3

A Review of the Fossil History of Staphylinoidea

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Abstract

The superfamily Staphylinoidea includes the families Hydraenidae, Ptiliidae, Agyrtidae, Leiodidae, Silphidae, and Staphylinidae and currently includes more than 400 described fossils. The geological history of the superfamily ranges from the Triassic to Cenozoic, and the lineage is well represented in multiple significant Lagerstätte. During the last several years, many new important fossils have been described, and for most Staphylinidae subfamilies, their geological history extends into the Cretaceous. I summarize the most important fossil discoveries for families and subfamilies from compressions/impressions and amber inclusions. I discuss the diversity of Staphylinoidea though time, and I provide a summary phylogeny of Staphylinoidea with fossil constraints, updated from previously published works. Additionally, I discuss the apparent bradytely in many lineages and possible future steps to expand our knowledge of fossil Staphylinoidea.

3.1 Introduction

The superfamily Staphylinoidea is composed of the families Agyrtidae, Leiodidae, Hydraenidae, Ptiliidae, Silphidae, and Staphylinidae. Currently there are almost 70,000 species described in these families, including more than 400 fossils (see Table 3.1). The status and relationships between the families were recently reviewed by McKenna et al. (2015) and Newton (2016). Besides the families listed above, the family Jacobsoniidae and the extinct family Ptismidae have been discussed as potentially belonging in Staphylinoidea (Yamamoto et al. 2017; Kirejtshuk et al. 2016), and these two subfamilies are discussed briefly below in Sect. 3.3.

In the past, four informal groups of subfamilies (omaliine, tachyporine, oxyteline, and staphylinine groups; Lawrence and Newton 1982; Thayer 2016) were recognized in Staphylinidae. However, the usefulness of these informal groups may have come to an end, since none of these are monophyletic (McKenna et al. 2015). While the phylogeny of McKenna et al. (2015) is not ideal (it was based only on two molecular markers: 28S rDNA and the nuclear protein-coding gene CAD), it is the only nearly complete molecular phylogeny of Staphylinoidea available in terms of subfamily coverage. It is also much more resolved and/or inclusive than previous phylogenies of Staphylinidae/Staphylinoidea (e.g., Newton and Thayer 1995;

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Table 3.1 Number of extinct and extant species of Staphylinoidea

Families/superfamily	Number of extinct species	Number of extant species
Hydraenidae	8	1962
Ptiliidae	6	776
Agyrtidae	9	72
Leiodidae	10	4167
Silphidae	21	187
Staphylinidae	374	62,480
Staphylinoidea	428	69,644

Data provided by Alfred Newton (Newton unpublished database) and are valid as of October 17, 2016

Hansen 1997; Ballard et al. 1998; Caterino et al. 2005; Grebennikov and Newton 2009, 2012) and certainly more realistic than previously published "phylogenetic schema" (Thayer 2005; Newton 2011; Chatzimanolis et al. 2012; Thayer 2016). Given that these informal groups of subfamilies are not monophyletic, I have decided not to use them in this review and by doing so perhaps drawing the ire of my fellow rove beetle systematists. I have used the phylogeny produced by McKenna et al. (2015) as the basis for Fig. 3.4 (that maps the earliest fossils for all major staphylinoid lineages) and as a guide on how to list the various families.

Below I provide a quick summary of the early paleontological works in Staphylinoidea, and then I review the most important fossils for each of the families/subfamilies. If there has been a recent review of the paleontological history for a particular group (e.g., Scydmaeninae by Jałoszyński 2016), then I reference the review and spent less time on that group. Following that section, I briefly discuss the diversity of fossils through time and stasis in the fossil record and provide brief remarks on future directions.

3.2 History of Staphylinoid Paleontology

The first fossil rove beetle was described by Gravenhorst in 1806 (Herman 2001). For the next 150 years or so, the record of new staphylinoid fossil descriptions was scant with just a few fossils being described. Early on, the most fossils, by far, were described by Samuel H. Scudder, perhaps the most prominent and influential American insect paleontologist of the nineteenth century. These fossils were from the Early Eocene Green River Formation in Wyoming/Utah/Colorado and the late Eocene-Oligocene Florissant Formation in Colorado (Scudder 1876, 1878, 1890, 1900). And while Scudder was instrumental in bringing all these fossils to light, many of his descriptions and identifications are typical of the era: short, incomplete, and inaccurate. Another paleontologist working in Florissant around the same time was H. F. Wickham who also described several taxa (Wickham 1913a, b). Figures 3.1 and 3.2c illustrate five of the species described by Scudder and Wickham from Florissant and Green River.

Other important early fossil contributions (individual fossils discussed below in Sect. 3.3) were made by Giebel (1856) and Oustalet (1874) who described fossils from Aix-en-Provence, France, and Heer (1847, 1862) who described Miocene insects from Oeningen, Germany, and the Firkanten Formation of Svalbard (Heer 1870). von Heyden and von Heyden (1866) described several taxa from the Rott Formation of Germany, and Schaufuss (1890) described many species from Baltic amber.

The last part of the twentieth century saw many important fossil discoveries from Asia. These included taxa described by Tikhomirova from the Jurassic of Karatau, Kazakhstan (Tikhomirova 1968), by Ponomarenko from the former Soviet Union (Ponomarenko 1977, 1980, 1985), by Ryvkin from the Russian Federation (1985, 1988, 1990), and Zhang from China (Zhang 1988, 1989).

One important characteristic of all the previously listed scientists is that they were (with few

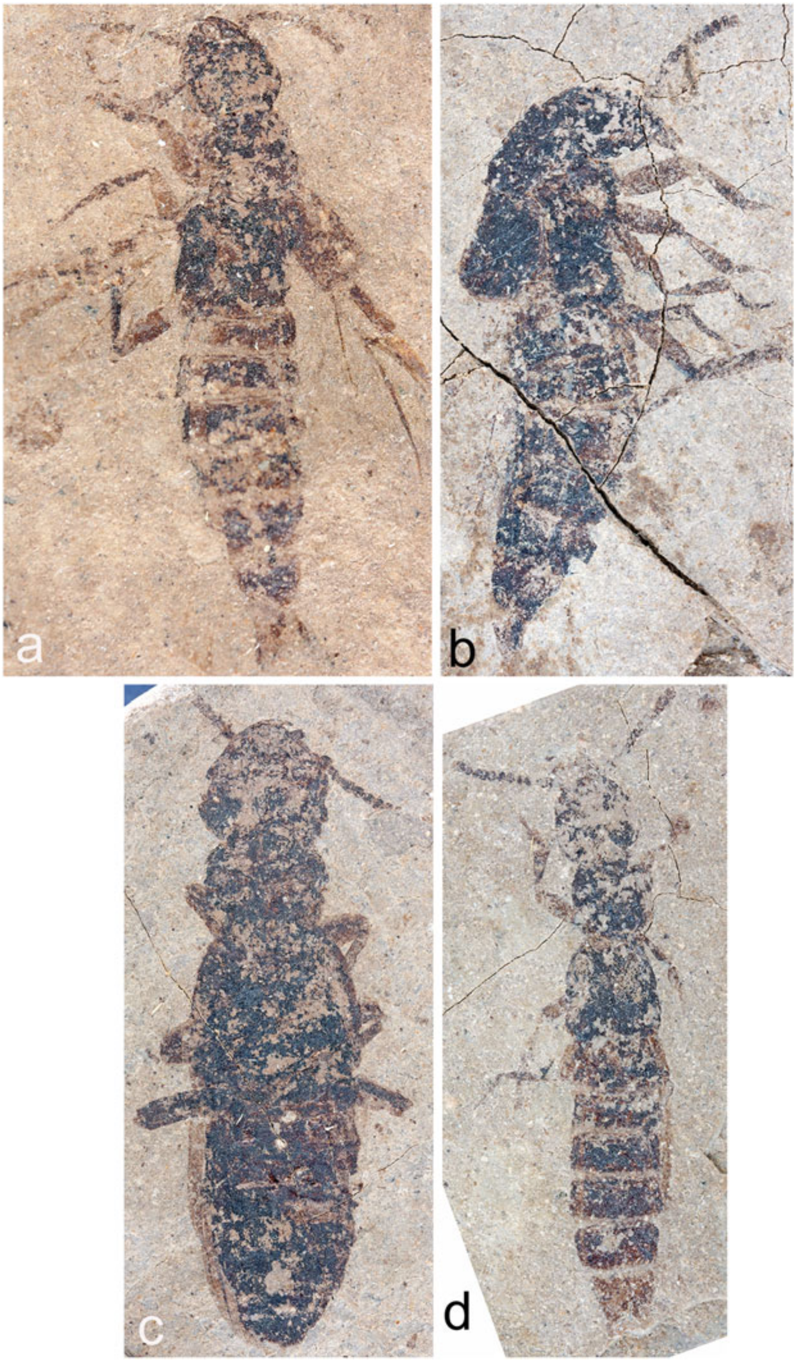

Fig. 3.1 Compression fossils of Staphylininae from Florissant, Colorado. (**a**) *Philonthus marcidulus* Scudder, USNM 1529, (**b**) *Staphylinus lesleyi* Scudder, USNM 1519; Herman (1986) suggested that this species probably belongs in *Bledius* Leach; (**c**) *Staphylinus vetulus* Scudder, USNM1537, (**d**) *Staphylinus vulcanus* Wickham, USNM 59636. While all these specimens were labeled as "types," they are syntypes because Scudder and Wickham designated multiple specimens in the type series without specifying one as holotype (see text for more details)

exceptions) paleontologists who did not work with Recent taxa. The past generations of rove beetle systematists spent very little time describing new fossil taxa or critically reviewing taxa described by the early paleontologists. There are many reasons why this happened: the false dichotomy between paleontologists and neontologists was much more prevalent in the

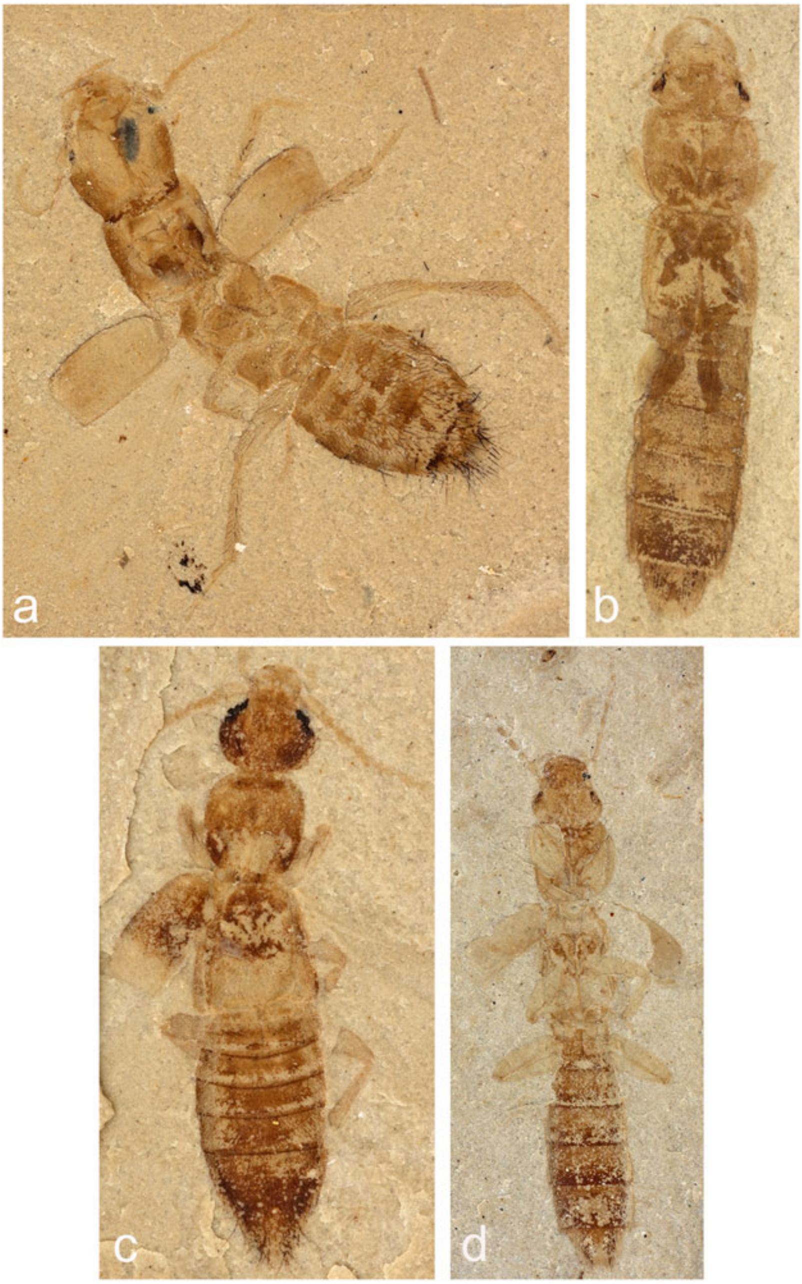

Fig. 3.2 Compression fossils of Paederinae from Green River. (**a**) Cryptobiina, USNM 58386; (**b**) Pinophilini, USNM 53181; (**c**) *Lathrobium absessum* Scudder, USNM 18593b; (**d**) *Palaminus*? USNM53181

past, and one had to be a paleontologist to look at a fossil; rove beetle taxonomy (even today) is a tangled mess, and it is hard to assign fossil taxa to higher-level groups; there are many extant species still awaiting descriptions, and most systematists prefer those than fossils; many modern techniques such as confocal microscopy or synchrotron microtomography that allow visualization of fossils were not available; and the absence of modern systematic methodology allows the incorporation of fossil taxa into phylogenetic analyses.

Another reason that might have discouraged the previous generation of rove beetle systematists to work with fossils is the frequent mistakes in identifying and assigning fossils to higher groups by the early paleontologists. A particular problem with fossils is that it is easy to fall into the trap of assigning similarities between fossils or between fossils and Recent taxa based on the reduction or loss of structures. This is especially true because without a proper phylogenetic analysis of all the subfamilies (such as the one produced by McKenna et al. 2015), it is hard to figure out which structures are apomorphies or plesiomorphies. Many paleontologists in the past had tried to fit fossils into Recent genera (Engel pers. comm.), rather than describing new fossil genera. For example, many fossils described by paleontologists such as Heer, Scudder, or Wickham in the nineteenth or twentieth century were placed incorrectly in Recent taxa and that created several problems: first, the geological age of the Recent taxa was incorrectly expanded by several million years (but see discussion below on stasis). Second, the generic limits were altered producing in some cases paraphyletic groupings; and, third, as mentioned above, these fossil taxa became unappealing to neontologists. Some of these early paleontologists even placed taxa in the wrong orders, describing, for example, earwigs as rove beetles (e.g., see Chatzimanolis and Engel 2010, for an attempt to correct some of these mistakes).

In recent years, there has been an important increase in the rate and quality of new fossil rove beetle descriptions. Herman (2001) in the introduction of his Catalogue of Staphylinidae mentioned that there had been 173 fossil taxa described between 1806 and 1999. Seventeen years later, the number of described fossil taxa has more than doubled with 374 described species as of October 17, 2016 (see Table 3.1). Many of these new descriptions incorporate high-quality images done with confocal microscopy or synchrotron X-ray microtomography, and we slowly start to see the incorporation of rigorous phylogenetic techniques in fossil studies (e.g., Solodovnikov et al. 2013).

3.3 Paleontological Record of Staphylinoidea

The purpose of this section is not to provide a complete catalogue of fossil staphylinoids; rather I attempt to synthesize some of the previous key works. Readers interested in more complete listings are encouraged to consult Herman (2001), Fossilworks (http://fossilworks.org), Mitchell (2013), and the forthcoming online catalogue of staphylinoids by Newton (unpublished). The age range (from Fossilworks) is given for the first time when a particular Lagerstätte is mentioned. However, the discussion below does not include Quaternary fossils or subfossils.

Besides the families listed below, two additional families might belong in this superfamily, the families Jacobsoniidae and the extant Ptismidae. Yamamoto et al. (2017) described a fossil Jacobsoniidae from Burmese amber (99.7–94.3 Ma) as the oldest member of this family. Ptismidae was described from Lebanese amber (130–124.45 Ma; Kirejtshuk et al. 2016) in Staphyliniformia and possibly in Staphylinoidea, although the fossil is rather difficult to interpret without a proper phylogenetic analysis.

3.3.1 Hydraenidae

Four species have been described in the genus *Ochtebiites* Ponomarenko (Ponomarenko 1977, 1980, 1985), and species in this genus are known from the Jurassic of Kazakhstan (Karatau Formation, 164.7–155.7 Ma), the Jurassic of the Russian Federation (189.6–155.7 Ma), and the Cretaceous of Mongolia (125.45–112.6 Ma). Whether or not these taxa truly belong in this family is not clear since the descriptions and drawings are rather vague. Additional species have been described in the extant genus *Ochthebius* Leach from the Rott Formation of Germany (28.4–23.03 Ma; von Heyden and von Heyden 1866) and the Firkanten Formation of Svalbard (66–58.7 Ma; Heer 1870).

3.3.2 Ptiliidae

While there are many undescribed ptiliids in amber from all major amber Lagerstätten (Shockley and Greenwalt 2013; see also for review of all described taxa), just six specimens have been described to species. Four of the described species are from Baltic (37.2–33.9 Ma) or Rovno (54.8–33.7 Ma) amber, while one species was described from the Rott Formation of Germany and another from the Kishenehn Formation of Montana (46.2–43.5 Ma).

3.3.3 Agyrtidae

A surprising number of fossil Agyrtidae (nine) have been described given that there are only 72 extant species known (see Table 3.1). The oldest fossils belong in the genus *Mesecanus* Newton (replacement name for *Mesagyrtes* Ponomarenko) from the Jurassic of the Russian Federation and the Jurassic of China (Hanshan Formation 171.6–164.7 Ma). Other fossils are known from the Turga Formation of the Russian Federation (125.45–122.46 Ma), the Chijinqiao Formation of China (125.45–112.6 Ma), the Eocene of Germany (Geiseltal, 48.6–40.4 Ma), and Baltic/Bitterfeld amber. A review of the fossil Agyrtidae was provided by Newton (1997) who questioned the placement of all fossil taxa currently in the family except *Mesecanus*.

3.3.4 Leiodidae

The oldest taxon in Leiodidae, *Mesagyrtoides fulvus* Perkovsky, is known from the Jurassic of Mongolia (Shar Teg: 152.1–145 Ma), but its placement in the family was recently disputed by Perreau (2012). Wickham (1913a) described a couple of species from the Florissant Formation in Colorado (37.2–33.9 Ma), while the majority of other taxa have been described from Baltic/Rovno (Perreau 2012) and Dominican amber (20.43–13.65 Ma; Perkovsky 2000).

3.3.5 Silphidae

Until recently, fossil Silphidae were only known from the Cenozoic. Several taxa were known from the Florissant Formation, and some of these taxa were described in the extant genus *Silpha* Linnaeus by Scudder and Wickham. Other Cenozoic taxa included species from the Geiseltal Formation of Germany, the Oligocene of France (Caylux, 28.4–23.03 Ma), the Miocene of Croatia (Radoboj, 12.7–11.6 Ma), and the Miocene of Germany (Oeningen, 12.7–11.6 Ma).

Recently, several Mesozoic Silphidae were reported by Cai et al. (2014a) from three different Lagerstätten: the Jurassic Daohugou Formation of China (164.7–155.7 Ma), the Cretaceous Yixian Formation of China (125.45–122.46 Ma), and the Burmese amber. While these taxa have not been described to species yet, many are well-preserved and undoubtedly will be eventually described.

3.3.6 Staphylinidae

Given the number of taxa in Staphylinidae, I will first discuss below the taxa that have been described as Staphylinidae *incertae sedis* and then provide details about the fossil history of each subfamily. Previous attempts to synthesize parts of the geological history of the family were made by Herman (2001), Cai and Huang (2010), Chatzimanolis and Engel (2011, 2013), Chatzimanolis et al. (2012), and Peris et al. (2014a).

The oldest described staphylinoid beetle is *Leehermania prorova* Chatzimanolis et al. from the Triassic Cow Branch Formation (221.5–205.5 Ma; Chatzimanolis et al. 2012). While some disagreement exists regarding the placement of *Leehermania* (Grebennikov and Newton 2012), the fossil has been used to calibrate several recent molecular phylogenies of Coleoptera as the oldest rove beetle (e.g., Misof et al. 2014; Toussaint et al. 2017). Of course, Chatzimanolis et al. 2012) could have been wrong about the placement of the fossil in

Staphylinidae, but without additional specimens showing its ventral view, the arguments in favor of the placement of the fossil in Hydroscaphidae as presented by Grebennikov and Newton (2012) are weak and rely on plesiomorphies (e.g., small size, short elytra, lack of abdominal paratergites, short antennae and legs).

Jurassic Staphylinidae *incertae sedis* are known from Karatau, Kazakhstan, and China. The genera *Tunicopterus* Tikhomirova and *Sulcelytrinus* Tikhomirova (Tikhomirova 1968) were recently reviewed by Solodovnikov et al. (2013) in a context of a phylogenetic analysis, and it was determined that they were not preserved well enough to assign them to a subfamily. Cai and Huang (2010) reviewed the Jurassic Staphylinidae from China and indicated that there are many more well-preserved genera awaiting formal description. Many Cretaceous compression fossils have been described as Staphylinidae *incertae sedis*, and several of those will be discussed below along with the subfamilies that are closely related to.

The various subfamilies are presented below in the order they appear on Fig. 3.4 which is based on the sister group relationships in the latest staphylinoid phylogeny by McKenna et al. (2015). Fossils formally described to species (non-Quaternary) are not known from the following subfamilies: Empelinae, Habrocerinae, Leptotyphlinae, Microsilphinae, Neophoninae, Protopselaphinae, Pseudopsinae, and Trichophyinae.

Tachyporinae Yamamoto (2016a) recently reviewed the Mesozoic Tachyporinae. The oldest Tachyporinae is known from the Jurassic of Jiulongshan, China (164.7–155.7 Ma). It is a specimen illustrated in Hong (1983) as "*Protostaphylinus mirus*" Lin, but according to Cai and Huang (2010) and Yamamoto (2016a), it is a different taxon than the one described by Lin (1976). Other Jurassic tachyporines are known from Karatau, Kazakhstan (Tikhomirova 1968), and the Talbragar beds in Australia (155.7–150.8 Ma; Cai et al. 2013a). This last fossil, *Protachinus minor* Cai et al., is significant because it provides a good early calibration point for the tribe Tachyporini. There are multiple known Cretaceous compression fossils (e.g., Yue et al. 2009; Cai et al. 2011), but only a couple in Cretaceous amber: *Mesotachyporus puer* Gusarov from New Jersey amber (94.3–89.3 Ma; Gusarov 2000) and *Procileoporus burmiticus* Yamamoto from Burmese amber (Yamamoto 2016a). Several taxa are known from the Cenozoic, including compression fossils from the Green River Formation (50.3–46.2 Ma; Chatzimanolis pers. obs.), Florissant (Scudder 1900), and amber fossils from Baltic and Dominican amber (e.g., Pasnik and Kubisz 2002; Yamamoto and Takahashi 2016).

Oxyporinae The oldest Oxyporinae are known from the Yixian Formation where three taxa have been described: *Cretoxyporus extraneus* Cai and Huang, *Protoxyporus grandis* Cai and Huang (Cai and Huang 2014a), and *Oxyporus yixianus* Solodovnkov and Yue (Yue et al. 2011). Additional fossils are known from the Cenozoic, but only *Oxyporus impressus* Piton (from Menat, France, 58.7–55.8 Ma; Piton 1940) and *Oxyporus vulcanus* von Heyden and von Heyden (from the Rott Formation; von Heyden and von Heyden 1866) definitely belong in *Oxyporus* according to Yue et al. (2011). The remaining species (*Oxyporus blumenbachi* Gravenhorst, *Oxyporus seuberti* Heer, and *Oxyporus stiriacus* Scudder) should be reexamined and probably removed from Oxyporinae (Yue et al. 2011).

Steninae Clarke and Chatzimanolis (2009) reviewed the geological history of Steninae. Two species of *Stenus* are known from the Mesozoic, *Stenus inexpectatus* Schlüter from French amber (99.7–94.3 Ma; Schlüter 1978) and *Stenus imputribilis* Ryvkin from Obeshchayushchiy, Russian Federation (84.9–70.6 Ma; Ryvkin 1988). Several other species of fossil *Stenus* are known from the Cenozoic, with many described by Puthz (2010). Cai et al. (2014b) described the only non-*Stenus* Steninae from the Eocene of France (Alès-Monteils, 37.2–33.9 Ma; *Eocenostenus fossilis* Cai et al.).

Euaesthetinae As above, Clarke and Chatzimanolis (2009) reviewed the geological history of Euaesthetinae. While several taxa have been attributed to this family (see Puthz 2008 and Fig. 3.3b on this chapter), only two taxa have been formally described: *Nordenskioldia pentatarsus* Lefebvre et al. (from Lebanese amber; Lefebvre et al. 2005) and *Octavius electrospinosus* Clarke and Chatzimanolis (from Burmese amber; Clarke and Chatzimanolis 2009).

Solieriinae The fossil Solieriinae all belong in the genus *Prosolierius* Thayer et al. Three species are known from Burmese amber (Thayer et al. 2012) and one species from Spanish amber (112.6–109 Ma; Peris et al. 2014a), while another undescribed species is known from Lebanese amber (Thayer et al. 2012).

Scydmaeninae The geological history of Scydmaeninae was recently reviewed by Jałoszyński (2016) and Jałoszyński and

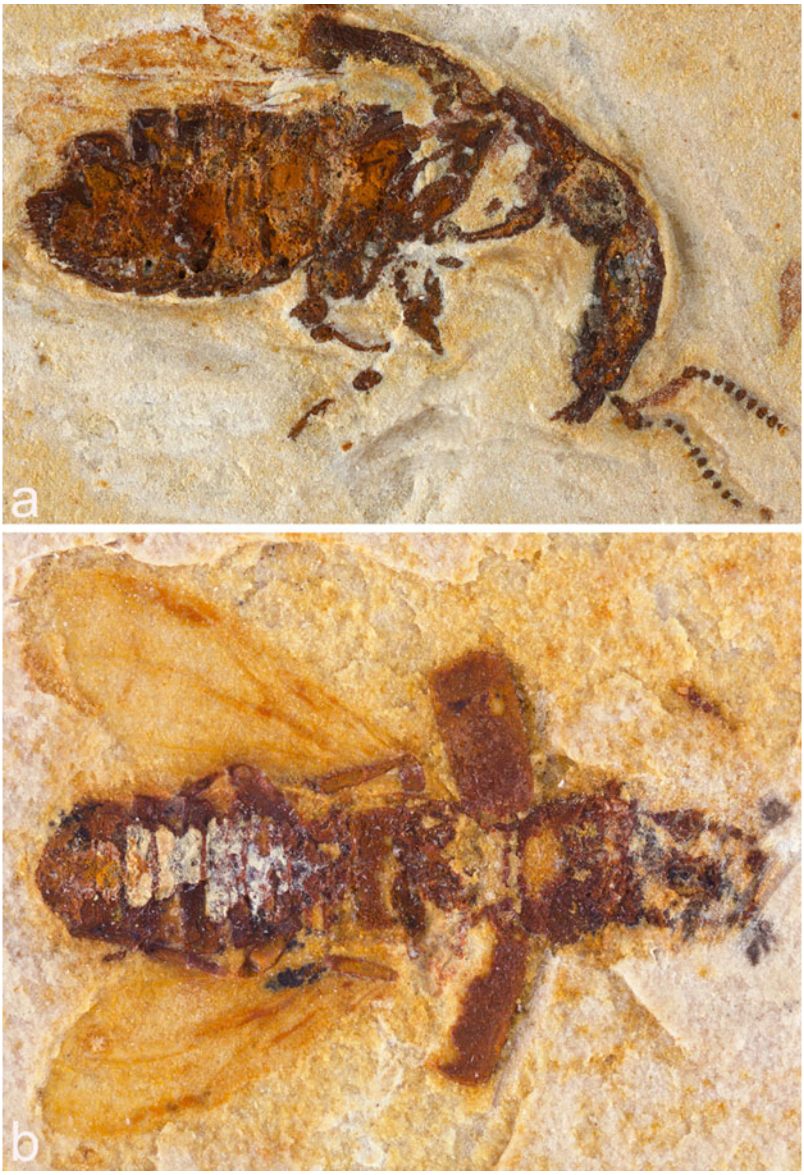

Fig. 3.3 Compression fossils of Staphylinidae from Crato, Brazil. (**a**) The oldest known specimen of Cryptobiina (Paederinae), AMNH SA46271; (**b**) a possible Paederinae, AMNH SA46246

Perkovsky (2016). A large number of fossils have been described from most major amber deposits with many more taxa remaining undescribed. The oldest taxa are known from Spanish amber, and all supertribes are known from the Cretaceous (Cai and Huang 2016; Jałoszyński and Peris 2016; Jałoszyński et al. 2017).

Aleocharinae More than 20 species of fossil Aleocharinae have been described (Yamamoto et al. 2016). The oldest taxa are known from Burmese amber from where two species were recently described: *Cretodeinopsis aenigmatica* Cai and Huang (Cai and Huang 2015a) and *Mesosymbion compactus* Yamamoto et al. (Yamamoto et al. 2016). That latter fossil is of particular importance because it had specialized morphological adaptations to coexist with social insects. The remaining taxa are known from Cenozoic amber and compression deposits. While many more taxa exist in Burmese, Baltic, and Dominican ambers (Chatzimanolis pers. obs.), the taxonomic chaos of recent taxa prohibits the rapid description of new fossil species. Unfortunately, for the same reason, all fossil taxa described in Recent genera should be reevaluated, particularly the taxa described by Scudder (1876, 1890) and Wickham (1913b) from Eocene compression fossils.

Phloeocharinae The only fossil species known from this subfamily is *Phloeocharis agerata* Chatzimanolis et al. described from New Jersey amber (Chatzimanolis et al. 2013).

Osoriinae Cai and Huang (2015b) described a fossil species, *Mesallotrochus longiantennatus* Cai and Huang, from Burmese amber. Other species are known from the Eocene of India (Cambay amber, 55.8–48.6 Ma; Ortega-Blanco et al. 2013), Dominican amber (Irmler 2003), and Shanwang, China (15.97–11.608 Ma; Zhang 1989).

Dasycerinae Yamamoto (2016b) described the only known fossil, *Protodasycerus aenigmaticus* Yamamoto, from Burmese amber. According to Yamamoto (2016b), the fossil seems to combine many features of Dasycerinae and Neophoninae.

Pselaphinae There are multiple species of Pselaphinae known from the Cenozoic and particularly from Baltic/Bitterfeld/Rovno amber and Dominican amber, either described or simply mentioned in the literature. Most of the species in Baltic amber were described by Schaufuss (1890), and Poinar and Poinar (1999) mentioned several species of Pselaphinae in Dominican amber. More recently, Peris et al. (2014a) described two species of Pselaphinae from Spanish amber, Parker and Grimaldi (2014) a species from Cambay amber, and Parker (2016) other species from Burmese amber.

Micropeplinae The oldest fossil of the subfamily was described by Cai and Huang (2014b) from Burmese amber. Three other species have been described in *Micropelpus* Latreille, two from Lava Camp Mine of Alaska (7.246–2.588; Mathews 1970) and another one from Willershausen clay pit in Germany (3.6–2.588; Gersdorf 1976).

Olisthaerinae Both fossils known of these peculiar beetles are from the Jurassic: Ryvkin (1985) described *Anicula inferna* Ryvkin from Novospasskoye of the Russian Federation (161.2–155.7 Ma) and Cai et al. (2015) described *Protolisthaerus jurassicus* Cai et al. from the Daohugou Formation of China. Cai et al. (2015) expressed some concern that *Anicula* might not belong in this subfamily but did not officially remove it. Another genus, *Megolisthaerus* Solodovnikov and Yue (Yue et al. 2010b), was described as closely related to Olisthaerinae, but Cai and Huang (2013b) transferred it to Staphylininae.

Paederinae The oldest described Paederinae are known from the Yixian Formation in the genus *Mesostaphylinus* Zhang (Solodovnikov et al. 2013). Other undescribed Mesozoic Paederinae are known from Spanish amber (Peris et al.

2014a) and from the Crato Formation of Brazil (122.46–112.6 Ma; Fig. 3.3a depicts the oldest record, still not formally described, for the subtribe Cryptobiina, A. Schomann pers. comm.). Multiple species have been described from Florissant, Colorado (e.g., Scudder 1890, 1900) and Baltic amber (e.g., Pasnik and Kubisz 2002), and most of those have been described (incorrectly) in the genus *Lathrobium* Gravenhorst. Other notable Cenozoic taxa are known from the Aix-en-Provence, France (11.6–7.2 Ma; Oustalet 1874), the Rott Formation of Germany (von Heyden and von Heyden 1866), and Shanwang, China (Zhang 1989).

Many new taxa are awaiting description from Burmese amber, Green River (see Fig. 3.2), and Kishenehn Formations in North America (Chatzimanolis pers. obs.). However, much work is needed on the classification of Paederinae before these taxa can be reliably described to an existing genus or subtribe (see also discussion below). The genus *Apticax* Schomann and Solodovnikov was described from the Crato Formation and was initially placed as closely related to Paederinae + Staphylininae (Schomann and Solodovnikov 2012). A later phylogenetic analysis (Solodovnikov et al. 2013) indicated that the genus could not be placed with confidence in any subfamily.

Staphylininae Solodovnikov et al. (2013) described many new Mesozoic genera (*Paleothius* Solodovnikov and Yue, *Cretoprosopus* Solodovnikov and Yue, *Thayeralinus* Solodovnikov and Yue, *Paleowinus* Solodovnikov and Yue, and *Durothorax* Solodovnikov and Yue) from the Yixian Formation, China. Other Cretaceous taxa include the genus *Cretoquedius* Ryvkin (Ryvkin 1988), originally described from Obeshchayushchiy, Russian Federation, but with additional taxa described from the Yixian Formation, China (Solodovnikov et al. 2013). The genus *Laostaphylinus* Zhang from the Laiyang Formation, China (125.45–112.6 Ma; Zhang, 1988), does not belong in the Staphylininae + Paederinae lineage according to Solodovnikov et al. (2013). A species described in *Quedius* Stephens by Cai and Huang (2013c) from the Yixian Formation likely belongs in *Cretoquedius* and could be a synonym of one of the taxa described by Solodovnikov et al. (2013). But even if that is not the case, the taxonomic concept of *Quedius* has changed dramatically over the last few years (Solodovnikov 2006; Brunke et al. 2016), and assigning that fossil to *Quedius* is problematic to say the least.

Many fossils have been described in this subfamily, at least in part because early paleontologists tried to describe fossils into Recent common genera. As such, many taxa from Florissant Colorado have been described in *Leptacinus* Erichson, *Philonthus* Curtis, *Quedius*, and *Xantholinus* Dejean (e.g., Scudder 1890, 1900; see Fig. 3.1). A common problem with these taxa is that multiple specimens were included in the type series, and sometimes these specimens are not conspecific. Needless to say, the generic assignment for all these fossils needs to be reevaluated. Other notable Cenozoic taxa include a species of *Tympanophorus* Nordmann from the Kishenehn Formation (Brunke et al. 2017); a species of *Platydracus* from Florissant (Cai et al. 2014d), Colorado; a species of *Algon* from the Miocene of China (Zhang 1989); and a species of *Leistotrophus* from the Green River Formation (Scudder 1876). Brunke et al. (2017) indicated that the *Leistotrophus* fossil is misidentified and does not belong in Staphylinina but most likely in either Acylophorina, Cyrtoquediina, Indoquediina, or Quediina. Chatzimanolis and Engel (2011, 2013) reviewed the taxa described in Baltic and Dominican amber.

Proteininae Vetuproteinus cretaceus Cai et al. (Cai et al. 2016) was recently described as the first definitive fossil representative of this subfamily from Burmese amber. Other fossils known include an undescribed *Proteinus* Latreille from Baltic amber (Cai et al. 2016).

Omaliinae Many Mesozoic fossils are known from this subfamily. Ryvkin (1985) described

Morsum abdominale Ryvkin from the Middle Jurassic of Kubekovo, Russian Federation (171.6–164.7 Ma). Other Jurassic records are known from Daohugou China (Cai and Huang 2013d), from the Karatau Formation of Kazakhstan (Tikhomirova 1968), and from Novospasskoe, Russia (161.2–155.7 Ma; Ryvkin 1985). Cretaceous Omaliinae are known from Daya (150.8–145.5 Ma) and Turga (125.45–122.46 Ma), Russian Federation, and were described by Ryvkin (1990). Recently, Peris et al. (2014b) described an Omaliini from French Cretaceous amber. Cenozoic records for the subfamily include many taxa, including species described from Baltic amber (Schaufuss 1890, Zanetti et al. 2016) and from Florissant, Colorado (e.g., Scudder 1900, Wickham 1913b).

Glypholomatinae Only two fossil species are known, and both belong in the Jurassic genus *Juroglypholoma* Cai et al. *Juroglypholoma antiquum* Cai et al. was described from the Daohugou Formation of China (Cai et al. 2012) and *Juroglypholoma talbragarense* Cai et al. from the Talbragar beds in Australia (Cai et al. 2013a).

Scaphidiinae The oldest Scaphidiinae are known from the Jurassic Formation of Solnhofen in Germany (150.8–145.5 Ma) and were described in the extinct genus *Scaphidiopsis* Handlirsch (Weyenbergh 1869). Other species were described from Oeningen, Germany, by Heer (1847, 1862).

Apateticinae While there are no formal fossil species described in Apateticinae, Newton (1997) suggested that *Miosilpha necrophiloides* Wickham (originally attributed to either Silphidae or Agyrtidae) from Florissant resembles the extant *Apatetica* Westwood and should be placed in that family. *Mesoapatetica aenigmatica* Cai et al. from Daohugou China was described as closely related to Apateticinae and Trigonurinae and more specifically as “a basal member of the Apateticinae and Trigonurinae clade” (Cai et al. 2014c). Unfortunately, the latest staphylinoid phylogeny of McKenna et al. (2015) does not support the hypothesis of a sister group relationship between these two subfamilies, and the fossil is interpreted here (see Fig. 3.4) as a stem group of the clade containing Apateticinae, Trigonurinae, and other subfamilies. Grebennikov and Newton (2012) and Cai and Huang (2013a) discussed the presence of Apateticinae in the Daohugou Formation but it is unclear if they were referring to *Mesoapatetica* or other fossils.

Trigonurinae The oldest known fossil is *Abolescus glabratus* Tikhomirova (Tikhomirova 1968) from the Jurassic Karatau Formation of Kazakhstan that was moved to this subfamily from Piestinae by Grebennikov and Newton (2012). Other fossils include *Triguna lata* Ryvkin (Ryvkin 1990) from Unda, Russian Federation (150.8–145.5 Ma), and *Kovalevia onokhoica* Ryvkin from Onokhoy, Russian Federation (125.45–112.6 Ma).

Megalopsidiinae The only fossil known is *Megalopinus extinctus* Yamamoto and Solodovnikov (Yamamoto and Solodovnikov 2016) from Burmese amber.

Piestinae Yue et al. (2016) recently described two species in the genus *Paleosiagonium* Yue et al. from the Yixian Formation of China. A fossil described much earlier, *Siagonium crassum* (Giebel), from Aix-en-Provence, France (Giebel 1856) has received little attention since the original description and might belong here.

Oxytelinae The fossil history of Oxytelinae was recently reviewed by Lü et al. (2017). Thirty-two Oxytelinae fossils have been described, ranging from 157.3 Ma to 5.3 Ma (not including the Quaternary taxa). All but two of these taxa, *Dolichoxenus newtoni* Engel and Chatzimanolis (Engel and Chatzimanolis 2009) and *Prajna tianmiaoae* Lü et al. (Lü et al. 2017), are compression fossils with the majority described from Florissant, Green River, or Chaomidian, China. While some of the compression fossil Oxytelinae

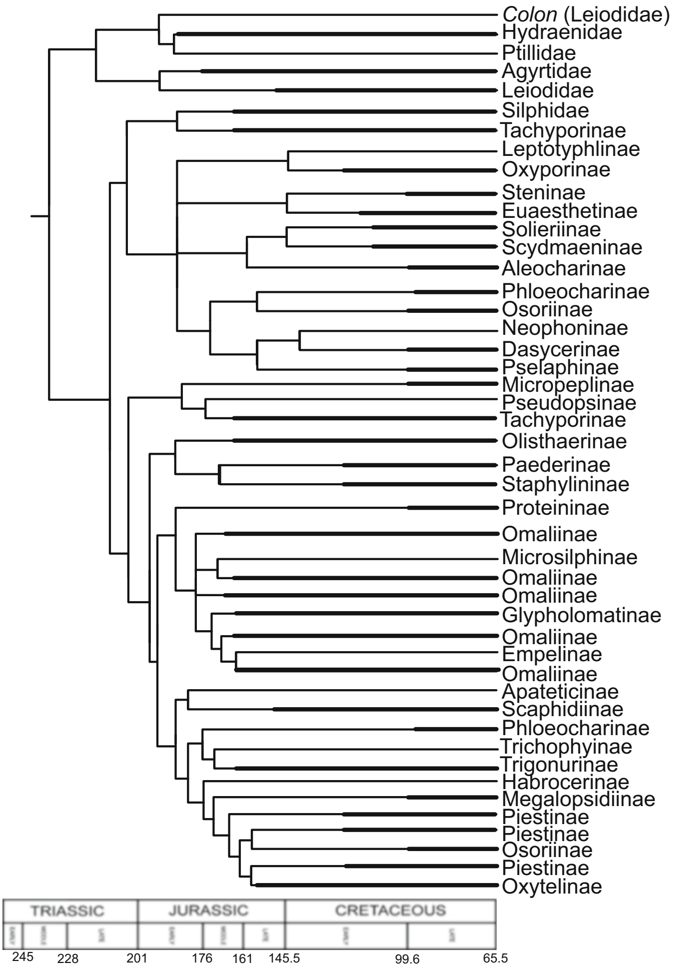

Fig. 3.4 Summary phylogeny of Staphylinoidea based on the Bayesian analysis of McKenna et al. (2015). The presence of Mesozoic fossils (based on records mentioned in the text) is indicated by thicker black bars. In the few instances where subfamilies were poly- or paraphyletic, all clades were treated as having the same geological history. Fossil taxa that were described as incertae sedis in Staphylinidae (such as *Leehermania*) are not included in this figure. Protopselaphinae was not included in the analysis of McKenna et al. (2015), but no fossils are known from the subfamily. See text (Sect. 3.4) for more details

are well-preserved (*Sinoxytelus:* Yue et al. 2010a; Cai et al. 2013b), others were poorly illustrated and described (especially taxa described in the nineteenth to twentieth century) and cannot really be used effectively in any comparative studies without a thorough review of the materials. Additionally, the status of all taxa described by Scudder (e.g., 1878, 1890, 1900) in Recent genera needs to be reevaluated.

†*Protactinae* This is the only extinct subfamily in Staphylinidae, containing two species from Oeningen, Germany (Heer 1847), in the genus *Protactus* Heer. The specimens are rather incomplete, and according to Yue et al. (2010b), they probably belong to a Recent subfamily.

3.4 Diversity Through Time

The origin of Staphylinidae by the Late Triassic is supported both by fossils (*Leehermania*, Chatzimanolis et al. 2012; other undescribed taxa mentioned in Fraser et al. 1996) and divergence estimates from molecular analyses (e.g., Toussaint et al. 2017). Given the phylogeny presented in McKenna et al. (2015), the oldest fossils known for the various subfamilies (presented in Sect. 3.3 and mapped on Fig. 3.4) and the various *incertae sedis* fossils in Staphylinidae, it is likely that almost all subfamilies currently recognized were present by Middle to Late Jurassic. While the timing of the Jurassic cladogenetic events presented in

Fig. 3.4 is hypothetical, it is likely that they all occurred during that period given the *incertae sedis* fossils for Staphylinidae known from that period. One potential problem with Middle Jurassic taxa is that it is hard to tell if these fossils belong in an existing subfamily or if they belong in a stem groups (e.g., see Cai et al. 2014c on the placement *Mesoapatetica aenigmatica* from Daohugou China).

As mentioned above, of all the existing subfamilies of rove beetles, we do not have fossils (formally described, non-Quaternary) for these: Empelinae, Habrocerinae, Leptotyphlinae, Microsilphinae, Neophoninae, Protopselaphinae, Pseudopsinae, and Trichophyinae. It will be probably hard to find Leptotyphlinae fossils (the extant members of this subfamily are so minute that it is difficult to see them with the naked eye), but given the long evolutionary history of Staphylinidae, it is probably just a matter of time before fossils for all the other subfamilies have been discovered. The current number of described fossils for the subfamilies Paederinae, Staphylininae, and Tachyporinae is higher than in most other subfamilies, but this is probably due to taxonomic bias of the work done by early paleontologists.

The majority of fossils have been described from Cenozoic formations, but there are some interesting surprises in the Cretaceous. For example, the subfamilies Olisthaerinae and Trigonurinae are only known from Jurassic and Jurassic/Cretaceous, respectively, with no known fossils from the Cenozoic. Other subfamilies with a Cretaceous-only record (no fossil Cenozoic taxa) include Apateticinae, Dasycerinae, Euaesthetinae, Glypholomatinae, Megalopsidiinae, Phloeocharinae, and Solieriinae. A lot of Cenozoic fossils still remain undescribed, and it is likely that we will discover fossil taxa for all these subfamilies. For example, there are yet to be described fossil Euaesthetinae and Megalopsidiinae from the Green River Formation (Chatzimanolis pers. obs.).

Recent fossil discoveries have altered our views on the biogeography and evolution of certain lineages. It was hypothesized that at least some subfamilies in Staphylinidae and certainly several in the "omaliine" group could have a Gondwanan distribution (e.g., Newton 1985). However, the discovery of several fossils (Jurassic Glypholomatinae from China: Cai et al. 2012; Solieriinae from Burmese, Lebanese and Spanish amber: Thayer et al. 2012; Peris et al. 2014a; and Proteininae from Burmese amber: Cai et al. 2016) have busted the Gondwanan origin hypothesis of several extant austral-endemic groups, at least at the subfamily level. It appears that rove beetles have the opposite problem of plants: recently, Ruhfel et al. (2016) concluded that the Malpighiales plants are too young to have a Gondwanan vicariant distribution, while it seems that rove beetles are too old for such distribution since all subfamilies were likely present before the break up of Pangea.

3.5 Stasis in the Fossil Record

In recent years many taxa from Cenomanian/Albian ambers have been described in Recent genera, and the authors of these papers have attributed this phenomenon to bradytely, i.e., slow rates of morphological change. Clarke and Chatzimanolis (2009) described a species of the Recent genus *Octavius* Fauvel from Burmese amber and were one of the first papers to discuss bradytely in Staphylinoidea. Other examples of bradytely from Cretaceous include species of *Stenus* Latreille from French amber (Schlüter 1978) and from Obeshchayushchiy, Russian Federation (Ryvkin 1988); undescribed species of *Nicrophorus* Fabricius from Burmese amber (Cai et al. 2014a); a species of *Phloeocharis* Mannerheim from New Jersey amber (Chatzimanolis et al. 2013); a species of *Eutheia* from Taimyr amber (Jałoszyński and Perkovsky 2016), and a species of *Megalopinus* Eichelbaum from Burmese amber (Yamamoto and Solodovnikov 2016). Other taxa that perhaps exhibit bradytely are several species of *Oxyporus* Fabricius (but several with uncertain placement, see section above) and the Jurassic *Protolisthaerus* (Cai et al. 2015).

In addition to the taxa mentioned above, there are other more recent fossils from the Cenozoic that have been described in Recent genera, mainly from Green River and Florissant Formations and Baltic amber by earlier paleontologists. However, given that most of these taxa need to be reexamined to verify their taxonomic position, it is hard to identify concrete examples of bradytely. Another problem is that the taxonomic concept of genera frequently changes, and taxa that were described in one Recent genus may actually belong in another. An example was recently mentioned by Yamamato et al. (2016), where a species described in *Homalota* Mannerheim from Green River by Scudder (Scudder 1890) is a member of what we will identify today as *Atheta* Thomson.

As a hypothesis for the explanation of bradytely in staphylinoid genera, Clarke and Chatzimanolis (2009) proposed "the continuous presence of mesic habitats over geological time." For better or worse, all subsequent papers dealing with bradytely (see references above) have used this as an explanation for the phenomenon. While the hypothesis of Clarke and Chatzimanolis (2009) is possible, we should consider the percentage of rove beetles living in mesic habitats, the long-term availability of other types of habitats, and the fossilization process. The "mesic habitat" hypothesis has not been statistically tested, and perhaps we should do so before we perpetuate this hypothesis.

We also need to consider the following paradox: how is it possible that we discuss bradytely for a group of animals such as Staphylinidae that has (given the time of origin and the current number of species) some of the highest speciation rates? Clarke and Chatzimanolis (2009) argued that perhaps some lineages of Staphylinidae exhibit bradytely, while others exhibit tachytely (rapid evolutionary change), or differential fossilization, or even lower extinction rates. The latter hypothesis was suggested for taxa such as *Octavius* or *Stenus* that exhibit bradytely and have high speciation rates with ~250 and ~2900 described species (see Chap. 11), respectively (Clarke and Chatzimanolis 2009), but again without any statistical tests. Perhaps, it is due time that we move into the age of statistical testing and try to decipher the tempo of evolution (see Voje 2016) given all these examples of stasis, our recent molecular analyses of Staphylinoidea, and the available diversification rates.

3.6 Future Directions

While we have made significant headway in understanding the staphylinoid fossil biota, there is still a long way to go before we can achieve a complete picture. Below is a list of items that I believe can help us make significant progress.

Review the Work of Early Paleontologists We certainly need people who have access and are able to reexamine all fossils described by Scudder, Tikhomirova, and Wickham, just to name a few. Many of these fossils were published with short descriptions, incomplete illustrations, and, as I have mentioned multiple times already above, in the wrong genera. These reviews should include lectotype designations since multiple specimens were included in the original type series that are not conspecific. Ideally, these taxa should be reexamined with modern imaging techniques such as SEM or microCT to be able to distinguish as many characters as possible.

Incorporate Fossils into Phylogenetic Analyses Whenever possible, we should try to move away from single-species descriptive works. Instead, we should describe new fossil species in the context of revisionary works and place them into a phylogenetic context. Attempting to discuss relationships without a phylogenetic analysis produces just-so-stories, and it should not be acceptable anymore. Solodovnikov et al. (2013), Jałoszyński (2015), and Yamamoto et al. (2016) greatly enhanced their fossil discoveries by providing phylogenetic analyses that included both fossils and Recent taxa.

Explore New or Neglected Lagerstätten Many new important taxa are currently being described from Burmese amber and the Yixian Formation (see references above). However, there are other Lagerstätten that have received little attention in the last few years or have recently become available. These include the Jurassic Formations in China (Cai and Huang 2010) and Cambay amber (Rust et al. 2010; Ortega-Blanco et al. 2013) but also formations in North America such as the Kishenehn Formation of Montana (Greenwalt and Labandeira 2013; Greenwalt et al. 2016). The Eocene formations of Florissant and Green River received a lot of attention by Scudder, but many new fossils have been uncovered recently. Unfortunately, it will be rather difficult to work with these fossils before a thorough review of the existing taxa from these localities is completed. These Eocene N. America formations are particularly important from a conservation/climate change perspective because they can provide data on the fauna of N. America under an elevated temperature scenario. Additionally, while Eocene formations may not be as exciting for discovering key innovations at the subfamily level, they can be really useful in figuring out biogeographic or genus-level group relationships (Brunke et al. 2017).

Bridge the Gap Between Paleontologists and Neontologists If possible, we need rove beetle systematists who work with both Recent and extinct materials, systematists who are comfortable revising Recent genera and at the same time describing fossil taxa. Typically, paleontologists tend to be generalists (i.e., describing fossils in many orders) and do not have the understanding of plasticity and variation of characters (or character polarity) within rove beetles.

Produce Generic Revisions for all Staphylinoid Subfamilies Although I have no illusion that this is a formidable task, and unlikely to be completed anytime soon, we will never be able to correctly classify many fossils unless we sort out the classification of extant taxa. For example, many fossil Cryptobiina Paederinae (see Figs. 3.2 and 3.3a) from Green River and Crato Formations remain undescribed because the higher-level classification of Cryptobiina is in disarray and placing these fossil taxa is impossible. Of course, one can start creating new genera for all these fossils, but this is not a good practice. Similarly, there are many fossil Aleocharinae (Chatzimanolis pers. observ.) in every major Lagerstätte that are hard or impossible to place because of the current issues with the Aleocharinae classification.

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