3	31	✓	✓	✓	✓	✓
29	<i>Paracretocateres bellus</i>	Lophocaterinae	Huangbanjigou, Yixian Formation, China	125.5	32	✓	✓	✓	✓	✓
30	<i>Jurorhizophagus alienus</i>	Monotomidae	Daohugou, Nei Mongol, China	157.3	33	✓	✓	✓	✓	✓
31	<i>Cretoprionus liutiaogouensis</i>	Prioninae + Parandrinae	Liutiaogou, Yixian Formation, China	122.5	34	✓	✓	✓	✓	✓
32	<i>Mesopachymerus antiquus</i>	Bruchinae	Canadian amber, Grassy Lake, Canada	70.6	35	✓	✓	✓	✓	✓
33	Multiple fossils	Nemonychidae	Karatau-Mikhailovka, Kazakhstan	157.3	36	✓	✓	✓	✓	✓
34	<i>Cylindrobrotus pectinatus</i>	Scolytinae	Lebanese amber, Lebanon	122.5	37	✓	✓	✓	✓	✓

FC, fossil calibration number; CR, Parham *et al.* (2012) criteria; CR1, single/multiple operational taxonomic units (OTUs) with museum numbers; CR2, apomorphy-based or phylogenetic analysis; CR3, agreement of morphology and molecular data; CR4, detailed locality and stratigraphy data provided; CR5, radioisotopic age or numeric age references given. A more detailed justification after Parham *et al.*'s (2012) criteria is provided in File S3. References: 1, Kirejtshuk *et al.* (2014); 2, Crowson (1962); 3, Tan *et al.* (2006); 4, Kirejtshuk & Poinar (2006); 5, Ge *et al.* (2010); 6, Prokin *et al.* (2013a); 7, Cassola & Werner, (2004); 8, Cai *et al.* (2014a); 9, Cai *et al.* (2014b); 10, Fikáček *et al.* (2014); 11, Nikolajev & Ren (2010); 12, Nikolajev & Ren (2011); 13, Bai *et al.* (2014); 14, Jin *et al.* (2013); 15, Pan *et al.* (2011); 16, Cai *et al.* (2015a); 17, Peris *et al.* (2015a); 18, Prokin & Ren, (2011); 19, Cai *et al.* (2015b); 20, Peris *et al.* (2014); 21, Peris *et al.* (2015b); 22, Kirejtshuk & Nel (2012); 23, Kirejtshuk *et al.* (2009a); 24, Perrichot *et al.* (2004); 25, Batelka *et al.* (2006); 26, Falin & Engel (2010); 27, Engel & Grimaldi (2008); 28, Liu *et al.* (2007); 29, Grimaldi & Engel (2005); 30, Kirejtshuk *et al.* (2012); 31, Liu *et al.* (2015); 32, Yu *et al.* (2015); 33, Cai *et al.* (2015c); 34, Wang *et al.* (2014); 35, Poinar (2005); 36, Legalov (2013); 37, Kirejtshuk *et al.* (2009b).

The chronogram derived from the new fossil calibration set is available with full annotations in File S5 and summarised in Fig. 1. We recovered large differences between our estimates and the estimates of MCK15 (Figs 1, 2 and Table 2). The root of the

tree (crown Holometabola) was found at 385.27 Ma with a 95% credibility interval (CI) of 365.49–400.00 Ma. We recovered the split between Strepsiptera and Coleoptera at 356 Ma (95% CI: 336–375 Ma) in the Early Carboniferous. The estimated origin

Table 2. Median crown age estimates and 95% credibility intervals recovered in the present study and McKenna *et al.* (2015) (MCK15).

Crown group taxon	Median age (Ma) in the present study (95% CI)	Median age (Ma) in MCK15 (95% CI)
Holometabola (Neuropteroidea + Hymenoptera)	385.27 (400.00 to 365.49)	297.97 (318.95 to 281.96)
Neuropteroidea (Coleoptera + Neuropterida + Strepsiptera)	375.56 (394.27 to 355.87)	289.77 (304.06 to 278.31)
Coleopterida (Coleoptera + Strepsiptera)	356.04 (375.03 to 336.81)	278.33 (288.28 to 271.89)
Coleoptera	332.85 (349.21 to 317.12)	252.89 (267.68 to 238.78)
Archostemata + Adephaga + Myxophaga	317.75 (335.42 to 300.34)	242.01 (256.67 to 230.37)
Archostemata + Myxophaga	300.43 (319.60 to 281.69)	219.55 (237.45 to 204.51)
Archostemata	249.30 (267.80 to 231.87)	157.82 (192.43 to 122.62)
Myxophaga	272.99 (295.37 to 247.29)	197.18 (221.87 to 170.13)
Adephaga	248.32 (267.96 to 231.33)	196.58 (217.84 to 174.74)
Geadephaga	220.26 (239.62 to 199.75)	172.50 (196.99 to 148.61)
Hydradephaga	237.29 (257.73 to 220.28)	183.89 (208.15 to 160.58)
Polyphaga	313.87 (328.95 to 299.69)	229.2 (246.57 to 213.49)
Scirtoidea + Derodontoidea s.s.	300.04 (317.56 to 281.63)	219.72 (237.74 to 199.33)
Core Polyphaga	298.07 (311.27 to 284.81)	212.21 (227.13 to 199.0)
Derodontoidea s.s.	223.31 (255.37 to 191.82)	172.13 (200.19 to 139.36)
Staphyliniformia	288.34 (302.28 to 274.09)	200.23 (216.96 to 182.84)
Staphylinioidea (+Jacobsoniidae)	280.42 (294.88 to 265.46)	193.16 (210.26 to 175.26)
Staphylinidae (+Silphidae and <i>Colon</i>)	245.58 (261.04 to 230.71)	165.03 (~180 to 150)
Scarabaeoidea	221.22 (241.76 to 201.90)	141.11 (161.0 to 116.87)
Hydrophiloidea s.l.	253.49 (272.86 to 233.15)	168.31 (187.52 to 151.09)
Hydrophiloidea s.s.	190.35 (214.68 to 168.95)	123.93 (151.66 to 88.34)
Histeroidea	203.60 (226.50 to 179.36)	131.60 (156.60 to 106.09)
Elateriformia (+ <i>Nosodendron</i>)	273.07 (287.43 to 258.61)	189.45 (205.74 to 175.0)
Elateroidea	246.02 (260.12 to 231.35)	166.18 (181.57 to 151.83)
Dascilloidea	179.92 (212.39 to 149.25)	120.47 (155.79 to 82.36)
Buprestoidea	184.06 (206.24 to 164.18)	111.76 (141.94 to 74.96)
Byrrhoidea	238.65 (254.67 to 222.21)	160.03 (176.96 to 142.85)
Bostrichoidea (here = Bostrichiformia)	263.46 (281.83 to 241.72)	181.65 (200.53 to 161.39)
Cucujiformia	274.64 (287.21 to 262.29)	189.76 (202.06 to 179.03)
Coccinelloidea	252.57 (267.14 to 238.60)	171.18 (187.0 to 157.09)
Tenebrionoidea + Lymexyloidea	259.18 (272.03 to 246.86)	175.15 (187.75 to 163.74)
Tenebrionidae	165.74 (178.80 to 153.83)	105.14 (~120 to 80)
Cleroidea (+Biphylidae and Byturidae)	252.07 (266.63 to 237.31)	169.02 (184.68 to 152.9)
Cucujoidea s.s. (–Biphylidae and Byturidae)	244.79 (258.67 to 231.66)	167.08 (178.4 to 156.24)
Phytophaga (Chrysomeloidea + Curculionoidea)	239.87 (252.13 to 227.58)	161.66 (169.54 to 155.56)
Chrysomeloidea	218.46 (234.63 to 203.25)	145.14 (159.47 to 124.55)
Chrysomelidae	206.18 (222.82 to 187.56)	132.38 (~160 to 110)
Cerambycidae (+Disteniidae and <i>Vesperus</i>)	162.03 (176.56 to 148.93)	90.66 (~110 to 70)
Curculionoidea	226.88 (239.70 to 215.30)	149.64 (160.70 to 138.46)
Curculionidae	160.29 (170.21 to 150.76)	93.45 (~110 to 80)

of extant beetle clades was found to be as old as 332 Ma (95% CI: 317–349 Ma) in the Mid Carboniferous. Most superfamilies were found to have originated in the Permian or Triassic (Fig. 2). In a substantial number of clades, the credibility intervals we recovered do not overlap with the ones estimates in MCK15, as highlighted in Fig. 2.

Discussion

Evolutionary history of beetles in the light of a new molecular timeframe

Our recalibrated time tree of Coleoptera based on MCK15 sequence data and topology, and a revised set of fossil calibrations resulted in node ages significantly older than in MCK15

and in other dated phylogenies focusing on the whole beetle tree of life (e.g. Hunt *et al.*, 2007; McKenna & Farrell, 2009; Misof *et al.*, 2014). However, our estimates are more in agreement with the few recent studies that looked at divergence times of major beetle clades (e.g. Zhang & Zhou, 2013; Ahrens *et al.*, 2014; Bloom *et al.*, 2014; Kergoat *et al.*, 2014; Kim & Farrell, 2015; Bocák *et al.*, 2016; Gunter *et al.*, 2016). Our estimates place the origin of Coleoptera during the Mid Carboniferous. We also infer an origin of the four extant beetle suborders in the Late Carboniferous to Early Permian, and an origin of many principal clades (series and superfamilies) predating the End-Permian Mass Extinction. Finally, our results support an origin of the large phytophagan families Curculionidae, Cerambycidae and Chrysomelidae during the Late Triassic to Mid Jurassic. These new age estimates and derived credibility

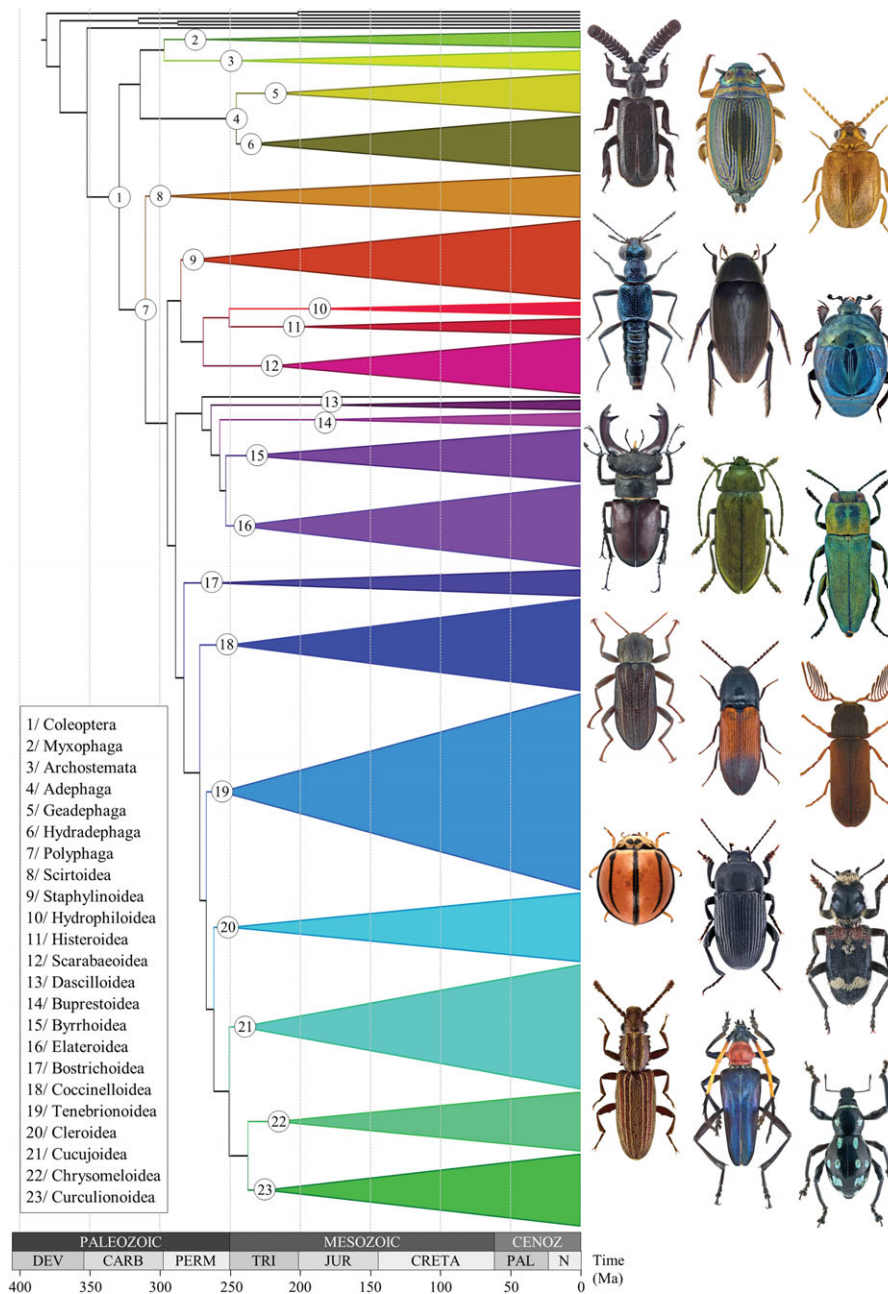


Fig. 1. Evolution of the main beetle clades through geological time. The chronogram shows the median ages derived from the BEAST dating analyses conducted on the dataset of McKenna *et al.* (2015) (MCK15) with new fossil calibrations (see text). Tips have been lumped into triangles representative of the sampling effort of the higher rank clades numbered in the tree. Triangles represent crown groups and not stem groups that would be older, as summarised in Fig. 2 and Table 2. A habitus picture of a species belonging to each of the 20 clades (except Myxophaga and Archostemata) is presented on the right of the topology in order of appearance. All pictures taken by Udo Schmidt. From top to bottom: *Arthropterus* sp. (Geodephaga), *Aulonogyrus concinnus* (Hydradephaga), *Prionocyphon serricornis* (Scirtoidea), *Dianous biformis* (Staphylinoidea), *Hydrophilus piceus* (Hydrophiloidea), *Saprinus splendens* (Histeroidea), *Lucanus cervus* (Scarabaeoidea), *Dascillus cervinus* (Dascilloidea), *Anthaxia diadema* (Buprestoidea), *Stenelmis canaliculata* (Byrrhoidea), *Ampedus balteatus* (Elateroidea), *Ptilinus pectinicornis* (Bostrichoidea), *Declivitata olivieri* (Coccinelloidea), *Colpotus godarti* (Tenebrionoidea), *Clerus mutillarius* (Cleroidea), *Oryzaephilus mercator* (Cucujoidea), *Pachyteria kurosawai* (Chrysomeloidea), *Metapocyrtus elegans* (Curculionoidea). [Colour figure can be viewed at wileyonlinelibrary.com].

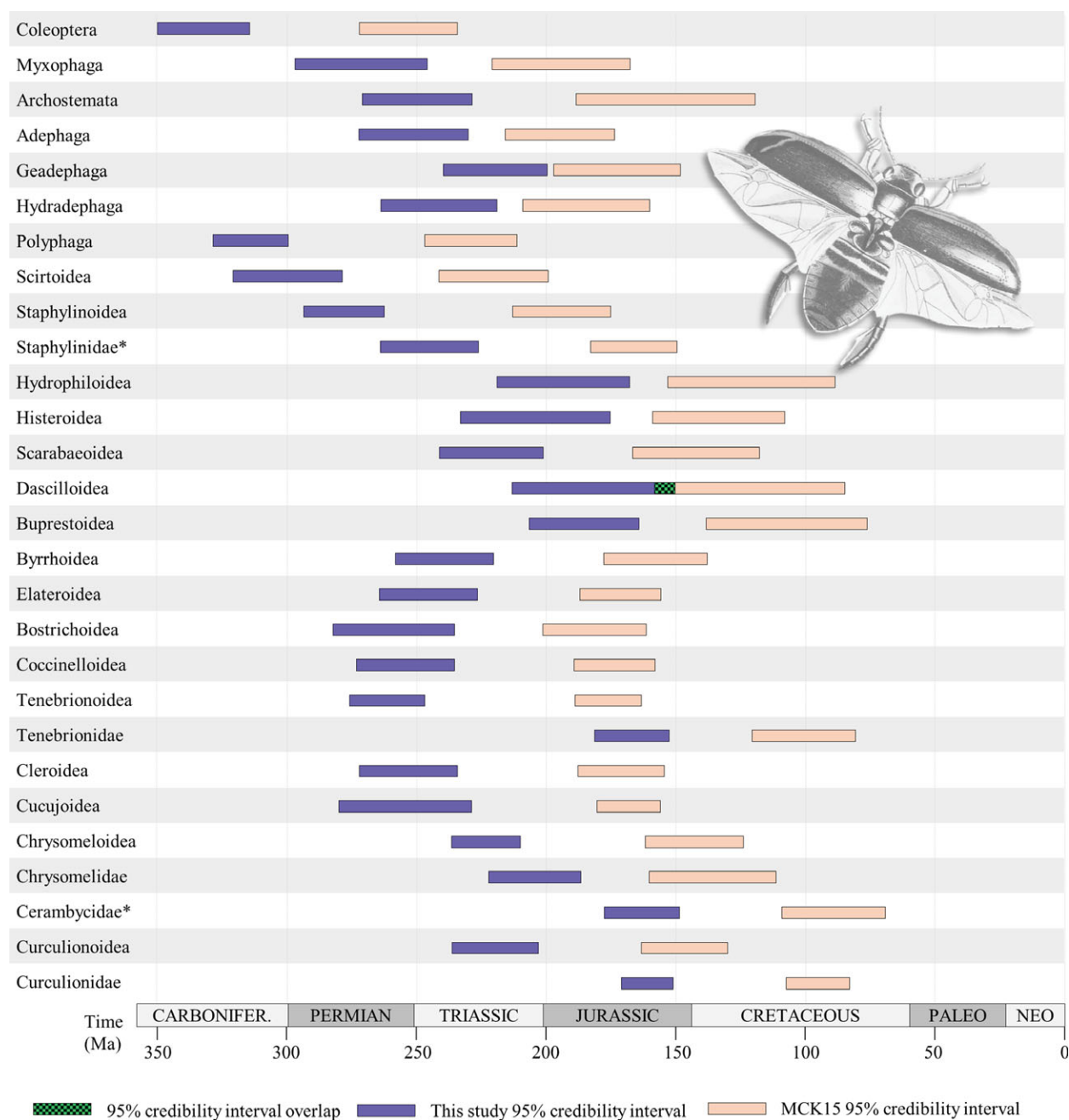


Fig. 2. Comparison of divergence time estimates for crowns of main beetle clades between McKenna *et al.* (2015) (MCK15) and the present study. Graph showing the 95% credibility intervals for the crown age of major beetle clades (see Table 2) in MCK15 and in the present study. The asterisk following the name of certain taxa indicates that these have been recovered as paraphyletic in MCK15 (see Table 2 and MCK15 for more information). On the top right corner is presented a drawing of *Dytiscus dimidiatus* taken from James Duncan's notorious book *The Natural History of Beetles* (1852). [Colour figure can be viewed at wileyonlinelibrary.com].

intervals are consistent with the latest dating for the crown of flowering plants in the Jurassic (e.g. Bell *et al.*, 2010; Clarke *et al.*, 2011; but see Beaulieu *et al.*, 2015). These estimates push back in time the old hypothesis of coevolution between phytophagan beetles and angiosperms (e.g. McKenna *et al.*, 2009). The ancestral plant association of phytophagan beetles therefore

remains somewhat enigmatic as their origin largely pre-dates the diversification and dominance of angiosperms in the Cretaceous (Friis *et al.*, 2011).

The Mid Carboniferous origin of Coleoptera is older than all previous estimates that dated it back to the Late Carboniferous/Early Permian (Hunt *et al.*, 2007; McKenna &

Farrell, 2009; Misof *et al.*, 2014, MCK15). On one hand, a Mid–Late Carboniferous origin was suggested in recent studies for major holometabolan lineages including Hymenoptera – the clade strongly supported as sister to other Holometabola (Ronquist *et al.*, 2012; Misof *et al.*, 2014). On the other hand, the oldest definite beetle fossils with clearly developed elytra (i.e. bearing the principal apomorphy of the order) are known from the Early Permian deposits of Germany, Russia, Czech Republic and USA dated as 295 to 260 Ma (Kukalová, 1969; Ponomarenko, 1969; Lubkin & Engel, 2005; Beckemeyer & Engel, 2008; Kirejtshuk *et al.*, 2014). This indicates a *c.* 35–40 Ma-long gap between the supposed origin of Coleoptera and the oldest confirmed fossil of the clade (*Coleopsis archaica*, ~295 Ma; see Table 1 and File S3), which is comparable to the gaps between the estimated origin and oldest fossil of other holometabolan orders (e.g. Hymenoptera, see Ronquist *et al.*, 2012).

The Late Carboniferous to Early Permian origin of all four beetle suborders (Adephaga, Archostemata, Myxophaga and Polyphaga) and the Late Permian origin of several major clades (superfamilies) are the most surprising result of our analysis. If accurate, this suggests that the basic diversity of Coleoptera evolved during the Late Paleozoic, with 8–11 modern lineages surviving the End-Permian Mass Extinction (Fig. 1). Our analysis dates the divergences of most principal polyphagan clades in a rather narrow window in the Late Permian and Early Triassic, around the Palaeozoic–Mesozoic boundary. These results stand in contrast to the current understanding of the Permian–Triassic fossil record of Coleoptera, in which the oldest definite representatives of all four modern suborders date to Early Triassic or earliest Middle Triassic (Ponomarenko, 1969, 1977, 1992; Lawrence, 1999; Chatzimanolis *et al.*, 2012; Grebennikov & Newton, 2012; Tan *et al.*, 2012; Lawrence & Ślipiński, 2013; Prokin *et al.*, 2013a, 2013b).

The crown ages of the superfamilies as well as origins of families pre-date the first fossils known for these groups, and our estimates at this level differ from those of MCK15, in which origins of many clades were younger than known fossils of the respective clade. For example, the crown age of Hydrophiloidea s.s. in MCK15 was estimated as 124 Ma (CI: 88–155 Ma) and the divergence of modern hydrophiloid families was dated to *c.* 100 Ma (CI not provided). However, the oldest fossils of the modern hydrophiloid families Helophoridae, Spercheidae and Hydrophilidae are already known from the Late Jurassic (*c.* 145–155 Ma; Prokin, 2009; Fikáček *et al.*, 2012a, 2012b, 2014). Increased congruence between estimates of family-level divergence times in our analysis and the fossil record were expected, as we mainly used fossils reliably assigned to the deeper nodes of modern clades (subfamilies, tribes, genera) to calibrate the divergence dates at family/subfamily levels. Consequently, we also estimate a much older origin for the largest beetle families (e.g. Staphylinidae: Late Triassic; Tenebrionidae: Early Jurassic) including the phytophagous groups (Middle Triassic origin of stem chrysomeloids and curculionoids, and Late Triassic origin of Chrysomelidae and Mid–Late Jurassic origins of Curculionidae and Cerambycidae). These results

are largely congruent with the time tree analyses of phytophagous clades by Wang *et al.* (2014) based on a recently discovered fossil prionine beetle, and of Tenebrionidae by Kergoat *et al.* (2014) based on combination of fossil and geological calibrations.

Reliability of divergence time estimates and analytical considerations

The exercise of this paper was to provide an alternative temporal framework of beetle evolution given the MCK15 topology by comparing the fossil set of MCK15 with a new and more comprehensive one. To do so, we replicated the analyses of MCK15 using two sets of fossils. However, we want to emphasise that we do not believe some of the parameter settings used in MCK15 (and therefore in this study) are the most appropriate considering the latest developments in molecular dating (some of which were not available at the time of MCK15). For instance, recent studies have shown that the effect of clock partitioning on estimates of evolutionary rates and timescales can be important in empirical datasets (e.g. Duchêne & Ho, 2014). Some methods have been introduced to take into account this issue, by identifying the best clock partitioning strategy in a Bayesian framework (Duchêne *et al.*, 2014). Likewise, the choice of fossil calibration prior densities should be examined in a comparative framework (Ho & Phillips, 2009). At a minimum, it is recommended to conduct comparative approaches using different prior densities to understand their impact on posterior age estimates, in particular when maximum ages are not easy to justify (Toussaint & Condamine, 2016). The fit of different parameter settings to empirical datasets can be tested by comparing the marginal likelihoods of different analyses using statistical tests (e.g. Bayes Factors; Kass & Raftery, 1995). The latest developments of dating programs such as BEAST (Drummond *et al.*, 2012) incorporate means to estimate these marginal likelihoods in a more sensitive and sound way than before (Baele *et al.*, 2012), thereby improving the robustness of the statistical framework in which comparative dating analyses are conducted.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12198

File S1. BEAST chronogram derived from the replicated analysis of MCK15. Divergence time estimates recovered from the BEAST analysis conducted with the same set of fossil calibrations used in MCK15 and the same node constraints as described in MCK15 (the topology was unfixed). This analysis replicated that performed in MCK15 with 300 million generations, a sampling every 3000 cycles and a burn-in of 50%. The posterior median age in million years is given at each node of the topology.

File S2. BEAST chronogram derived from the analysis with the set of calibration of MCK15 but a fixed topology. Divergence time estimates recovered from the BEAST analysis conducted with the same set of fossil calibrations used in MCK15 but with the final BEAST topology of MCK15 as a fixed input (all parameters allowing topology changes were unchecked in BEAUTi. This analysis was performed with 300 million generations, a sampling every 3000 cycles and a burn-in of 50%. The posterior median age in million years is given at each node of the topology.

File S3. Detailed information of fossil calibrations and justification after Parham *et al.* (2012) criteria.

File S4. BEAUTi .xml file used for the new analysis based on the set of 34 beetle fossils.

File S5. Maximum Clade Credibility Tree of Toussaint *et al.* fully annotated.

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