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Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles

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Abstract. The beetle series Staphyliniformia exhibits extraordinary taxonomic, ecological and morphological diversity. To gain further insight into staphyliniform relationships and evolution, we reconstructed the phylogeny of Staphyliniformia using DNA sequences from nuclear *28S* rDNA and the nuclear protein-coding gene *CAD* for 282 species representing all living families and most subfamilies, a representative sample of Scarabaeiformia serving as a near outgroup, and three additional beetles as more distant outgroups. Under both Bayesian inference (BI) and maximum likelihood inference (MLI), the major taxa within Staphyliniformia are each monophyletic: (i) Staphylinoidea, (ii) Hydrophiloidea s.l., and the contained superfamilies (iii) Hydrophiloidea s.s. and (iv) Histeroidea, although Staphylinoidea and Hydrophiloidea s.l. are not strongly supported by MLI bootstrap. Scarabaeiformia is monophyletic under both methods of phylogenetic inference. However, the relative relationships of Staphylinoidea, Hydrophiloidea *s.l.* and Scarabaeiformia differ between BI and MLI: under BI, Staphyliniformia and Scarabaeiformia were sister groups; under MLI, Hydrophiloidea *s.l.* and Scarabaeiformia were sister groups and these together were sister to Staphylinoidea. The internal relationships in Scarabaeiformia were similar under both methods of phylogenetic inference, with Cetoniinae, Dynastinae + Rutelinae, Hybosoridae, Passalidae, Scarabaeidae and Scarabaeinae recovered as monophyla. Histeridae comprised two major clades: (1) Abraeinae, Trypanaeine and Trypeticinae; and (2) Chlamydopsinae, Dendrophilinae, Haeteriinae, Histerinae, Onthophilinae, Saprininae and Tribalinae. The relationships among early-divergent Hydrophiloidea differed between BI and MLI, and overall were unresolved or received only moderate to low nodal support. The staphylinoid families Agyrtidae, Hydraenidae and Ptiliidae were recovered as monophyletic; the latter two were sister taxa, and Staphylinidae + Silphidae was also monophyletic. Silphidae was placed within Staphylinidae in close relation to a subset of Tachyporinae. Pselaphinae and Scydmaeninae were both recovered within Staphylinidae, in accordance

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with recent analyses of morphological characters, although not always with recently proposed sister taxa. None of the four major groups of Staphylinidae proposed by Lawrence and Newton (1982) was recovered as monophyletic. Certain highly specialized staphyliniform habits and morphologies, such as abdominal defensive glands and reduced elytra, have arisen in parallel in separate lineages. Further, our analyses support two major transitions to an aquatic lifestyle within Staphyliniformia: once within Staphylinoidea (Hydraenidae), and once within Hydrophiloidea *s.l.* (Hydrophiloidea *s.s.*). On a smaller scale, the most common transition is from litter to subcortical or to periaquatic microhabitats and the next most common is from litter to carrion and to fungi. Overall, transitions to periaquatic microhabitats were the most numerous. The broad picture in Staphyliniformia seems to be a high level of evolutionary plasticity, with multiple possible pathways to and from many microhabitat associations, and litter as a major source microhabitat for diversification. In Scarabaeiformia, the most common transitions were from litter to foliage, with flowers to litter, litter to flowers, and litter to dung being next, and then litter to roots, logs or carrion. Litter is again the largest overall source microhabitat. The most common transitions were to foliage and flowers. It thus seems that the litter environment presents ecological and evolutionary opportunities/challenges that facilitate entry of Staphyliniformia and Scarabaeiformia into 'new' and different ecological adaptive zones.

Introduction

Staphyliniformia (Fig. 1; clown, water scavenger, carrion and rove beetles, and relatives) is an infraorder (series) of beetles in the suborder Polyphaga. With more than 74 000 described extant species (A.F. Newton, unpublished data, 20 August 2013), Staphyliniformia contains nearly 20% of extant beetle species (Newton & Thayer, 1992), and is the most species-rich infraorder of largely nonphytophagous beetles. The feeding habits of Staphyliniformia are highly varied, encompassing nearly all habits known among beetles; however, most species can be functionally classified as saprophages, mycophages or predators (e.g. Newton, 1984; Hansen, 1997a). Herbivory is notably quite rare, and saprophagy is the presumed plesiomorphic habit (Hansen, 1997a). Specialized habits abound, including parasitoidism, inquilinism (with vertebrates or social insects), ectoparasitism, myxomycophagy, phytophagy (rarely), algophagy, sporophagy and pollenivory (Crowson, 1981; Hansen, 1997a). Staphyliniformia vary considerably in size, from the smallest and lightest of all beetles (Ptiliidae Erichson: *Nanosella* Motschulsky; adults ~0.35 mm and ~0.5 mg) to some of the largest and heaviest. Staphyliniformia can be found in all biogeographic regions except Antarctica, and inhabit nearly all terrestrial and nonmarine aquatic habitats (Moore & Legner, 1976; Lawrence & Britton, 1994; Hansen, 1997a; Thayer, 2005). The oldest reported fossil Staphyliniformia (family Staphylinidae Lameere) are from Upper Triassic strata (Carnian Stage: 225–230 Ma) (Fraser *et al.*, 1996; Chatzimanolis *et al.*, 2012); the attribution of these fossils to Staphylinidae has been questioned (Grebennikov & Newton, 2012), but unequivocal staphylinids certainly occur by the Middle Jurassic Period (Cai *et al.*, 2012; Chatzimanolis *et al.*, 2012) and a molecular clock analysis by Zhang & Zhou (2013) suggested that Staphylinidae arose around the Early Triassic and that many lineages of the family began radiating in the Late Jurassic.

The classification of Staphyliniformia remains unsettled, and branching patterns among its constituent supra-generic groups remain contested. Most recent workers (e.g. Ohara, 1994; Hansen, 1997a,b; Archangelsky, 1998; Archangelsky *et al.*, 2005; Caterino *et al.*, 2005) recognize three superfamilies: Histeroidea Gyllenhal (clown beetles and relatives), Hydrophiloidea Latreille (water scavenger beetles and relatives) and Staphylinoidea Latreille (rove beetles and relatives). If infraorder Scarabaeiformia (=Scarabaeoidea Latreille; dung beetles, scarab beetles, stag beetles and allies) is derived from within Staphyliniformia, together forming the group Haplogastra *sensu* Kolbe (1908), as suggested by other recent studies (e.g. Kukalová-Peck and Lawrence, 1993; Scholtz *et al.*, 1994; Hansen, 1997a,b; Beutel & Komarek, 2004; Korte *et al.,* 2004; Beutel & Leschen, 2005; Caterino *et al.*, 2005; Hunt *et al.*, 2007; Song *et al.*, 2010), it is most likely the sister group of Histeroidea + Hydrophiloidea, the three together forming the sister group of Staphylinoidea (Hansen, 1997b; Caterino *et al.*, 2005). Morphological character support for such a placement is detailed in Hansen (1997b), Beutel & Leschen (2005) and Caterino *et al.* (2005). Lawrence *et al.* (2011), in contrast, recovered Staphylinoidea as two early-divergent polyphagan clades: (1) Staphylinidae (including Scydmaeninae Leach) + Silphidae Latreille, and (2) Hydraenidae Mulsant + Ptiliidae and Leiodidae Fleming + Agyrtidae Thomson (with agyrtids nested within leiodids), with a paraphyletic Jacobsoniidae Heller at the base of (2). The superfamilies Hydrophiloidea (including Histeroidea) and Histeroidea were monophyletic, but as in some other morphological and molecular studies (Beutel, 1999; Bernhard *et al.*, 2009) the histeroids nested within Hydrophilidae Latreille in the broad sense.

Fig. 1. Series Staphyliniformia and near relatives (series Scarabaeiformia). (A) Silphidae: *Diamesus osculans* (Photo © Piotr Naskrecki, used by permission), (B) Hydrophilidae: *Hydrophilus* (Photo © John Pickles, used by permission), (C) Staphylinidae: Scydmaeninae (Photo © Alex Wild, used by permission), (D) Scarabaeidae: *Pelidnota punctata* (Photo © Alex Wild, used by permission), (E) Staphylinidae: Staphylininae: *Philonthus caeruleipennis* (Photo © Stephen Luk, used by permission), (F) Histeridae: *Hololepta* (Photo © Alex Wild, used by permission), (G) Staphylinidae: Tachyporinae: *Vatesus* sp. with *Eciton* ants (Photo © Alex Wild, used by permission), (H) Scarabaeidae: *Dynastes granti* (Photo © Alex Wild, used by permission), and (I) Leiodidae: *Agathidium* sp. (Photo © Joyce Gross, used by permission).

Morphological and molecular characters have been used both separately (e.g. Hansen, 1997b; Beutel, 1999; Korte *et al.*, 2004; Beutel & Leschen, 2005; Lawrence *et al.*, 2011) and in combination (e.g. Caterino *et al.*, 2005) in attempts to reconstruct the phylogeny of Staphyliniformia. Although some previously uncertain relationships have been reinforced or resolved by these studies –including the monophyly of Staphylinoidea and the placement of Hydraenidae in close relation to Ptiliidae (not within Hydrophiloidea) – very few other higher-level taxonomic groups have received strong nodal support. Caterino *et al.* (2005), in the most taxonomically extensive molecular phylogenetic study of Staphyliniformia to date, reconstructed relationships among 62 species of Staphyliniformia and 48 additional species from across Coleoptera (including a representative sample of 23 Scarabaeoidea) using morphological character data and nearly complete *18S* rDNA sequences. Notable results included the placement of Scarabaeiformia within Staphyliniformia (exact placement unclear), and the recovery of Hydraenidae as a close relative of Ptiliidae. However, their analyses (like other studies to date) recovered relatively little well-supported resolution, particularly among higher-level taxonomic groups.

Hydrophiloidea s.s. (containing the families Epimetopidae Zaitzev; Georissidae Laporte; Helophoridae Leach; Hydrochidae Thomson; Hydrophilidae; and Spercheidae Erichson; more than 3400 species overall) and Histeroidea (containing the families Histeridae Gyllenhal; Sphaeritidae Shuckard; and Synteliidae Lewis; nearly 4500 species overall) are generally considered to be sister groups, based primarily on strong larval similarities (e.g. Böving & Craighead, 1931; Lawrence & Newton, 1982, 1995; Newton, 1991; Hansen, 1995, 1997b). The monophyly of each clade's constituent families has not been questioned recently (Hansen, 1991, 1997b). The name Hydrophiloidea is sometimes applied to the larger clade formed by these presumed sister groups [hereafter, Hydrophiloidea s.l.] (Lawrence & Newton, 1982, 1995). Adult Hydrophiloidea (except Sphaeridiinae Latreille) are typically aquatic and usually feed on detritus or algae (Archangelsky *et al.*, 2005). Adult Histeroidea are typically terrestrial predators (Kovarik & Caterino, 2005). Larvae of both superfamilies usually occur in the same habitats as adults and are predators.

Phylogenetic studies have contributed substantially to our understanding of relationships in Hydrophiloidea and Histeroidea; however, none of these studies have included sufficient

samples or adequate sequences to fully test all relationships of interest. Multiple studies have reconstructed hydrophiloid and/or histeroid relationships using morphological character data (Beutel, 1994; Hansen, 1997b; Archangelsky, 1998; Beutel, 1999; Ślipiński & Mazur, 1999; Anton & Beutel, 2004; Beutel & Komarek, 2004; Mađarić *et al.*, 2013), DNA sequence data (Caterino & Vogler, 2002; Korte *et al.*, 2004; Caterino *et al.*, 2005; Bernhard *et al.*, 2006; Hunt *et al.,* 2007; Short & Fikáček, 2013) or both (Caterino & Vogler, 2002; Caterino *et al.*, 2005; Bernhard *et al.*, 2009). Caterino *et al.* (2005) found no support for a sister-group relationship between Hydrophiloidea and Histeroidea in analyses of *18S* rDNA sequences alone. Under parsimony inference, Hydrophiloidea and Histeroidea formed a paraphyletic grade with respect to the remaining Haplogastra. Analysis under maximum likelihood inference (MLI) yielded a similar result, adding Agyrtidae + Leiodidae in a position sister to Histeroidea. Analysis under Bayesian inference (BI) recovered a similar topology, but with Geotrupidae Latreille (*Geotrupes* Latreille and *Lethrus* Scopoli; Scarabaeiformia) sister to Hydrophiloidea.

Bernhard *et al.* (2009) recovered strong support for many internal relationships in Hydrophiloidea (18 exemplars) and Histeroidea (4 exemplars) in a combined analysis of data from *18S*, *28S*, *12S*, *16S*, cytochrome oxidase I (*COI*), cytochrome oxidase II (*COII*) and morphology under BI; however, other analytical methods recovered relatively little well-supported resolution. A Bayesian analysis of molecular data alone (Bernhard *et al.*, 2006) recovered Spercheidae as the sister group of the remaining Hydrophiloidea, and recovered strong support for most relationships within Hydrophiloidea and Histeroidea. Hydrophiloidea excluding Spercheidae was recovered as two major clades: (1) the 'helophorid lineage' comprising Epimetopidae, Georissidae, Helophoridae, and Hydrochidae, and (2) the family Hydrophilidae. Although limited taxon sampling limits the robustness of their results, they were consistent with a single origin of the aquatic lifestyle in Hydrophiloidea, and with numerous secondary transitions to terrestrial habitats and tertiary changes to aquatic habitats within Sphaeridiinae (Bernhard *et al.*, 2006).

Short & Fikáček (2013) reconstructed the phylogeny of Hydrophilidae s.s. based on DNA sequence data from *COI*, *COII*, *16S*, *18S*, *28S* and arginine kinase, and found strong support for significantly different higher-level relationships in several instances, most notably the largely terrestrial Sphaeridiinae plus Rygmodinae Orchymont being nested within aquatic lineages. They made numerous changes to the classification (especially at the subfamily level) and provided morphological diagnoses of the higher taxa.

Caterino & Vogler (2002) reconstructed the phylogeny of Histeroidea through phylogenetic analyses of adult and larval morphological characters and *18S* rDNA sequences. Separate and combined analyses recovered *Sphaerites* Duftschmid (Sphaeritidae) as sister to all other Histeroidea, and *Syntelia* Westwood (Synteliidae) as sister to Histeridae. Ovoid, mainly generalist forms occupied early-divergent positions within Histeridae. The highly specialized cylindrical subcortical forms of Histeridae were derived from within more generalized lineages. Decay indices were reported, and were generally low, particularly for nodes deep in the tree. Nodal estimates of parsimony bootstrap support were noted to be similar to the decay indices, but were not reported.

Staphylinoidea, with more than 66 100 described species (A.F. Newton, unpublished data), account for the majority of species of Staphyliniformia, and approximately one out of every seven described beetle species. Contained within this large group are the primitive carrion beetles (Agyrtidae), minute moss beetles (Hydraenidae), round fungus beetles (Leiodidae), feather-winged beetles (Ptiliidae), carrion beetles (Silphidae) and rove beetles (Staphylinidae; including the ant-like stone beetles, Scydmaeninae, ant-like mold beetles, Pselaphinae Latreille, and several other smaller former families). Staphylinoidea are known from nearly every type of habitat used by beetles, and their diets and life histories are similarly varied; for instance, in addition to saprophagy, which is considered to be the plesiomorphic habit for the superfamily (Hansen, 1997a), many Staphylinoidea are mycophagous or predatory (Leschen, 1993; Betz *et al.,* 2003). Numerous highly specialized habits and life histories are known, including the only beetle species known to be an obligate ectoparasite of mammals [the leiodid *Platypsyllus castoris* Ritsema which is associated with American beaver *Castor canadensis* Kuhl and the European beaver *C. fiber* Linnaeus (Wood, 1965)]. Bi-parental care and other forms of sociality are known from several different taxonomic groups of Staphylinoidea (Hinton, 1944; Wyatt, 1986; Eggert & Muller, 1997), and the production and deployment of toxic and/or other defensive secretions is widespread, primarily in Staphylinidae, but little-studied for most groups (e.g. Schildknecht *et al.*, 1975; Dettner, 1993). The monophyly of Staphylinoidea is widely accepted, but has not yet received strong statistical support in analyses of DNA sequence data.

The families of Staphylinoidea are often divided into three groups: the Leiodid Group (Agyrtidae and Leiodidae), the Ptiliid Group (Hydraenidae and Ptiliidae) and the Staphylinid Group (Silphidae and Staphylinidae) (Lawrence & Newton, 1982; Hansen, 1997b). Agyrtidae is a small seemingly relict family (*c.* 70 species) occurring in the Holarctic region and New Zealand (Newton, 1997). Agyrtids are mostly associated with, and feed on, carrion, fungi or intertidal wrack, although some are predaceous (Newton, 2005c). Leiodidae (*c.* 3970 species) are found worldwide (Newton, 1998). Adults and larvae generally feed on fungi or on rotting plant or animal material (Newton, 2005d), and some specialize on slime molds. Some species are common in bird nests or mammal dens, and many are cavernicolous. Hydraenidae (nearly 1900 described species worldwide) are generally found crawling in vegetation or on stones at the margin of water, but members of the family occur in a great variety of habitats, including riparian and intertidal zones, phytotelmata, rotting plant material, carrion and dung. Adult and larval Hydraenidae are typically grazers on microflora such as algae, bacteria or other microorganisms (Jäch *et al.*, 2005). Ptiliidae (*c.* 680 described species) have a worldwide distribution. Adults and larvae are found in association with polypore or other fungi or in a diversity of other habitats containing rotting or damp organic material; most are probably fungivorous (Hall, 2005). Ptiliidae includes the smallest of all

beetles (<0.35 mm long). The Leiodid and Ptiliid Groups form a clade (or nearly so) in most analyses of morphological and/or molecular data to date (e.g. Lawrence *et al.*, 2011).

The constitution and phylogeny of Staphylinidae (more than 59 000 described species) remain somewhat controversial (e.g. Ganglbauer, 1895; Crowson, 1955; Coiffait, 1972; Lawrence & Newton, 1982, 1995; Naomi, 1985; Newton & Thayer, 1988, 1995; Hansen, 1997b; Caterino *et al.*, 2005; Thayer, 2005). The family Silphidae (nearly 190 species, mostly associated with and/or feeding on carrion; Sikes, 2005), which along with Staphylinidae comprises the Staphylinid Group of Lawrence & Newton (1982; also Hansen, 1997b), is considered by some recent authors to be derived from within Staphylinidae (e.g. Lawrence & Newton, 1982; Newton & Thayer, 1995; Hansen, 1997b; Ballard *et al.*, 1998; Grebennikov & Newton, 2009 – molecular data only) or a sister group to Staphylinidae (Grebennikov & Newton, 2012). The Staphylinid Group is supported by morphological characters of both adults and larvae (Hammond, 1979; Lawrence & Newton, 1982; Newton & Thayer, 1995; Beutel & Molenda, 1997; Hansen, 1997b; Thayer, 2005; Grebennikov & Newton, 2012), and at least one series of analyses of DNA sequence data (Ballard *et al.*, 1998).

Lawrence & Newton (1982) proposed four major lineages within the Staphylinid Group, which they later modified slightly (Lawrence & Newton, 1995) to the following: the Omaliine Group [subfamilies Dasycerinae Reitter; Empelinae Newton & Thayer; Glypholomatinae Jeannel; Micropeplinae Leach; Microsilphinae Crowson; Neophoninae Fauvel; Omaliinae MacLeay; Proteininae Erichson; Protopselaphinae Newton & Thayer; and Pselaphinae (as Pselaphidae)]; the Tachyporine Group (subfamilies Aleocharinae Fleming; Habrocerinae Mulsant & Rey; Olisthaerinae Thomson; Phloeocharinae Erichson; Tachyporinae MacLeay; Trichophyinae Thomson; and – in 1982 – Pseudopsinae Ganglbauer, now placed in the Staphylinine Group); the Oxyteline Group (subfamilies Apateticinae Fauvel; Osoriinae Erichson; Oxytelinae Fleming; Piestinae Erichson; Scaphidiinae Latreille; and Trigonurinae Reiche, the first and last of these being included in Piestinae in 1982); and the Staphylinine Group (subfamilies Euaesthetinae Thomson; Leptotyphlinae Fauvel; Megalopsidiinae Leng; Oxyporinae Fleming; Paederinae Fleming; Pseudopsinae Ganglbauer; Solieriinae Newton & Thayer; Staphylininae Latreille; and Steninae MacLeay; and possibly Scydmaeninae, and Silphidae). The Omaliine Group was supported using morphological data by Thayer (1985, 1987), Newton & Thayer (1995) and Lawrence *et al.* (2011) (with very limited taxon sampling), but not by Beutel & Molenda (1997).

None of the four major proposed staphylinid lineages/groups was recovered as monophyletic in recent well-sampled molecular or morphological phylogenetic studies (e.g. Hansen, 1997b; Ballard *et al.*, 1998; Beutel & Leschen, 2005; Caterino *et al.*, 2005). Members of the Omaliine Group collectively exhibit a diversity of habits, with many observed or inferred to be predaceous, but others facultatively or obligately saprophagous, mycophagous or pollenivorous (Newton, 1984; Newton & Thayer, 1995; Thayer, 2005). Some Pselaphinae are social insect inquilines fed by their hosts through trophallaxis. Members of the Tachyporine Group are predominantly predaceous, although several clades of Aleocharinae and some Tachyporinae are mycophagous, and one tachyporine and numerous aleocharine lineages are social insect inquilines, some fed by their hosts. This group has no clear synapomorphies and needs further study (Lawrence & Newton, 1982; Newton, 1984; Ashe & Newton, 1993; Ashe, 2005; Thayer, 2005). Members of the Oxyteline Group are saprophagous or mycophagous as adults and larvae (Lawrence & Newton, 1982, 1995; Thayer, 2005), and both stages have an elongated and looped gut compared to other staphylinids. Lawrence *et al.* (2011) found the group monophyletic, albeit with very limited sampling. Grebennikov & Newton (2012) found Apateticinae and Trigonurinae falling at the base of Staphylinidae, outside the Oxyteline Group, which they recognized in a more restricted sense (although they did not include the aforementioned characters of the gut in their analysis). With the exception of the mycophagous Oxyporinae, adults and larvae of the Staphylinine Group are exclusively predaceous, as far as known, and many (including Oxyporinae) have mouthpart modifications correlated with highly specialized feeding via extraoral digestion (e.g. Evans, 1965; Kasule, 1970; Leschen & Newton, 2003; O'Keefe, 2005; Jałoszyński & Beutel, 2012; Jałoszyński & Olszanowski, 2013). Grebennikov & Newton (2009), based mainly on morphological data for adults and larvae, confirmed the inclusion of Scydmaenidae in this group (as a subfamily), but excluded Silphidae and considered inclusion of Oxyporinae to be only weakly supported.

The phylogenetic position of Scarabaeiformia with respect to Staphyliniformia remains unclear. Korte *et al.* (2004), Caterino *et al.* (2005) and Hunt *et al.* (2007) recovered molecular evidence for the placement of Scarabaeiformia within Staphyliniformia (forming the traditional group Haplogastra Kolbe), but nodal support for this placement was low in all three studies. Studies of morphological characters, for example by Kukalová-Peck & Lawrence (1993) and Hansen (1997b), also suggest that Scarabaeiformia might belong within Staphyliniformia. Bocak *et al.* (2014) analyzed DNA sequences from two nuclear (*18S* & *28S* rDNA) and two mitochondrial (*rrnL* & *COI*) genes. They recovered Scarabaeiformia as a monophyletic member of a grade consisting of polyphyletic assemblages of staphyliniform, bostrichiform and elateriform taxa. In Smith *et al.* (2006), Hydrophiloidea was recovered as the sister group of Scarabaeiformia, but no additional details were provided on this aspect of their study.

Although the focus of this paper is Staphyliniformia, our sampling of Scarabaeiformia allows us to examine the relationships within that group to some extent. Consisting of a single superfamily, Scarabaeoidea, this taxon contains approximately 35 000 described species from all regions of the world. The fossil record of the superfamily dates back to the Upper Jurassic (Grimaldi & Engel, 2005). Scarabaeoids are known to feed on a wide range of living, dead and decomposing plant and animal matter. Unlike Staphyliniformia, many Scarabaeoidea are phytophagous (e.g. Cetoniinae, Dynastinae, Melolonthinae and Rutelinae), although many are coprophagous, saprophagous

(e.g. Aphodiinae, Scarabaeinae) or mycophagous (e.g. Geotrupidae) (Jameson & Ratcliffe, 2002; Scholtz & Grebennikov, 2005). Scarabaeoidea are typically free living and solitary, but some are known to provide brood care, live as inquilines in the nests of social insects [e.g. Cetoniinae Leach: Cremastocheilini Burmeister and Schaum, some Aphodiinae Leach (Scholtz & Grebennikov, 2005)] or burrowing vertebrates (Aphodiinae: Gordon & Skelley, 2007), or exhibit sub-social behaviours (e.g. Passalidae Leach: Schuster & Schuster, 1985; Scarabaeinae Latreille: Scholtz, 1990; Halffter, 1997). Most larval and many adult Scarabaeoidea are highly modified for living in subterranean or other dense-substrate microhabitats. The classification of Scarabaeoidea remains unsettled, and the status of many higher-level groups (families, subfamilies, etc.), including their interrelationships, remains contentious despite considerable study (e.g. Howden, 1982; d'Hotman & Scholtz, 1990; Browne & Scholtz, 1995, 1999). Smith *et al.* (2006) reported the results of parsimony analyses of *28S* and *18S* rDNA sequence data from a large sample of Scarabaeoidea, including representatives of most families and subfamilies. Although most lower-level groupings (tribes, subfamilies) received strong nodal support, higher-level relationships were poorly supported.

The present study was designed to reconstruct the higher-level phylogeny of Staphyliniformia and to assess the validity of the informal staphylinoid groups of Lawrence & Newton (1982). With our extensive sampling of Scarabaeiformia as a near-outgroup, we also had an opportunity to examine the relationships within that taxon. However, the relationships between Staphyliniformia and Scarabaeoidea and the placement of Staphyliniformia within Polyphaga as a whole will require a more extensive sampling of other Polyphaga than we have included here. Nonetheless, our taxon sample is the largest to date for a molecular phylogenetic study of Staphyliniformia and Scarabaeiformia, and to our knowledge this is the first broad study of staphyliniform or scarabaeiform phylogeny to include data from a nuclear protein-coding (NPC) gene.

Materials and methods

Taxon sampling

We sampled three taxa known to be outgroups: two adephagans (*Bembidion perspicuum* LeConte: Carabidae Latreille, and *Laccophilus pictus* Laporte: Dytiscidae Leach) and one species from the early-divergent polyphagan superfamily Scirtoidea Fleming (*Scirtes* Illiger sp.: Scirtidae Fleming) (Table S1). These were selected based on Hunt *et al.* (2007) and McKenna & Farrell (2009). We also included a representative sample of Scarabaeoidea (12/13 families; lacking Belohinidae Paulian), for a total sample of 3 distant outgroups, 47 scarabaeoids and 232 staphyliniforms (282 total species; Table S1). Our ingroup taxon sample included one or more exemplars from all ten staphyliniform families, 66/70 subfamilies, and a broad sampling of tribal-level diversity. We were unable to obtain suitable specimens of Horelophinae Hansen (Hydrophilidae), Horelophopsinae Hansen (Hydrophilidae), Prosthetopinae Perkins (Hydraenidae), and Protopselaphinae Newton and Thayer (Staphylinidae) for DNA, although the aforementioned two hydrophilid subfamilies were recently synonymized with others by Short & Fikáček (2013). The taxonomy used here for Staphyliniformia follows Newton & Thayer (2005), with some subsequent changes as recognized in Bouchard *et al.* (2011), which is the source used for Scarabaeiformia. Specimens were identified by M. Caterino, D. Hawks, D. Maddison, D. McKenna, A. Newton, M. Paulsen (University of Nebraska, Lincoln), A. Seago, A. Short, A. Smith (Canadian Museum of Nature) or M. Thayer. Voucher specimens for most Staphyliniformia are deposited at the Field Museum of Natural History (FMNH) in Chicago, IL, U.S.A., the Harvard University Museum of Comparative Zoology (MCZ) in Cambridge, MA, U.S.A. (those from which DNA was extracted), and the Santa Barbara Museum of Natural History (SBMNH). Most scarabaeoid vouchers are deposited at the University of California, Riverside (UCR), the Canadian Museum of Nature (CMN), or the University of Nebraska, Lincoln (UNL); the vouchers of more distant outgroups are deposited in the Oregon State Arthropod Collection (OSAC).

DNA extraction, amplification and sequencing

Specimens for DNA were collected as adults (unless otherwise noted in Table S1) and preserved in 100% EtOH. Total genomic DNA was extracted from each specimen (thorax, legs, or entire specimen) using the QIAquick DNeasy Tissue Kit (Qiagen, Inc., Germantown, MD, U.S.A.), following the manufacturer's protocol. PCR amplification was carried out in 25-μL reactions, typically containing 11.6 μL HPLC water, 5 μL 5X buffer, 0.2 μL 10 mM dNTP's, 1.5 μL MgCl2, 0.2 μL Taq DNA Polymerase (all from Qiagen) and 1 μL of each primer (10 mM). Five μL of Q solution (Qiagen) was added to each reaction for 28S. We targeted approximately 2200 bp of double-stranded DNA sequence data for each specimen, including approximately 1300 bp of the nuclear ribosomal gene *28S* and an approximately 900 bp fragment of the NPC gene carbamoyl-phosphate synthase domain (*CAD*).

28S was amplified with the paired primers ZX1 (sense; ACCCGCTGAATTTAAGCATAT; Van der Auwera *et al.*, 1994) and OP2 (antisense; CAGACTAGAGTCAAGCTCAACAGG; Mallatt & Sullivan, 1998), yielding a *c.*2900-bp product. The first approximately 1300 bp comprising the 5′ end of this amplification product was sequenced with the primers ZX1 and rd5b (antisense; CCACAGCGCCAGTTCTGCTTAC; Whiting, 2002). We also used the primers ZX1 and rd5b for amplification in situations where the initial primers (ZX1 and OP2) failed. Several additional primers were occasionally used for amplification and/or sequencing when these failed. These included ZR1 (sense; GTCTTGAAACACGGACCAAGGAGTCT; Mallatt & Sullivan, 1998), rd4.2b (antisense; CCTTGGTCCGTGTTTCAAGACGG; Whiting, 2002) and rd7b1 (antisense; GACTTCCCTTACCTACAT; Whiting, 2002). Typical amplification conditions for *28S* included a single incubation at 94°C for 1.30 min, followed by six cycles at each of the following

six annealing temperatures (a touchdown profile): 94°C for 30 s, 65°C/63.5°C/62°C/60.5°C/59°C/57.5°C for 1 min, 72°C for 2.30 min, with a single extension step of 7 min at 72°C. We gel extracted all *28S* amplification products using the Qiagen QIAquick Gel Purification Kit.

For *CAD* we performed a hemi-nested amplification using the primers CD338F (sense; ATGAARTAYGGYAATCGTGGH-CAYAA; Moulton & Wiegmann, 2004) and CD688R (antisense; TGTATACCTAGAGGATCDACRTTYTCCATRTTRCA; Wild & Maddison, 2008), followed by CD338F and CD668R (antisense; ACGACTTCATAYTCNACYTCYTTCCA; Wild & Maddison, 2008) using 1 μL of product from the first amplification reaction. Amplification conditions included a single incubation at 94°C for 1.30 min, followed by 30 cycles of 94°C for 30 s, 50°C annealing for 1 min, and 72°C extension for 1 min, followed by a single extension of 7 min at 72°C at the end of the amplification program. The *CAD* amplification products were purified using shrimp alkaline phosphatase and exonuclease I (GE Healthcare), or were gel purified using the QIAquick Gel Purification Kit. *CAD* was sequenced using the primers CD338F and CD668R. *28S* was sequenced using the primers ZX1, rd4.2b, ZR1 and rd5b. We used the ABI PRISM BigDye Terminator Cycle Sequencing Kit, v3.1 (Applied Biosystems), and cycle sequencing reactions were carried out on an ABI PRISM 3730 automated sequencer (Applied Biosystems). The DNA sequences used in this study are deposited at DDBJ/EMBL/GenBank under the accession numbers KJ844878-KJ845337.

Sequence alignment

Sequences were assembled and edited using Sequencher v4.7 (Gene Codes). The *28S* sequences were initially aligned using the E-INS-i algorithm in MAFFT v6.8 (Katoh *et al.*, 2002; Katoh & Toh, 2008) with default alignment parameters and then refined manually in Mesquite v2.75 (build 575) (Maddison & Maddison, 2011). The *CAD* sequences were viewed as amino acids in Mesquite and aligned manually. Nucleotide positions with unique indels and those that could not be unambiguously aligned were removed in Mesquite. The resulting aligned *28S* and *CAD* matrices were concatenated in Mesquite to produce a supermatrix containing 3430 aligned nucleotide positions.

Data partitions, model selection, and phylogenetic analyses

We used PartitionFinder v1.0.1 (Lanfear *et al.*, 2012) to select a partitioning scheme and best-fitting substitution model for each partition using the Bayesian information criterion (Posada & Crandall, 2001). A scheme with four unlinked partitions (*28S*, *CAD* first, second and third positions), employing the GTR + I + Gamma model of nucleotide substitution for all partitions, was identified as optimal.

We executed an analysis under BI using MrBayes v3.2 (Huelsenbeck & Ronquist, 2001; Ronquist *et al.*, 2012) on the Harvard University Faculty of Arts and Sciences Research Computing Odyssey cluster, using the four data partitions and models defined above, with default priors. We ran eight simultaneous runs, each with 32 chains, together occupying 256 nodes on Odyssey (estimated base frequencies; four gamma categories; default heating; trees sampled every 10^3 generations). The analyses ran for 98 520 500 generations. To diagnose convergence, determine an appropriate burn-in, and otherwise check performance and accuracy of the analyses, we performed graphical and statistical analyses on the resulting eight log files in the program Tracer v1.4 (Rambaut & Drummond, 2007). These analyses indicated that the runs had converged by 50 000 000 generations. Based on this information we applied a conservative burn-in and combined the last 10 000 trees from each of the eight runs (for a total of 80 000 trees) and used these to estimate node posterior probabilities (BPP) and to obtain a 50% majority-rule consensus tree. We rooted the resulting tree with the two adephagan outgroups (*Bembidion* and *Laccophilus*). Posterior probabilities ≥0.95 were considered to constitute strong nodal support, whereas BPP values ≥0.75 and <0.95 were considered to constitute moderate nodal support.

A partitioned MLI rapid bootstrap analysis (1000 replicates; GTR + I + Gamma model) and MLI search (ten replicates) were executed on the combined matrix, using the same partitioning scheme as the BI analysis, in the program RAxML GUI v1.2 (RAxML v7.3.2) (Stamatakis, 2006; Stamatakis *et al.*, 2008; Silvestro & Michalak, 2011). Bootstrap (MLB) values ≥75 were considered to constitute strong nodal support, whereas MLB values ≥50 and <75 were considered to constitute moderate nodal support.

Microhabitat ancestral state reconstruction

Microhabitat data for Staphyliniformia (generally at the generic level) were compiled from the sources cited by Thayer (2005: table 2B), field and collection experience of MKT and AFN, and Archangelsky *et al.* (2005), Hall (2005), Jäch *et al.* (2005), Kovarik & Caterino (2005), Newton (2005a,b,c), O'Keefe (2005) and Sikes (2005), and for Scarabaeiformia (at the family or subfamily level) from Scholtz & Grebennikov (2005). The data are presented as a nexus file (File S1). Categories used were largely the major categories of Thayer (2005: table 2B, column headings), with a few added as required to cover Scarabaeiformia. Mesquite v2.75+ (build 579) (Maddison & Maddison, 2011) was used to perform parsimony-based ancestral state reconstruction on both the Bayesian 50% majority rule consensus tree and the maximum likelihood tree. There are many (over 10^{18}) Most Parsimonious Reconstructions (MPRs) for these microhabitat types upon each of these two trees. To tabulate the relative frequencies of different sorts of microhabitat transitions on a tree, 100 000 MPRs were sampled using Mesquite's Summarize Changes in Selected Clade Over Trees feature, with the average number of each sort of transition being calculated. State transitions between nodes in that reconstruction were tallied in a weighted manner, because many reconstructed nodes were ambiguous (two to occasionally five states).

A transition from unambiguous state A at node X to unambiguous state B at descendant node X + 1 was counted as 1 change of A to B; if either or both nodes had more than one state, all possible transition permutations were assumed equiprobable and weighted accordingly; no-change transitions were used only for determining weights and were not recorded as changes. For example, if node X was reconstructed as (A, B) and its descendant node X + 1 was reconstructed as (B, C, D), there are six possible transitions from X to X + 1, one of which is a no-change (B to B). This pair of nodes was counted as contributing 0.17 change (0.1666, rounded off for simplicity) each to the tallies for changes A to B, A to C, A to D, B to C, and B to D, for a total of 0.85. If node X's other descendant node X + 2 was reconstructed as (C), X to X + 2 would contribute 0.5 each to transitions A to C and B to C. Thus only pairs of ancestor–descendant nodes that were reconstructed as having a single unambiguous change counted as a whole step for that state-to-state transition, and pairs of nodes with one or more shared reconstructed states (i.e. one or more no-change permutations) contributed less than a whole step total.

Separately for Staphyliniformia and Scarabaeiformia, transitions between pairs of states were summed as described above over all nodes to yield matrices of 'From-microhabitat' by 'To-microhabitat'. These matrices are presented in Tables S2, S4, S6 and S8. Tables S3, S5, S7 and S9 show the percentage of total transitions (for the infraorder) found for each transition pair. Figures S1–S4 present Tables S3, S5, S7 and S9 in graphical form.

Results and discussion

Staphyliniformia & Scarabaeiformia

The phylogeny recovered under BI showed more resolution with strong nodal support than the phylogeny recovered under MLI. Both analyses recovered the monophyly of Staphyliniformia + Scarabaeiformia (1.0 BPP, 95 MLB) and Scarabaeiformia (1.0 BPP, 93 MLB) (Figs 2–5). However, the BI and MLI trees differed in the placement of Hydrophiloidea s.l. relative to Scarabaeiformia and Staphylinoidea. Under BI, Hydrophiloidea s.l. was sister to Staphylinoidea, forming the traditional Staphyliniformia, and Scarabaeiformia was sister to Staphyliniformia. However, under MLI, Hydrophiloidea s.l. was sister to Scarabaeiformia, rendering Staphyliniformia paraphyletic. Nodal support for the placement of Hydrophiloidea s.l. was low under both methods of phylogenetic inference (i.e. in both phylogenetic trees). It therefore remains unclear whether Scarabaeiformia is the sister group of Hydrophiloidea s.l., and these together are sister to the Staphylinoidea, or whether Scarabaeiformia is the sister group of Staphyliniformia. We should caution, though, that our taxon sampling did not provide a strong challenge to the monophyly of Staphyliniformia + Scarabaeiformia, as we included none of the taxa within Polyphaga that might be intermingled between these two taxa [e.g. Jacobsoniidae (Derodontiformia), see Lawrence *et al.*, 2011; D.D. McKenna *et al.*, unpublished data]. A proper examination of the relative relationships of Staphyliniformia to Scarabaeiformia will require extensive sampling of Bostrichiformia, Cucujiformia, Derodontiformia and Elateriformia. The distance of the far outgroups (a scirtoid and two adephagans) from these two taxa may also limit their ability to provide rooting information for Staphyliniformia + Scarabaeiformia, and thus our results about superfamily relationships should also be viewed as preliminary.

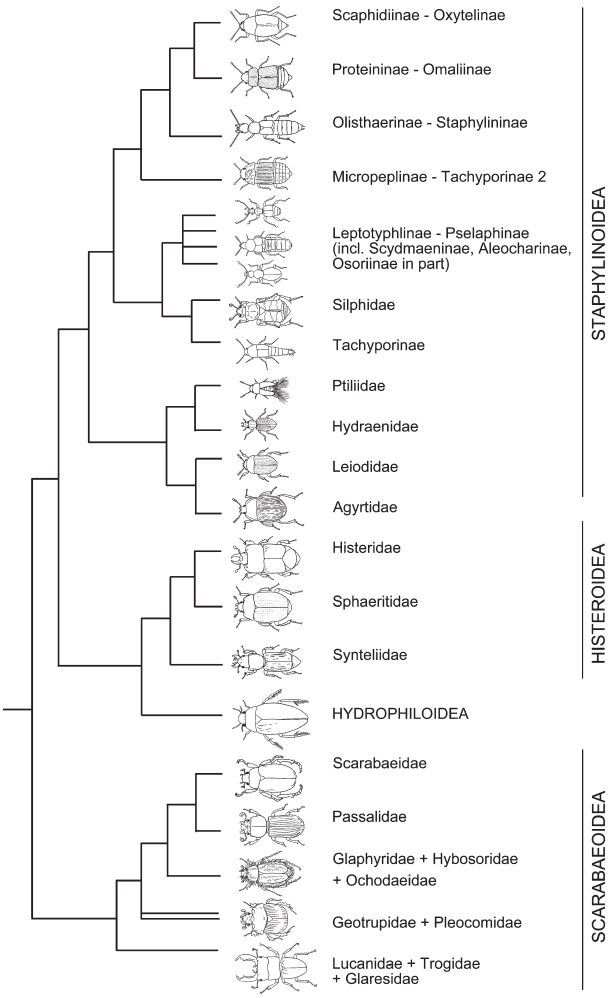

Fig. 2. Summary tree showing the arrangement of selected families, supra-familial taxonomic groups and subfamilies of Staphylinidae (with exemplar habitus images) recovered in the Bayesian phylogenetic analysis. Taxon labels indicate the scope of each multi-group clade reading from bottom to top in the detailed tree (Fig. 3).

Hydrophiloidea & Histeroidea

Hydrophiloidea (1.0 BPP, 97 MLB) and Histeroidea (1.0 BPP, 88 MLB) were monophyletic sister groups, forming the clade Hydrophiloidea s.l. (0.63 BPP, <50 MLB). *Sphaerites* (Sphaeritidae) was sister to Histeridae, and *Syntelia* (Synteliidae) was sister to all other Histeroidea. This conflicts with

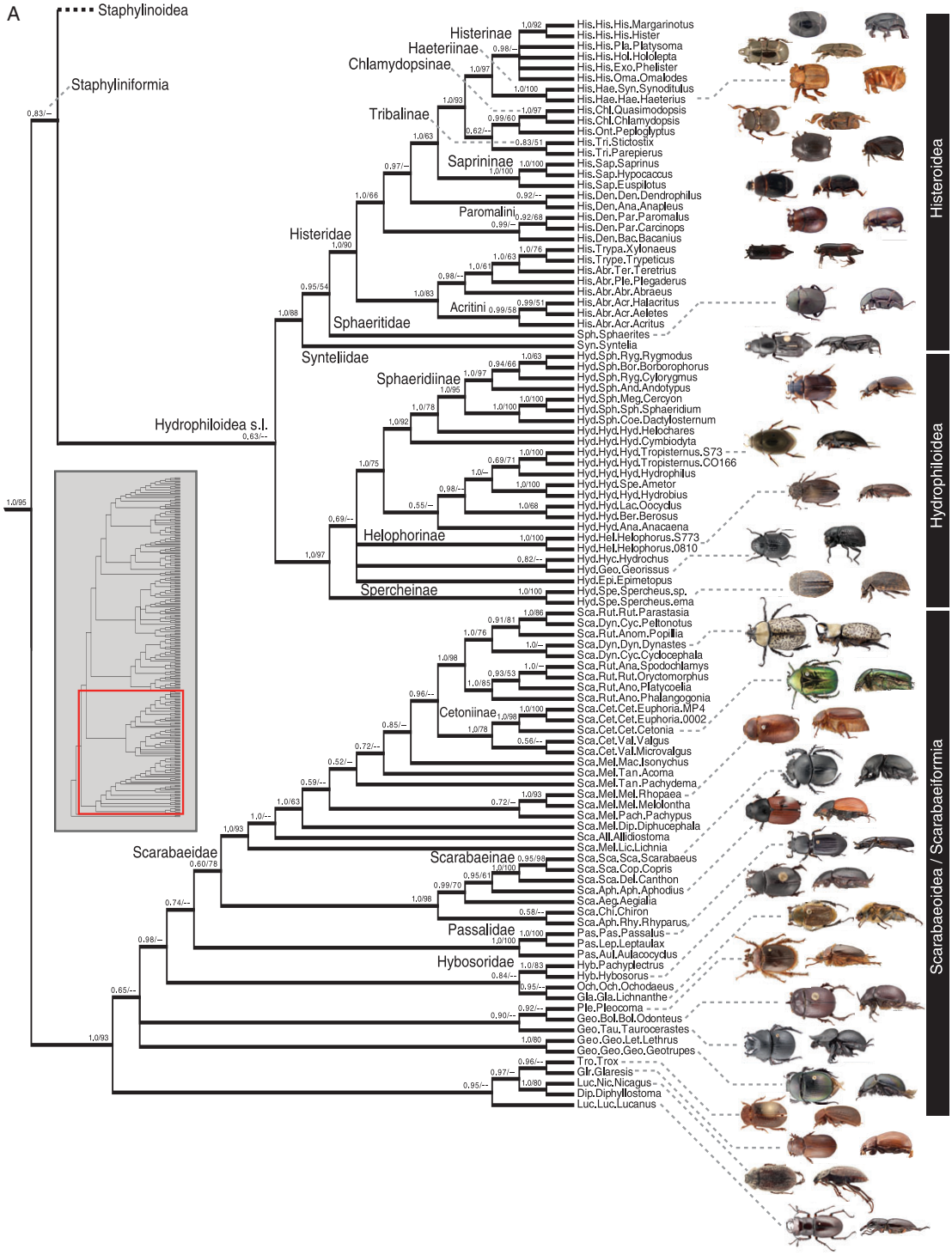

Fig. 3. (A) Bayesian 50% MR consensus tree showing the relationships among major lineages of beetles in the infra-ordinal groups Staphyliniformia and Scarabaeiformia (location in phylogeny indicated by inset). Bayesian posterior probabilities (first/left number) and partitioned maximum likelihood bootstrap support (second/right number) are shown above branches. This tree is based on analyses of DNA sequence data from *28S* rDNA and the nuclear protein-encoding gene *CAD* for 232 ingroup, 47 near outgroup and 3 far outgroup taxa (far outgroups not shown) (see Table S1 for more information). Photos of exemplars are not to scale. (B) Continuation of Bayesian 50% MR consensus tree showing the relationships among major lineages of beetles in the infra-ordinal groups Staphyliniformia and Scarabaeiformia (location in phylogeny indicated by inset). Photos of exemplars are not to scale. (C) Continuation of Bayesian 50% MR consensus tree showing the relationships among major lineages of beetles in the infra-ordinal groups Staphyliniformia and Scarabaeiformia (location in phylogeny indicated by inset). Photos of exemplars are not to scale.

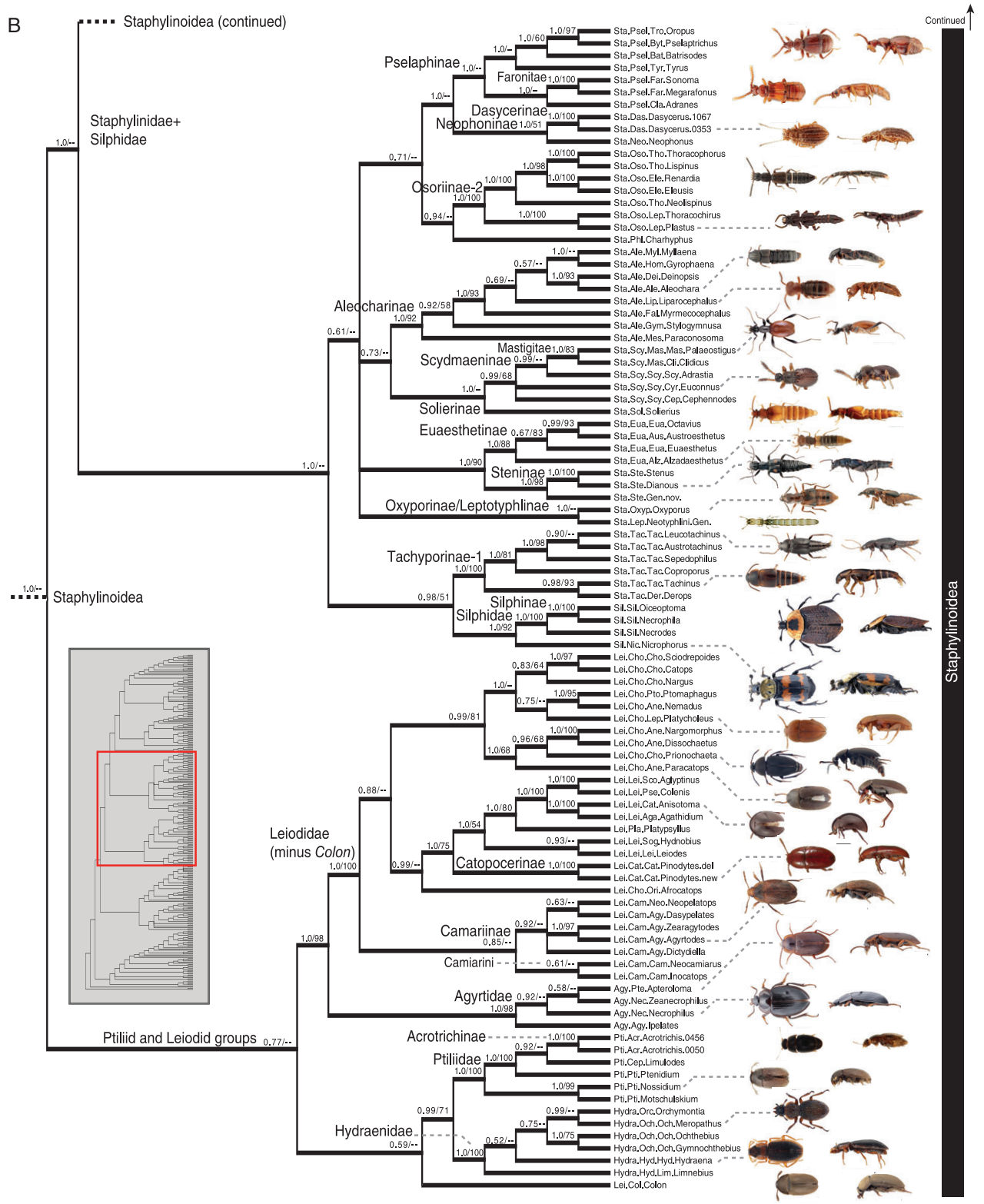

Fig. 3. Continued.

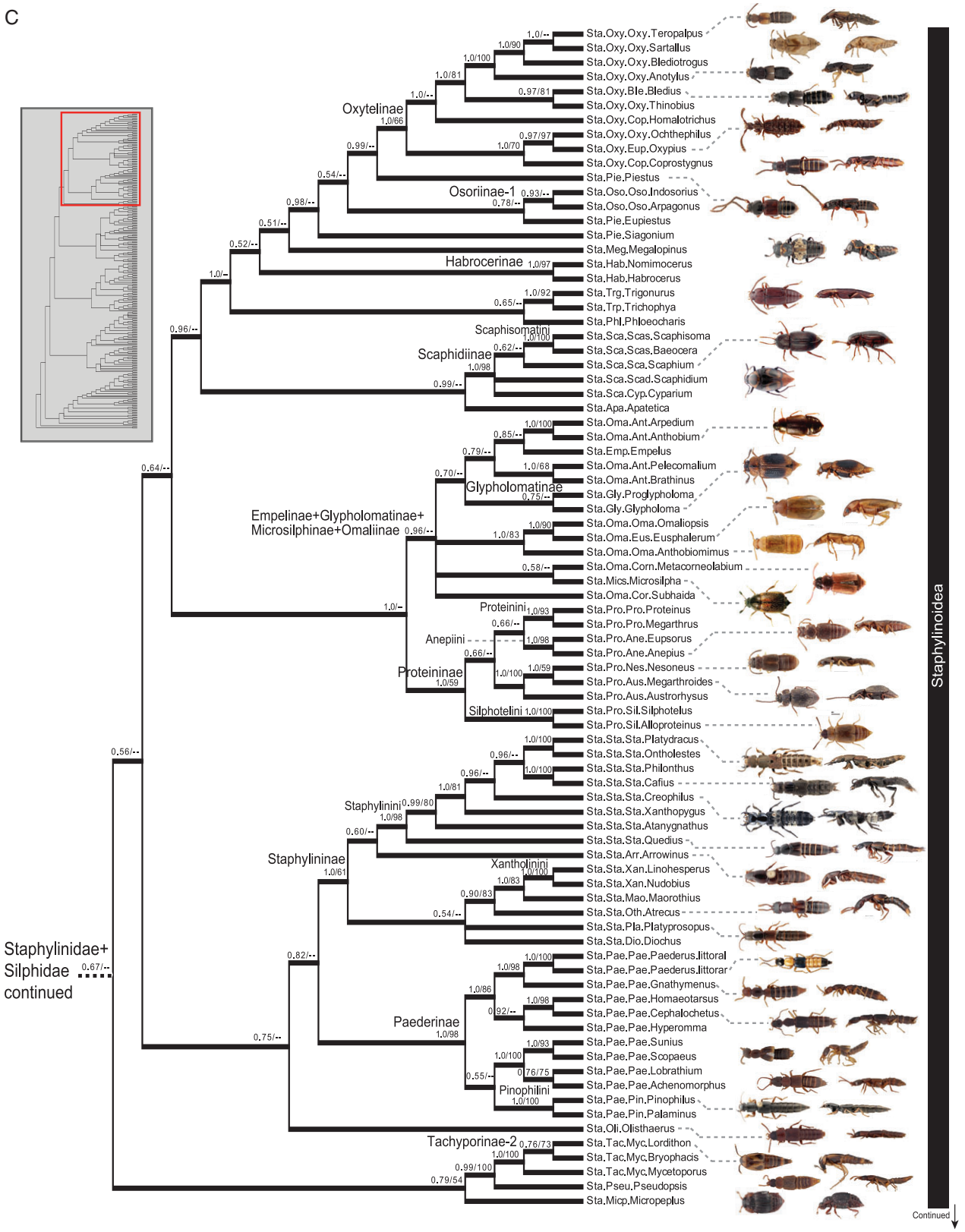

Fig. 3. Continued.

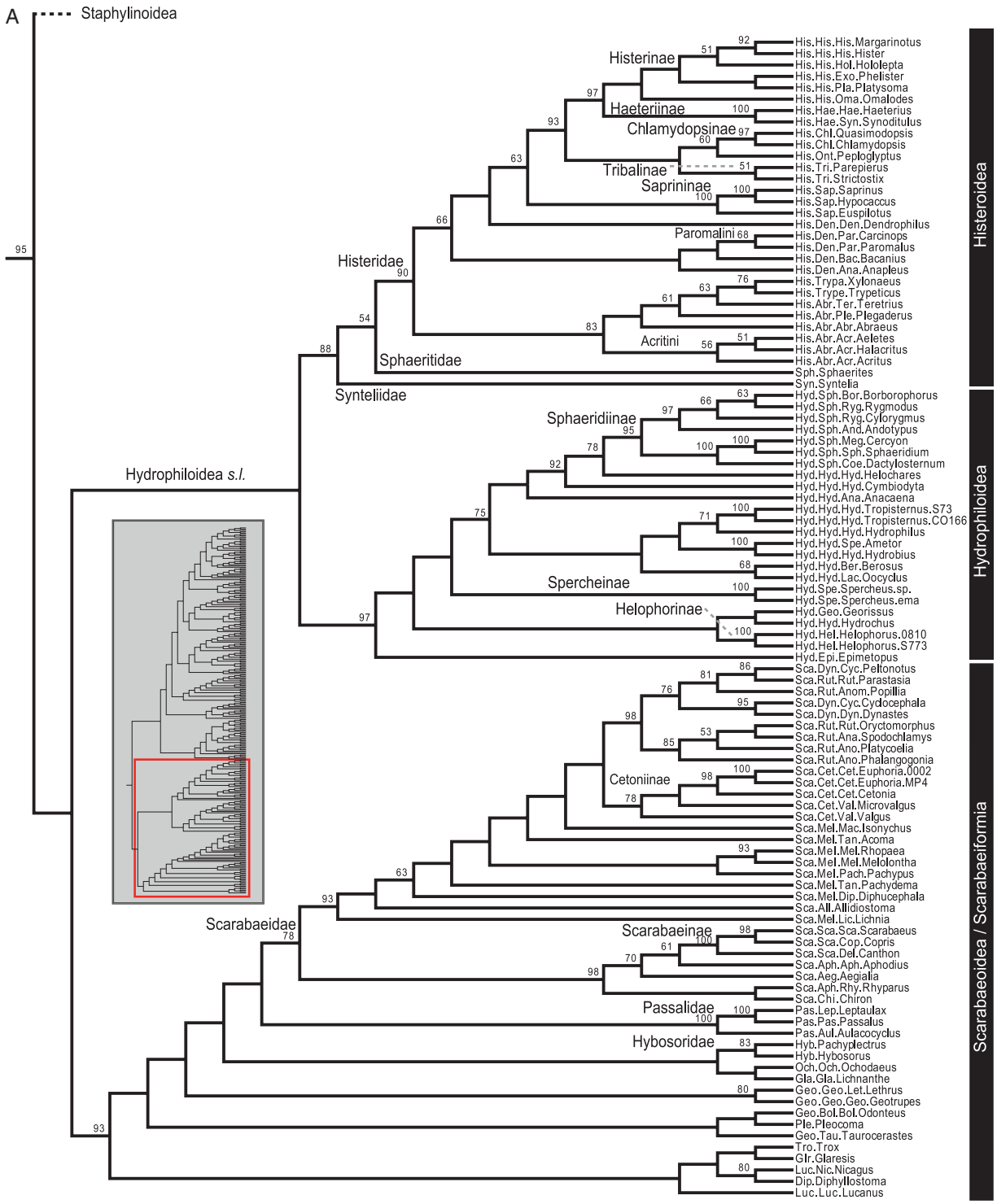

Fig. 4. (A) Maximum likelihood phylogram showing the relationships among major lineages of beetles in the infra-ordinal groups Staphyliniformia and Scarabaeiformia (location in phylogeny indicated by inset). Partitioned maximum likelihood bootstrap support is shown above branches. This tree is based on analyses of DNA sequence data from 28S rDNA and the nuclear protein-encoding gene CAD for 232 ingroup, 47 near outgroup, and 3 far outgroup taxa (far outgroups not shown) (see Table S1 for more information). (B) Continuation of maximum likelihood phylogram showing the relationships among major lineages of beetles in the infra-ordinal groups Staphyliniformia and Scarabaeiformia (location in phylogeny indicated by inset). (C) Continuation of maximum likelihood phylogram showing the relationships among major lineages of beetles in the infra-ordinal groups Staphyliniformia and Scarabaeiformia (location in phylogeny indicated by inset).

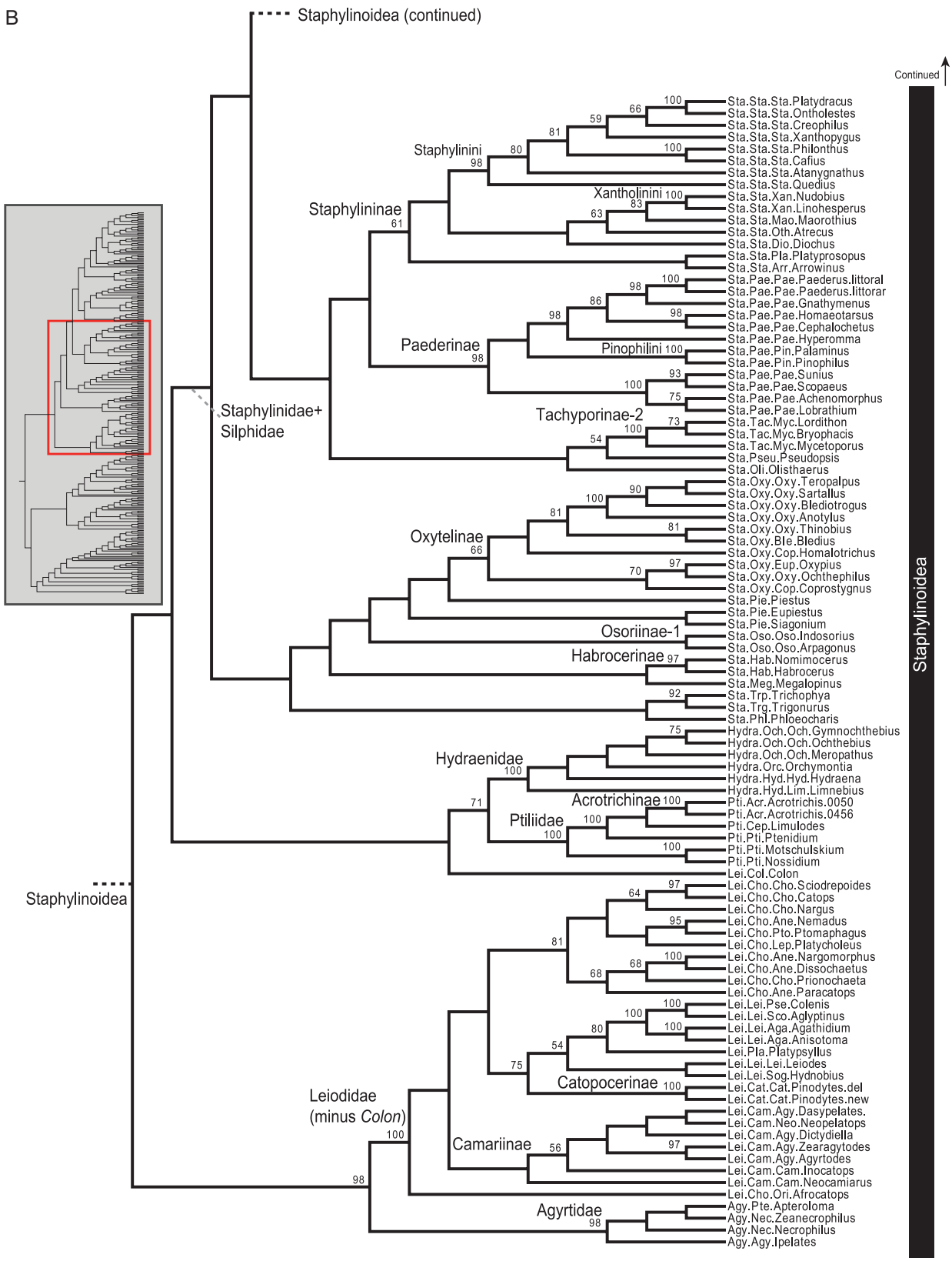

Fig. 4. Continued.

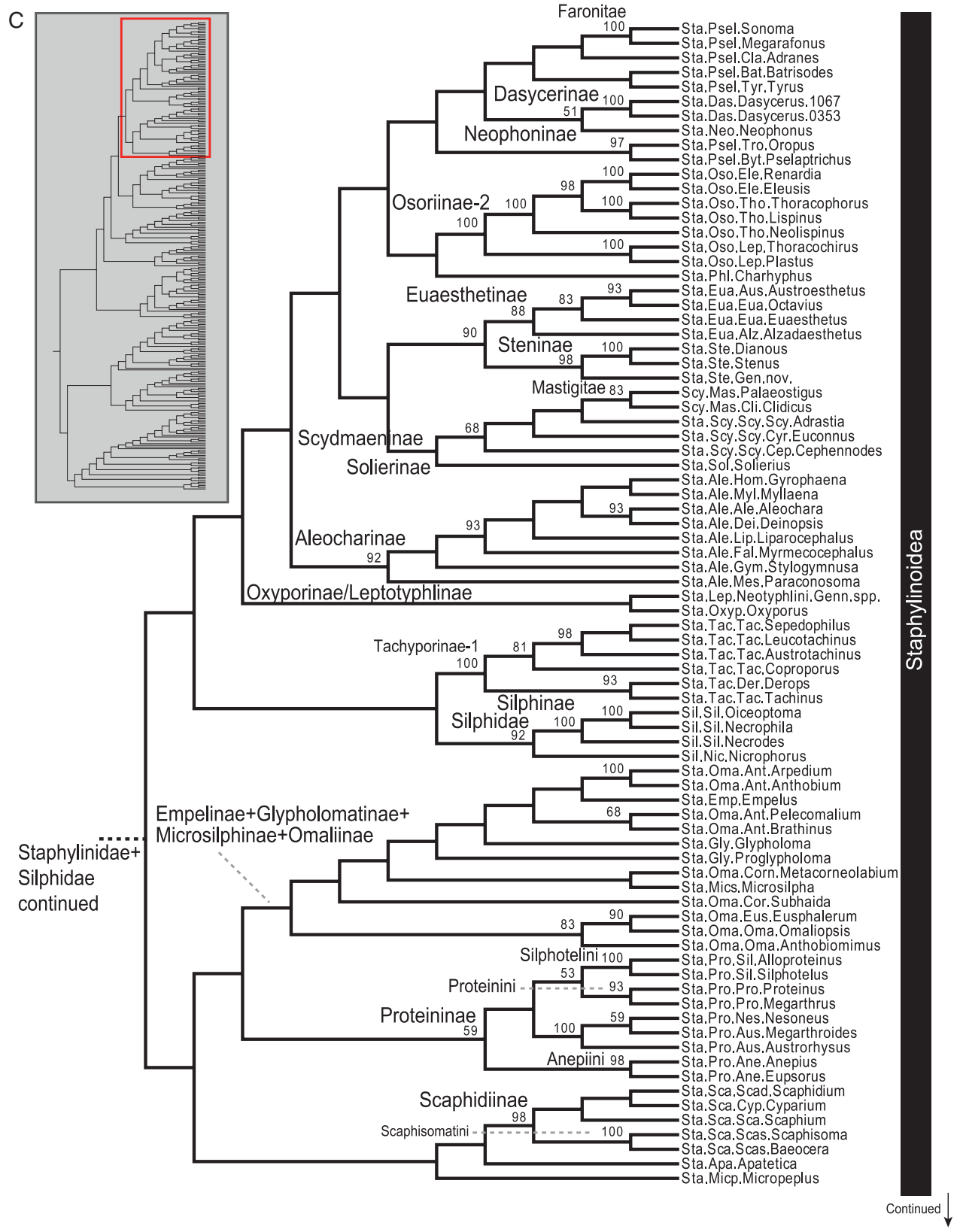

Fig. 4. Continued.

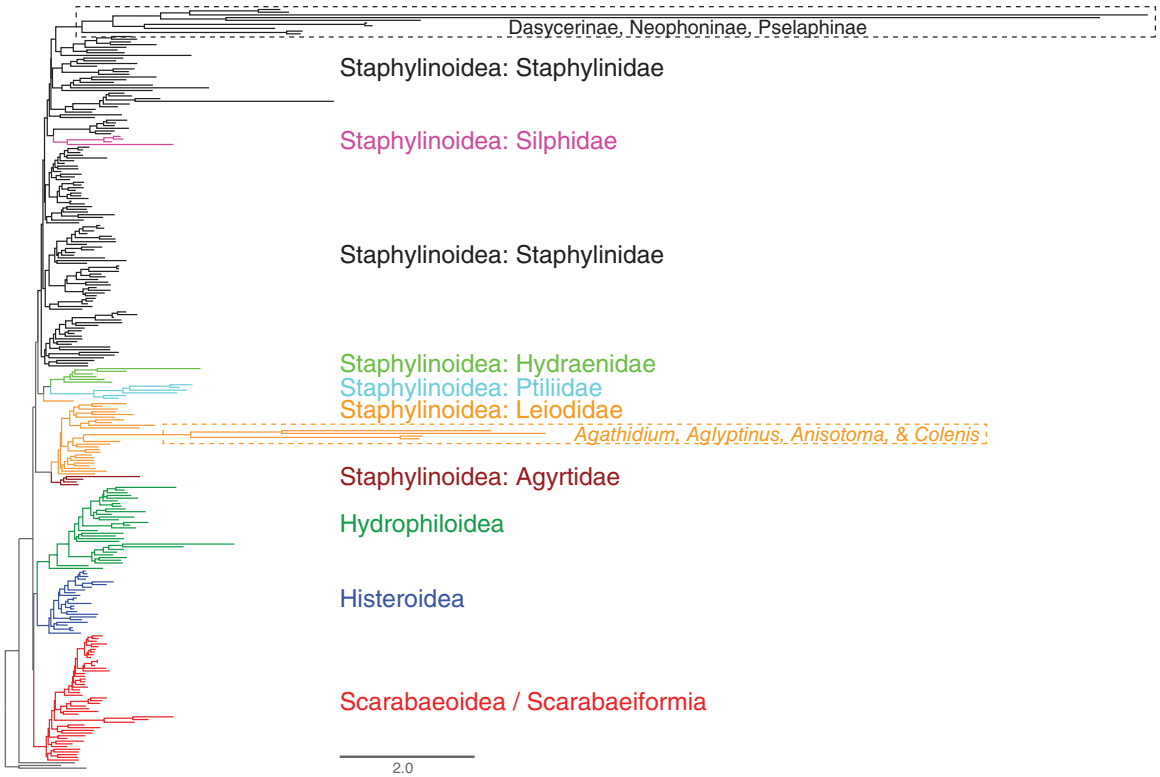

Fig. 5. Maximum likelihood phylogram showing the tree in Fig. 4, with branch lengths proportional to the number of nucleotide substitutions.

previous results (summarized by Newton, 2005a,b,c,d), which have found Sphaeritidae as sister to Synteliidae plus Histeridae. Histeridae (1.0 BPP, 90 MLB) comprised two major clades: (1) Abraeinae MacLeay, Trypanaeinae Marseul and Trypeticinae Bickhardt (1.0 BPP, 83 MLB); and (2) Chlamydopsinae Bickhardt, Dendrophilinae Reitter, Haeteriinae Marseul, Histerinae Gyllenhal, Onthophilinae MacLeay, Saprininae Blanchard and Tribalinae Bickhardt (1.0 BPP, 66 MLB). Consistent with other workers (e.g. Lawrence & Newton, 1995; Caterino & Vogler, 2002), we recovered Trypanaeinae and Trypeticinae as sister taxa (one exemplar of each; 1.0 BPP, 76 MLB), well within the Abraeinae, and sister to *Teretrius* Erichson (Teretriini Bickhardt) (1.0 BPP, 63 MLB). The Dendrophilinae formed a paraphyletic grade, consistent with other workers who have noted its non-monophyly (e.g. Lawrence & Newton, 1995; Caterino & Vogler, 2002). Saprininae (1.0 BPP, 100 MLB) was sister (1.0 BPP, 63 MLB) to a clade comprised of Tribalinae (two exemplars; 0.83 BPP, 51 MLB), *Peploglyptus* Lee (Onthophilinae) and the enigmatic Chlamydopsinae (two exemplars; 1.0 BPP, 97 MLB). Haeteriinae (two exemplars; 1.0 BPP, 100 MLB) was sister to Histerinae (two exemplars; 0.98 BPP, <50 MLB). All sampled tribes of Histeroidea were recovered as monophyla.

Within Hydrophiloidea, Spercheidae (two species of *Spercheus* Illiger were sampled) was sister to the remaining Hydrophiloidea under BI, whereas analyses under MLI recovered *Epimetopus* Lacordaire (Epimetopidae) in this position. Overall, supra-generic relationships among early-divergent hydrophiloids (*Epimetopus, Georissus* Latreille, *Helophorus* Fabricius, *Hydrochus* Leach and *Spercheus*) were unresolved or received only low nodal support in both BI and MLI analyses. The monophyly of Hydrophilidae was supported, although Hydrophilinae Latreille was rendered paraphyletic by Sphaeridiinae in both analyses. Although our results for the early-divergent hydrophiloids differed, our results within Hydrophilidae s.s. were almost entirely consistent with the results of Short & Fikáček (2013) based on more taxa and genes.

Staphylinoidea: the Ptiliid and Leiodid groups

These clades together were sister to the Staphylinid Group under BI (0.77 BPP), but formed a paraphyletic grade subtending the Staphylinid Group under MLI (<50 MLB). Hydraenidae and Ptiliidae were sister groups (0.99 BPP, 71 MLB) and each was monophyletic (1.0 BPP, 100 MLB). Within Hydraenidae, Limnebiinae Mulsant was found to be sister to the remainder of the family, with Hydraeninae Mulsant sister to an Ochthebiinae Thomson + Orchymontiinae Perkins clade. Orchymontiinae was nested within Ochthebiinae in the Bayesian analysis, but sister to it under MLI. Within Ptiliidae, Acrotrichinae Reitter was monophyletic (1.0 BPP, 100 MLB), and Ptiliinae Erichson formed a paraphyletic grade, with Cephaloplectinae Sharp + Acrotrichinae nested within. *Colon* Herbst (Leiodidae: Coloninae Horn) was recovered in the unexpected position of

sister to Hydraenidae + Ptiliidae, but with low nodal support (0.59 BPP, <50 MLB). Leiodidae (minus *Colon*) (1.0 BPP, 100 MLB) and Agyrtidae (1.0 BPP, 98 MLB) were sister groups (1.0 BPP, 98 MLB). Only the leiodid subfamilies Catopocerinae Hatch (two species sampled from one genus; 1.0 BPP, 100 MLB) and Camiarinae Jeannel (seven species sampled from as many genera; 0.85 BPP, <50 MLB) were monophyletic; the latter is somewhat surprising, because no morphological apomorphies have been found to support it. Cholevinae Kirby was monophyletic (0.99 BPP, 81 MLB) except for the placement of *Afrocatops* Jeannel as sister (0.99 BPP, <50 MLB) to the clade comprising Catopocerinae + Leiodinae Fleming + Platypsyllinae Ritsema under BI. *Afrocatops* was sister to all other Leiodidae (minus *Colon)* under MLI, but with weak support at all inter-subfamilial nodes. Leiodinae was rendered paraphyletic by the surprising inclusion of *Platypsyllus* (Platypsyllinae).

Staphylinoidea: the Staphylinid group

Within the Staphylinid Group, monophyletic subfamily-level groups for which more than one species was sampled included Aleocharinae (8 genera sampled; 1.0 BPP, 92 MLB), Habrocerinae (both genera; 1.0 BPP, 97 MLB), Oxytelinae (10 genera; 1.0 BPP, 66 MLB), Paederinae (11 genera, 12 spp.; 1.0 BPP, 98 MLB), Proteininae (9 genera; 1.0 BPP, 59 MLB), Pselaphinae (7 genera; monophyletic under BI only, 1.0 BPP), Scaphidiinae (5 genera; 1.0 BPP, 98 MLB), Scydmaeninae (5 genera; 99 BPP, 68 MLB), Staphylininae (15 genera; 1.0 BPP, 61 MLB), Steninae (3 genera; 1.0 BPP, 98 MLB) and Euaesthetinae (4 genera; 1.0 BPP, 88 MLB). Monophyletic tribes or supertribes included Faronitae Reitter (2 genera; 1.0 BPP, 100 MLB), Mastigitae Fleming (2 genera; 1.0 BPP, 83 MLB), Mycetoporini Thomson (3 genera; 1.0 BPP, 100 MLB), Pinophilini Nordmann (2 genera; 1.0 BPP, 100 MLB), Proteinini Erichson (2 genera; 1.0 BPP, 93 MLB), Scaphisomatini Casye (2 genera; 1.0 BPP, 100 MLB), Staphylinini Latreille (8 genera; 1.0 BPP, 98 MLB) and Xantholinini Erichson (2 genera; 1.0 BPP, 100 MLB). Nonmonophyletic staphylinid subfamilies were Omaliinae (Empelinae, Glypholomatinae, and Microsilphinae were within it), Osoriinae [forming two distant clades: (1) Osorini Erichson and (2) Leptochirini Sharp + (Thoracophorini Reitter + Eleusinini Sharp)] and Tachyporinae [forming two distant clades: (1) Tachyporini MacLeay + Deropini Smetana, and (2) Mycetoporini Thomson]. Monotypic subfamilies sampled were Empelinae, Neophoninae and Solieriinae, and monogeneric subfamilies sampled were Dasycerinae (two individuals of the same species), Megalopsidiinae, Microsilphinae, Olisthaerinae, Oxyporinae, Trichophyinae and Trigonurinae. Subfamilies for which only one of multiple extant genera was sampled (for which we therefore could not assess monophyly) were Apateticinae, Leptotyphlinae, Micropeplinae, Phloeocharinae and Pseudopsinae.

Notable higher-level relationships within the Staphylinid Group included *Solierius* Bernhauer (Solieriinae) sister to Scydmaeninae (1.0 BPP, <50 MLB), Paederinae sister to Staphylininae (0.82 BPP, <50 MLB), and – unexpectedly – Silphidae sister to Tachyporinae: Tachyporini + *Derops* Sharp (Deropini) (0.98 BPP, 51 MLB), *Charhyphus* Sharp (Phloeocharinae) sister to Osoriinae-2 (0.94 BPP, <50 MLB) and Dasycerinae + Neophoninae + Pselaphinae sister to that pair (0.71 BPP, <50 MLB).

The Omaliine Group subfamilies Empelinae, Glypholomatinae, Microsilphinae, Omaliinae and Proteininae together formed a monophylum (1.0 BPP; <50 MLB) with Proteininae the sister of the rest and Omaliinae paraphyletic with respect to the other three. The Omaliine Group includes taxa often regarded as basal among Staphylinidae (e.g. Crowson, 1960; Newton & Thayer, 1995); but there is no evidence for this in our analyses. A close relationship among Glypholomatinae, Empelinae, Microsilphinae and Omaliiinae, as recovered here, is not surprising given similarities in larval and/or adult morphology (e.g. Newton & Thayer, 1995; Thayer, 1987, 1997, 2000, 2005), although placement of the aberrant Empelinae within Omaliinae: Anthophagini Thomson is quite unexpected. Morphological data are also consistent, with a close relationship between these subfamilies and Proteininae (Newton & Thayer, 1995; Thayer, 1987, 2005). Proteininae and Micropeplinae, widely separated in our analyses, share an ovariole structure unique within Staphylinidae (Welch, 1993).

Proteininae and Omaliinae defensive gland secretions remain little known, but their secretions are similar (typically including acids, to the extent that they have been studied), and may be a chemical synapomorphy for the entire clade (Empelinae + Glypholomatinae + Microsilphinae + Omaliinae + Proteininae) (Klinger & Maschwitz, 1977; Dettner & Reissenweber, 1991; Dettner, 1993), although secretions of the smaller subfamilies have not been analysed. The (weakly supported) sister-group relationship we found between Microsilphinae and Omaliinae: Corneolabiini Steel is unexpected based on adult morphology, but was strongly supported in a study based on larval morphology (Thayer, 2000). The monophyly of Dasycerinae + Neophoninae + Pselaphinae (1.0 BPP; <50 MLB) and placement of Neophoninae sister to Dasycerinae (1.0 BPP, 51 MLB) are consistent with morphology (e.g. all have tarsi with 3 tarsomeres; see Newton & Thayer 1995), although Hansen (1997a) recovered Neophoninae separate from the other two in some analyses; no defensive secretions from these taxa have been studied. Their separation from the rest of the Omaliine Group and placement as sister to Osoriinae-2 + *Charhyphus* is unexpected, however. The remaining Omaliine Group subfamily sampled, Micropeplinae, was in a moderately supported clade with Pseudopsinae and Mycetoporini (Tachyporinae) under BI (0.79 BPP) or with Scaphidiinae and Apateticinae under MLI (<50 MLB), differing strongly from analyses based on morphology, where Micropeplinae was the sister of Dasycerinae + Pselaphinae (e.g. Thayer, 1987; Hansen, 1997b) or of Microsilphinae (Newton & Thayer, 1995).

In our analyses, the Tachyporine Group, Tachyporinae and Phloeocharinae are each polyphyletic, consistent with morphological studies by Hammond (1975) and other authors [e.g. Ashe & Newton, 1993; Ashe, 2005 (N.B. Tachyporini only); Thayer, 2005]. The nonmonophyly of Tachyporinae is not surprising, but Tachyporini plus Deropini (1.0 BPP, 100 MLB) was unexpected sister to Silphidae in both BI and MLI trees (0.98

BPP, 51 MLB), widely separated from Mycetoporini, which were themselves unexpectedly sister to Pseudopsinae (0.99 BPP, 100 MLB). Habrocerinae and Trichophyinae adults and larvae share many morphological features (e.g. Ashe & Newton, 1993; Ashe, 2005; Thayer, 2005), but they did not form a clade in our trees, and Olisthaerinae, unexpectedly, was sister to Paederinae plus Staphylininae (BI, 0.75 BPP) or (with weak support) to Pseudopsinae plus Mycetoporini (MLI). Aleocharinae is monophyletic, but with tribal relationships only partly in accord with those supported by morphology (Ashe & Newton, 1993; Ashe, 1994, 2005). Most notably, Deinopsini Sharp was placed within the 'higher Aleocharinae' (Ashe, 2005) instead of as the sister of Gymnusini Heer and closer to the base of Aleocharinae.

The Oxyteline Group (subfamilies Apateticinae, Osoriinae, Oxytelinae, Piestinae, Scaphidiinae and Trigonurinae) formed a clade with the addition of *Megalopinus* Eichelbaum (Megalopsidiinae), *Phloeocharis* Mannerheim (Phloeocharinae), *Trichophya* Mannerheim (Trichophyinae) and Habrocerinae (0.96 BPP, <50 MLB). The Oxyteline Group in the narrowest sense (as used by Hansen 1997a) includes only Osoriinae, Oxytelinae and Piestinae, and is monophyletic in our trees (0.98 BPP, <50 MLB, excluding Osoriinae-2), albeit with different relationships among Piestinae and Osoriinae. Oxytelinae are monophyletic in our trees, but Piestinae are not, in both cases agreeing with Grebennikov & Newton (2012). The relationships we found within Oxytelinae differed from those of Newton (1982b) based on morphology, although our sampling of Euphaniini (only *Oxypius*, expected to be the sister of all other Oxytelinae) and Coprophilini (*Coprostygnus*, *Homalotrichus*) was more limited than his. In contrast to our results, Grebennikov & Newton (2012) found a monophyletic Osoriinae. Our Osoriinae-2 (non-Osoriini) showed the same relationships under BI and MLI, as well as being the sister of *Charhyphus* (Phloeocharinae) (0.94 BPP, <50 MLB). Apateticinae and Scaphidiinae both have abdomens strongly tapering towards their apex (Leschen & Löbl, 1995), very long elytra (covering at least part of tergite V), mesocoxae widely separated, and wing-folding with reduced overlap (Thayer, 2005). They are sister groups in our trees (0.99 BPP, <50 MLB), but we found different relationships within Scaphidiinae under BI and MLI. In contrast, Grebennikov & Newton (2012) found weak support for Scaphidiinae as sister to the Oxyteline Group *sensu* Hansen (1997b) but no support for associating Apateticinae with this group; instead, they found Apateticinae + *Trigonurus* Mulsant (Trigonurinae) supported as sister taxa and together as sister to all remaining Staphylinidae. In our study, *Trigonurus*, inexplicably, formed a strongly supported clade with *Trichophya* (1.0 BPP, 92 MLB) and these two together with *Phloeocharis* Mannerheim a moderately or weakly supported clade under BI and MLI (0.65 BPP, <50 MLB); these taxa have never been suggested to be related based on morphology.

The Staphylinine Group was polyphyletic in our trees, although several subfamily groups well supported in BI and MLI are consistent with earlier studies. Euaesthetinae and Steninae are reciprocally monophyletic sister taxa, as supported by morphology (Clarke & Grebennikov, 2009), and together are part of a large polytomy (BI) or sister to Scydmaeninae plus Solieriinae (MLI). Neotyphlini Coiffait (Leptotyphlinae) was sister to *Oxyporus* Fabricius (Oxyporinae) (1.0 BPP, <50 MLB), these two being one of several lineages in a mixed staphylinid polytomy under BI (Fig. 3B) and under MLI sister to the rest of those lineages together (Fig. 4C). Scydmaeninae was recovered in a position sister to *Solierius* (Solieriinae) in both analyses for the first time, although this relationship was strongly suggested in the description of the first solieriine fossils (Thayer *et al.*, 2012). Together, Scydmaeninae + Solieriinae were sister to Aleocharinae under BI, and to Steninae + Euaesthetinae (as found by Grebennikov & Newton, 2009) under MLI. *Megalopinus* (Megalopsidiinae) was mixed with Tachyporine- and Oxtyeline-Group taxa, in BI sister to Piestinae + Osoriinae-1 + Oxytelinae, and in MLI to Habrocerinae, with that pair sister to Piestinae + Osoriinae-1 + Oxytelinae. *Pseudopsis* Newman (Pseudopsinae) appears in our trees as sister to Mycetoporini (Tachyporinae) (0.99 BPP, 100 MLB), with either *Micropeplus* Latreille (Micropeplinae) (0.78 BPP, <50 MLB) or *Olisthaerus* Dejean (Olisthaerinae, weak support) as their sister group.

Paederinae + Staphylininae (the restricted Staphylinine Group of Hansen, 1997a) were reciprocally monophyletic sister groups in both analyses, in agreement with recent morphological analyses (e.g. Solodovnikov & Newton, 2005; Grebennikov & Newton, 2009) and consistent with their nearly unique ovariole type (Welch, 1993; also in one Oxytelinae and a few Tachyporinae). Within Paederinae, Pinophilini is monophyletic, but Paederini Fleming is paraphyletic with respect to it in both analyses. In Staphylininae, the large tribe Staphylinini is monophyletic in both trees, in agreement with recent morphological (Solodovnikov & Schomann, 2009) and molecular (Chatzimanolis *et al.*, 2010) studies. The relationships among all seven staphylinine tribes in the MLI tree is nearly identical to that based on larval morphology in Solodovnikov & Newton (2005), with *Platyprosopus* Mannerheim (Platyprosopini Lynch) and *Arrowinus* Bernhauer (Arrowinini Solodovnikov) as sister taxa that together are sister to all remaining Staphylininae (MLI) or all except Staphylinini (Solodovnikov & Newton, 2005). In the BI tree, *Arrowinus* is sister to Staphylinini (as in the combined larval and adult analysis of Solodovnikov & Newton, 2005) and *Platyprosopus* forms a polytomy with *Diochus* Erichson (Diochini Casey) and a monophyletic clade including the remaining three tribes (Othiini Thomson + (Maorothiini Assing + Xantholinini)) that was recovered under both BI and MLI, as well as in the larval (but not combined) analysis of Solodovnikov & Newton (2005). Both of our analyses differ in some respects from those of Solodovnikov *et al.* (2013) based on fossil and extant taxa. Together, Paederinae + Staphylininae are sister to Olisthaerinae (BI, 0.75 BPP) or Mycetoporini + Pseudopsinae (MLI, weak support), rather than Pseudopsinae alone, as supported by morphology (e.g. Hansen, 1997b; Grebennikov & Newton, 2009).

Within the Staphylinine Group, abdominal defensive glands are known from: Steninae, some Pseudopsinae (Herman, 1975; Newton, 1982a), some Paederini (Paederinae) and some Staphylininae (Xantholinini and many Staphylinini). The function, structure and chemistry of these glands, as well as the abdominal defensive glands found in many subfamiles of the

Omaliine Group (see above), Oxytelinae, most Aleocharinae and some Piestinae (*Piestus* Gravenhorst only), suggest that they are of independent origin in or within each of these groups, and in Silphidae (e.g. Dettner, 1993; Thayer, 2005; Caron *et al.*, 2008; Schierling & Dettner, 2013). The placement of these groups in our analyses is consistent with this hypothesis of multiple independent origins of abdominal defensive glands within Staphylinidae, a situation that contrasts with that in Adephaga (Dettner, 1987) and in Tenebrionidae Latreille (Tschinkel & Doyen, 1980), where a single defensive gland system evidently originated very early in each of these groups and has been retained and modified throughout the history of the group.

Higher-level relationships within the Staphylinid Group differed somewhat between the BI and MLI trees. At the highest level, although Silphidae had the same (unexpected) sister group (Tachyporinae-1) in both trees, that sister pair was nested much deeper within the Staphylinid Group in the MLI than the BI tree. This reflects the fact that although the trees share a clade (differing in some internal relationships) shown as Silphidae to Pselaphinae in Figs 3B, 4C, in the BI tree that clade is sister to the rest of the Staphylinid Group (i.e. all of Fig. 3C), whereas in the MLI tree, it is sister only to the much smaller Scaphidiinae to Omaliinae clade shown in Fig. 4C. At the level of subfamily relationships, Pselaphinae are in a clade with Neophoninae and Dasycerinae in both analyses, but are only monophyletic in the BI tree. The clade Scydmaeninae + Solieriinae appears in both trees, but in the BI tree its sister group is Aleocharinae (not suggested by any morphological analyses) and in the MLI tree Euaesthetinae + Steninae (more congruent with morphological analyses). In the BI 50% majority rule consensus tree, Euaesthetinae + Steninae is part of a polytomy with representatives from all four subfamily groups. Aleocharinae was part of the same large clade in both analyses (Pselaphinae to Oxyporinae/Leptotyphlinae in Figs 3B, 4C); in the MLI analysis it was the second node from the base, but under BI is at least one node higher, and has a sister relationship to Scydmaeninae + Solieriinae. The taxa forming the large clade that occupies all of Fig. 3C (BI analysis) in the MLI analysis form a grade of successive sister groups to the Silphidae to Pselaphinae clade of Fig. 4C. The morphologically well-supported clade Paederinae + Staphylininae (e.g. Grebennikov & Newton, 2009) occurs in both of our analyses, but with somewhat different and unexpected sister groups: Olisthaerinae in BI and that plus Pseudopsinae + Tachyporinae-2 (Mycetoporini) in MLI, whereas morphological data support Pseudopsinae alone as sister of Paederinae + Staphylininae. The subfamily Micropeplinae was rather unstable in our analyses, appearing in the BI tree as sister to the strange clade Pseudopsinae + Tachyporinae-2 (Mycetoporini), at the base of one basal branch of the Staphylinid Group, but in the MLI tree embedded higher up in the Staphylinid Group, as the likewise unexpected sister to Scaphidiinae + Apateticinae, with that combined clade being the sister of most of the Omaliine Group. That Omaliine Group clade also appeared in the BI analysis, but as sister to the much larger Scaphidiinae–Apateticinae to Oxytelinae clade shown in Fig. 3C. The clade comprising Piestinae + Osoriinae-1 (=Osoriini) + Oxytelinae appeared in both trees with nearly the same perplexing sister groups (Megalopsidiinae then Habrocerinae in BI, or those two together in MLI) and is surprising mainly in its exclusion of Osoriinae-2 (=other tribes), which emerged equally oddly as sister to one Phloeocharinae and then Pselaphinae + Neophoninae + Dasycerinae in both analyses, but with different sister groups to that overall clade. There are numerous finer differences between the results of the BI and MLI analyses as well, such as relationships among Empelinae, Glypholomatinae, Microsilphinae and Omaliinae (partly unresolved under BI), and among the tribes of Staphylininae.

Scarabaeiformia

The internal relationships among Scarabaeiformia in the BI and MLI analyses were quite similar, with generally stronger nodal support under BI. The families Hybosoridae Erichson (1.0 BPP, 83 MLB), Passalidae (1.0 BPP, 100 MLB) and Scarabaeidae (0.6 BPP, 78 MLB), were each monophyletic, along with the subfamilies Cetoniinae (1.0 BPP, 78 MLB) and Scarabaeinae Latreille (1.0 BPP, 100 MLB). The families Geotrupidae and Lucanidae Latreille were not recovered as monophyletic in either analysis. Neither Dynastinae MacLeay nor Rutelinae MacLeay were reciprocally monophyletic, but together they formed a clade (1.0 BPP, 98 MLB) sister to the Cetoniinae. Dynastinae, Rutelinae and Cetoniinae formed a clade (0.96 BPP, <50 MLB) derived from within a paraphyletic grade formed by Melolonthinae Samouelle and *Allidiostoma* Arrow (Allidiostomatinae Arrow). The primarily dung-feeding Aphodiinae Leach, Chironinae Blanchard and Scarabaeinae Latreille formed a clade (1.0 BPP, 98 MLB) sister to the remaining Scarabaeidae. Passalidae and Scarabaeidae were recovered as sister groups (with low nodal support; 0.74 BPP, <50 MLB). Hybosoridae, Ochodaeidae Mulsant and Rey, and Glaphyridae MacLeay together were sister to Scarabaeidae plus Passalidae (0.98 BPP, <50 MLB). *Pleocoma* LeConte (Pleocomidae LeConte) was recovered as sister to *Odonteus* Samouelle (Geotrupidae: Bolboceratinae) (0.92 BPP, <50 MLB), and these together were sister to *Taurocerastes* (Geotrupidae: Taurocerastinae) (0.90 BPP, <50 MLB). *Lethrus* (Geotrupidae: Lethrinae) and *Geotrupes* (Geotrupidae: Geotrupinae Latreille) were sister groups (1.0 BPP, 80 MLB), and together with other Geotrupidae and *Pleocoma* formed a polytomy with the clade comprising Scarabaeidae + Passalidae + Hybosoridae, Ochodaeidae and Glaphyridae. *Trox* Fabricius (Trogidae MacLeay), *Glaresis* Erichson (Glaresidae Kolbe), *Nicagus* LeConte (Lucanidae Latrielle: Nicaginae LeConte), *Diphyllostoma* Fall (Diphyllostomatidae Holloway) and *Lucanus* Scopoli (Lucanidae), formed a clade sister to all other Scarabaeiformia, with Lucanidae being paraphyletic with respect to the other three families. The relatively derived assemblage of phytophagous Scarabaeidae (the 'pleurostict scarab' subfamilies Melolonthinae, Allidiostomatinae, Cetoniinae, Rutelinae and Dynastinae) is strongly supported as monophyletic. Most scarabaeiform taxa were recovered within major clades that corroborate published morphology- and DNA-based phylogenetic studies and the current classification

of scarabaeoid families and subfamilies. However, several of the present results contrast strikingly with both published and unpublished results on the higher-level composition of the Scarabaeiformia. For example, Smith *et al.* (2006), using only parsimony analyses, found a weakly supported clade consisting of Geotrupidae (including Bolboceratinae), Pleocomidae and Passalidae. Subsequent analyses by DCH and his collaborators (in preparation), using parsimony, BI and MLI analyses and over 1000 taxa, consistently recover a strongly-supported clade comprised of Passalidae and bolboceratine geotrupids. Members of the Passalidae and Hybosoridae are conspicuous in possessing extremely divergent rDNA sequences relative to all other members of the Scarabaeiformia. This potential for long-branch attraction among unrelated taxa, combined with the fact that we were unable to amplify CAD for many scarabaeoids (see Table S1), may have contributed to the poor resolution and generally weak nodal support among Scarabaeiformia in the analyses reported here.

Conclusions

Gaining an understanding of patterns of staphyliniform and scarabaeiform diversification is critical to understanding the macroevolution of beetle diversity. Within this truly megadiverse group – comprising 25–30% of all species of Coleoptera – typical phytophagy (i.e. feeding on live plant tissues) is restricted to derived lineages within Scarabaeidae, a relatively derived family of Scarabaeoidea, and a few scattered examples nested well within Staphylinoidea. This strongly implicates factors other than diversification in parallel with plant (angiosperm) radiation as the principal drivers of this large radiation. The relative uncertainty of the deep relationships in our results – at least partly conflicting with earlier results – makes it difficult to present more than a preliminary discussion of possible evolutionary pathways within the group; nonetheless, some interesting patterns emerge from our analyses.

Both of our analyses supported monophyly of Scarabaeoidea, Histeroidea, Hydrophiloidea s.s., Hydrophiloidea s.l. and Staphylinoidea, although the last two were strongly supported in only the Bayesian analysis. Monophyly of Staphyliniformia (Hydrophiloidea s.l. plus Staphylinoidea) and of Staphylinidae + Silphidae was supported in only the Bayesian analysis (and strongly so). Using the Bayesian results shown in Fig. 3 (with 264 supported nodes, *vs*. 164 under MLI, as shown in Fig. 4) as a framework, we can tentatively examine the possible evolutionary pathways of various aspects of Staphyliniformia and Scarabaeiformia life history, with a view particularly towards inferring the ancestral states of major clades.

Feeding habits within Staphyliniformia are, as noted above (*q.v.* for references), very diverse, encompassing primarily predation, saprophagy and mycophagy, and other more specialized habits to a lesser degree. Hydrophiloidea s.l. consists of Hydrophiloidea s.s., which are nearly always saprophagous as adults and predaceous as larvae, and Histeroidea, which are nearly always (and primitively) predaceous in both stages; this suggests that ancestral Hydrophiloidea s.l. were predaceous as larvae and either predaceous or saprophagous as adults. Within Staphylinoidea, the Ptiliid-Group + Leiodid-Group clade was probably ancestrally saprophagous or mycophagous, although lack of information about the feeding habits of *Colon* (sister to the Ptiliid Group in our analyses, although expected to be within Leiodidae) leaves some ambiguity in the ancestral state reconstruction. The sister group of that complex is Staphylinidae + Silphidae, which includes numerous predaceous, saprophagous and mycophagous lineages; it appears, however, that its common ancestor was probably predaceous, with parallel origins of saprophagy or mycophagy within several major lineages: some Tachyporinae, some Aleocharinae, Osoriinae-2, Dasycerinae + Neophoninae, and in one or more branches of the Proteininae to Oxytelinae clade of Fig. 4. Reconstruction within that large clade is hampered by our lack of knowledge of the feeding habits of several relatively small and/or obscure subfamilies. This leaves the ancestral state for Staphylinoidea ambiguous: either predaceous or saprophagous/mycophagous. Factoring in its sister group Hydrophiloidea s.l. (with hypothesized ancestrally predaceous larvae and predaceous and/or saprophagous adults) tips the balance slightly in favour of predaceousness.

The microhabitat associations of Staphyliniformia are similarly varied, and transitions among different microhabitats – the substrates or immediate surroundings in which beetles live – have evolved numerous times. This variation and the necessarily incomplete taxon sample here make any inference of ancestral states and transitions between them complex and somewhat tentative, even for relatively coarsely delimited states. Nonetheless, based on the BI tree in Fig. 3, it appears that ancestrally, Scarabaeiformia + Staphyliniformia, Staphyliniformia, Hydrophiloidea s.l., Histeroidea and Staphylinoidea were each associated with (usually forest) litter, whereas ancestral Hydrophiloidea s.s. shifted to being aquatic, with some secondary reversions to terrestriality (see below).

At the largest scale, our analyses of ancestral microhabitat associations support two major transitions to an aquatic lifestyle within Staphyliniformia: one within Staphylinoidea (Hydraenidae) and one within Hydrophiloidea s.l. (Hydrophiloidea s.s.). As all relatively basal branches within Hydrophiloidea s.s. in both of our analyses are associated with aquatic or submerged riparian habitats, the lack of support for a single resolved branching pattern within the group does not alter the two-transition scenario. Also of note, there are (likely numerous) secondary transitions back to terrestrial ways of life within both lineages, including: *Nucleotops* Perkins and Balfour-Browne and *Parhydraena* Orchymont within Hydraenidae (Perkins & Balfour-Browne, 1994); and Sphaeridiinae and some *Limnoxenus* Motschulsky within Hydrophilidae (Hansen, 1997a; Short & Liebherr, 2007; Short & Fikáček, 2013). Although numerous Staphylinidae are associated with waterside habitats (here termed periaquatic, as in, e.g., Newton *et al.*, 2000; Thayer, 2005; Webster & DeMerchant, 2012), including some that skate on water (at least some *Stenus* Latreille) or hunt in water-filled phytotelmata [e.g. some *Belonuchus* Nordmann, *Platydracus* Thomson and *Odontolinus* Sharp in *Heliconia* L. inflorescences, see Frank & Morón,

2012); and a *Hesperus* Fauvel in bamboo nodes (Schillhammer, 2002], none of that megadiverse assemblage is considered fully aquatic or known to swim or complete part of its life cycle submerged.

On a smaller scale, although recognizing that we are treating only a small sample of Staphyliniformia, reconstructing ancestral microhabitat states on the trees in Figs 3, 4 finds 71 (BI) or 70 (MLI) different state transitions (filled cells in Tables S2–S9), with the most common being from litter to fungi (11.8% BI, 12.7% MLI), litter to periaquatic (10.8% BI, 11.4% MLI), or litter to subcortical (10.8% BI, 10.4% MLI), and the next most common being from litter to carrion (6.9% BI, 7.4% MLI) and litter to nests (∼5.6% for both). All transitions from litter total 57.1% (BI) or 60.0% (MLI) of changes, reflecting the litter-based inferred ancestral states of the higher taxa noted above. After litter, transitions from carrion (10.7% BI, 8.4% MLI) or from nests (9.0% BI, 8.4% MLI) were next most common, but trailing far behind. Dung, flowers, marine-shore (mainly wrack), soil, foliage and logs seem to be more or less eco-evolutionary sinks, with <2% of all transitions occuring out of each (none from the last two). Aquatic microhabitats are evolutionarily nearly as closed, with just over 2% of all transitions occurring from them. Overall, transitions to periaquatic and fungi were the most numerous (17.1–17.6% for both), followed by those to subcortical (13.8% for both), carrion (10.5% BI, 12% MLI), litter (10.0% BI, 8.7% MLI) and nests (8.1% for both). The very low percentages of transitions to flowers, foliage and soil (≤2% BI and MLI) reflect the relatively rare occupation of those zones by staphyliniforms. In contrast, those microhabitats with more numerous transitions to them have supported numerous radiations across the infraorder.

Looking at the balance of transitions between staphyliniform microhabitats, net-source microhabitats (i.e. more transitions *from* than *to*) are, in descending order: litter (5.7:1 BI, 6.9:1 MLI), aquatic (1.5:1 for both) and nests (1.1:1 BI, 1.04:1 MLI), the last one being just barely net-source. Net-sink microhabitats (more transitions *to* than *from*) are: marine (8.3:1 BI, 6.5:1 MLI), dung (5.9:1 BI, 3.7:1 MLI), soil (2.6:1 BI, 7:1 MLI), periaquatic (3.6:1 BI, 3.4:1 MLI), subcortical (2.5:1 BI, 4.1:1 MLI), fungi (2.6:1 BI, 2.2:1 MLI), flowers (1.5:1 BI, 1.2:1 MLI) and carrion (1.4:1 MLI only), with foliage and logs being complete sinks (no transitions *from* them, at least in the current taxon sample). Carrion shows nearly equal transitions in both directions under BI, but is slightly net-sink under MLI. It is striking that nests (which here includes associations with social insects or vertebrates) are also a dynamic eco-evolutionary link (very slightly net-source), with transitions occurring from four and to seven other states. This is somewhat unexpected, because such interspecific relationships are generally regarded as specializations; clearly not all are irreversible ones, although not all inquilines are equally modified or integrated. The appearance of flowers being slightly a net-source microhabitat may reflect a sampling artifact; because of specimen availability, the exemplars of Staphylinidae: Omaliinae used in this study are disproportionately floricolous compared to the full array of microhabitats occurring in that subfamily, which influenced the ancestral character state reconstructions in the clade containing Omaliinae. The broad picture in Staphyliniformia seems to be a high level of evolutionary plasticity, with multiple possible pathways to and from many microhabit associations.

Our taxon sampling is more limited for Scarabaeiformia, which occupy a similar number (but with a slightly different array) of microhabitats, but we reconstructed fewer different transitions among those (23 BI, 20 MLI; filled cells in Tables S6–S9). The most common transitions were from litter to foliage (16.5% BI, 13.2% MLI), litter to dung (14.1% for both), litter to flowers (11.7% BI, 9.0% MLI) and litter to roots (10.0% BI, 9.3% MLI), then litter to logs (8.4% BI, 7.9% MLI) and litter to carrion (6.9% for both). Strikingly, litter is again the largest overall source microhabitat (76% BI, 66% MLI), even more so than for Staphyliniformia, but with flowers next (12% BI, 22.4% MLI) and all others far behind, including foliage, fruit and roots having no transitions from them. The most common transitions were to foliage (19.8% of all transitions for both), then to flowers (16.0% BI, 12.4% MLI), dung (∼15% for both) or roots (12.2% BI, 12.6% MLI), a very different pattern from Staphyliniformia, followed by carrion (both 10.4%) and logs (both 8.9%). Looking at the balance of transitions involving different microhabitats, net-source microhabitats (more transitions *from* than *to*) are: litter (15.9:1 BI, 8.2%:1 MLI) and flowers (1.8:1 MLI only). Net-sink microhabitats (more transitions *to* than *from*) are: dung (17.4:1 for both), nests (4.0:1 BI only), fungi (1.7:1 for both), flowers (1.3:1 BI only) and logs (1.3:1 for both), with carrion, foliage, fruit, periaquatic and roots being complete sinks (i.e. no transitions *from* them in the current taxon sample). Foliage, fruit and roots of angiosperms are microhabitats (and feeding substrates) that have supported tremendous radiations in the higher Scarabaeidae (Cetoniinae, Dynastinae, Melolonthinae, Rutelinae; Scholtz & Chown, 1995), and the lack of transitions from those niches could reflect a lack of selective pressure to switch general microhabitats or constraint (by specializations required to exploit those microhabitats) – or both.

Angiosperm-associated radiations have been used to explain diversification patterns in many insect groups, including beetles (e.g. Ehrlich & Raven, 1964; Mitter *et al.*, 1988; Farrell, 1998; McKenna & Farrell, 2006; McKenna *et al.*, 2009) and in the context of this study could be relevant to some Scarabaeoidea. On the other hand, the high species richness and asymmetrically distributed diversity of nonphytophagous insects, especially Staphylinoidea, clearly demand a different explanation, in view of their limited direct association with plants. Many nonphytophagous (e.g. saprophagous or predatory) beetles do not specialize on a particular species of host or prey, so 'arms-race' coevolution or parallel radiation paradigms are not readily applicable.

In the cases of both Staphyliniformia and Scarabaeiformia, the litter environment clearly played an important role in their taxonomic and ecological diversification. Litter is a complex habitat dominated (primarily) by dead and dying plant parts, and is inhabited (perhaps most notably in this case) by fungi, microbes, termites, ants and many other kinds of small animals. Environmentally, litter varies considerably in space and time in its composition, depth and moisture content. Litter likely presented early staphyliniforms with many ecological

opportunities (and challenges) in the form of un(der)utilized microhabitats and/or food resources. Adaptive evolution resulted in novel habits and/or morphologies that permitted staphyliniforms to exploit these un(der)utilized niches. These (pre)adaptations in turn allowed entry into new 'adaptive zones' outside litter, where taxonomic diversification continued/ensued. Thus, the diversity of Staphyliniformia may have arisen in large part as a consequence of the repeated evolution of novel ecological strategies among litter-inhabiting ancestors, followed by taxonomic diversification in newly colonized ecological niches to which they were preadapted. Recent phylogenetic studies of other nonphytophagous beetle groups suggest similar scenarios (e.g. Leschen & Buckley, 2007; Seago *et al.*, 2011), and similar patterns are seen in other species-rich insect groups that are not primarily phytophagous, perhaps most notably ants (Formicidae; e.g. Moreau *et al.*, 2006). It is worth noting, however, that angiosperms introduced (to the litter) a much larger diversity of leaf forms, sizes, textures and chemistry than gymnosperms, so the taxonomic diversification of angiosperms and their subsequent rise to widespread ecological dominance in the Cretaceous (Bell *et al.*, 2010) is likely to be an important factor in diversification of the litter fauna, including litter-associated Staphyliniformia and Scarabaeiformia. Although more detailed analyses are not yet available for the large and trophically diverse staphyliniform family Staphylinidae, similar recurring changes in feeding habits and microhabitat associations appear likely to have occurred in their evolutionary history. More broadly, it appears that an important element in the tremendous diversification of Staphyliniformia as a whole may have been a potential for flexibility (evolutionary plasticity) in adapting to a wide variety of feeding strategies and microhabitat associations, with multiple possible pathways to and from many microhabit associations, and litter as a major source microhabitat for diversification.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12093

Figure S1. Staphyliniformia: percentages of transitions between microhabitats under Bayesian inference; data from Table S3. Colour coding the same as in Figures S2–S4 for shared microhabitats.

Figure S2. Staphyliniformia: percentages of transitions between microhabitats under maximum likelihood; data from Table S5. Colour coding the same as in Figures S1, S3 and S4 for shared microhabitats.

Figure S3. Scarabaeiformia: percentages of transitions between microhabitats under Bayesian inference; data from Table S7. Colour coding the same as in Figures S1, S2 and S4 for shared microhabitats.

Figure S4. Scarabaeiformia: percentages of transitions between microhabitats under maximum likelihood; data from Table S9. Colour coding the same as in Figures S1–S3 for shared microhabitats.

Table S1. Taxonomic status, DNA code(s), and DDBJ/EMBL/GenBank accession numbers for each specimen sequenced. The taxonomy used here for Staphyliniformia follows Newton & Thayer (2005), with some subsequent changes as recognized in Bouchard *et al.* (2011), which is the source for Scarabaeiformia.

Table S2. Staphyliniformia: summed counts of transitions under Bayesian inference from microhabitats in left column to those in column headings, shaded by value: red highest, deep green lowest.

Table S3. Staphyliniformia: percentages of totals from Table S2 (BI), shaded by value: red highest, deep green lowest.

Table S4. Staphyliniformia: summed counts of transitions under Maximum Likelihood from microhabitats in left column to those in column headings, shaded by value: red highest, deep green lowest.

Table S5. Staphyliniformia: percentages of totals from Table S4 (ML), shaded by value: red highest, deep green lowest.

Table S6. Scarabaeiformia: summed counts of transitions under Bayesian inference from microhabitats in left column to those in column headings, shaded by value: red highest, deep green lowest.

Table S7. Scarabaeiformia: percentages of totals from Table S6 (BI), shaded by value: red highest, deep green lowest.

Table S8. Scarabaeiformia: summed counts of transitions under Maximum Likelihood from microhabitats in left column to those in column headings, shaded by value: red highest, deep green lowest.

Table S9. Scarabaeiformia: percentages of totals from Table S8 (ML), shaded by value: red highest, deep green lowest.

File S1. Nexus file containing microhabitat data for Staphyliniformia and Scarabaeiformia. Categories used were largely the major categories of Thayer (2005). See "Methods" for more information.

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