Systematics, Natural History, and Evolution of the Saw-Lipped Rove Beetles (Euaesthetinae): Progress and Prospects for Future Research

6

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Abstract

The rove beetle subfamily Euaesthetinae is reviewed and information on the systematics, ecology, and evolution presented. Key morphological features of adults and larvae are discussed, and the current state of morphology-based phylogenetics and paleontological research is reviewed. Natural history information is compiled for most genera, and general ecological trends are highlighted. Euaesthetinae are probably monophyletic but with a suprageneric taxonomic structure likely poorly reflected by the current classification. They are nearly globally distributed in most habitats, and collection data suggests that their ecological diversity is not yet fully known or confirmed. The southern hemisphere and high-elevation faunas globally comprise mostly flightless species restricted to ground litter of diverse habitats. A division into groups extending from the general ground litter into either soil (endogenous) or aboveground habitats (mediated by high-moisture microhabitats, typically dense bryophyte growths) is suggested. Although Euaesthetinae are generally found in mesic habitats, a group of seemingly "periaquatic" taxa are primarily found in Holarctic riparian and wetland sites. Probable "surface runners" and arboreal (foliage-dwelling) species form two other (overlapping) ecological groupings, and the occurrence of some species in vertebrate and ant nests requires further investigation. Biological inferences are drawn from several different morphological features of the group suggesting diverse life histories for these tiny beetles. Updated fossil information is provided, and this indicates needed taxonomic changes and suggests a greater extinct taxonomic diversity than previously known. The fossil record and ecology of the group suggest that euaesthetine lineages are resistant to extinction over geological time making these beetles well-suited to historical biogeographic studies.

6.1 Introduction

Euaesthetinae (Fig. 6.1), or "saw-lipped rove beetles" (on account of most included species having a serrate or denticulate labral margin), are a poorly known group of predatory ground-dwelling staphylinids occurring in forests and other habitats worldwide. Herman (2001) listed 724 species in 26 genera (762 spp. in Thayer 2005), with the current total standing at 1155 species (A. Newton unpub.). Although it is therefore a small group compared with some of the

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larger subfamilies, some genera present notable radiations. As most species are cryptic, occurring primarily in the leaf litter and similar microhabitats, finding them requires specialized collecting techniques, and so they are only rarely encountered in the field. Unsurprisingly, this practical issue has contributed to a much slower rate of increase in biological and ecological knowledge compared to related groups like Steninae for which significant biological knowledge has accumulated (e.g., Betz 1998a; Chap. 11 of this book). To date there has not been a focused study on any aspect of the biology of Euaesthetinae, and there may be only a single literature report on any aspect of their life history (Remillet 1969; an *Octavius* Fauvel, 1873 specimen fed diplurans for ~1 month). Available information is scattered in the primary literature and consists of specimen-level collection data reported in the context of taxonomic studies, with some larger contributions presenting valuable in-depth generalizations about the ecology of regional faunas (e.g., Orousset 1988, 2012). The development of evolutionary research on this group has therefore been impacted by this general paucity of biological information and has been further affected by both a lack of synthetic systematic studies and a slower discovery of well-preserved fossils than for other staphylinid groups. Given their cryptic habits and undersampling, the extant global diversity of Euaesthetinae is undoubtedly much greater than currently known. Systematic research is just beginning to advance beyond alpha taxonomic work on (mainly) the larger widespread genera following preliminary work by Leschen and Newton (2003), Clarke and Grebennikov (2009), and others to develop sets of phylogenetically informative morphological characters. Paleontological research on Euaesthetinae (and the closely related group Steninae) is in its infancy, but some notable recent papers reported on the existence of morphologically derived (crown-group) taxa as early as the Early Cretaceous, ~135–100 Ma (Lefebvre et al. 2005; Clarke and Chatzimanolis 2009). The author's ongoing work on the comparative morphology of Euaesthetinae (especially of their mouthparts), inter- and infra-generic morphological diversity, new fossil discoveries, and the synthesis of information presented herein confirms that the group is much more biologically and ecologically diverse than previously thought.

6.1.1 Recognition of Adults and Larvae of Euaesthetinae

Most species of Euaesthetinae are minute, ~1–2.5 mm long, but with size outliers occurring in both directions, such as in some undescribed species of *Protopristus* Broun, 1909 <0.5 mm and the "giant" *Edaphus goliath* Puthz, 2007 of South America, reaching 5.1 mm (Puthz 2007a). They are generally slender or tubular in form though as a group Euaesthetinae are morphologically diverse in characters and habitus considering their minute size (Fig. 6.1; see also Orousset 1988 for habitus illustrations of five genera). Euaesthetinae are closely related to Steninae (see below), but extant taxa are distinguished from this megadiverse and comparatively homogenous group (and other staphylinid subfamilies) by the combination of several characters including the evenly denticulate margin of the labrum (Fig. 6.2c; *Stenaesthetus* Sharp, 1874, *Schatzmayrina* Koch, 1934, and several species of *Edaphus* Motschulsky, 1857 are exceptional in having a smooth or nearly smooth margin; e.g., Fig. 6.2f), the well-developed pronotosternal suture (Fig. 6.2d, arrow), the pointed apex of the ninth sternite (male) or second gonocoxite (female) (Fig. 6.2g–h), and the conspicuous macrosetae (usually a row of 3–4) along the posterolateral edge of the metacoxa (Fig. 6.2e, arrow). Other characteristics include the falcate or otherwise slender-curved mandibles (Fig. 6.2a) that are hidden beneath the labrum in repose, the clubbed antennae (Fig. 6.2a; both shared with Steninae), and reduced tarsal segmentation in most genera [4-4-4 in the majority, e.g., Fig. 6.2i; 5-5-4 in Stenaesthetini; 5-5-5 only in *Edaphosoma* Scheerpeltz, 1976 and *Nordenskioldia* Sahlberg, 1880 (Nordenskioldiini), and in *Fenderia* Hatch, 1957 and *Stictocranius* LeConte, 1866 (Stictocraniini)]. Although generally distinct in both habitus and characters, no adult

Fig. 6.1 Habitus photos of select Euaesthetinae (**a**) Euaesthetini: *Edaphus* sp. (**b**) Austroesthetini: *Austroesthetus* sp. (**c**) Stenaesthetini: "EuaAUS." (**d**) Euaesthetini: *Octavius* sp. Scale bars = 1 mm

character has yet been found that is both present in all species of Euaesthetinae and apparently unique to the group (see below).

Larvae have been described for about one third of euaesthetine genera and are known (but not yet described) for several others (Fig. 6.4). Larval descriptions of varying detail have been contributed by several authors (e.g., Kasule 1966; Newton 1990; Clarke and Grebennikov 2009), with the most complete larval description being for that of a New Zealand *Agnosthaetus* species (Clarke 2011). Like the adults, larvae are generally characteristic but cannot easily be distinguished from other subfamilies by any single character alone. They lack a separate labrum (this has fused to the head capsule forming an apically toothed nasale), have abdominal terga that form entire plates (undivided at middle, except, exceptionally, in at least some Australian *Edaphus*), and, if present at all, have an unarticulated (fixed) maxillary mala. All three characters are shared with Steninae. From that subfamily, euaesthetine larvae can be most easily distinguished by the combination of their generally much smaller size, three-segmented antennae that are shorter than the head, longest leg seta located on the tibia, and the absence or strong reduction of the maxillary mala. Further, when the mala is present it is positioned somewhat dorsally (rather than projecting mesially) such that it is difficult to observe in ventral view (see Kasule 1966: fig. 60; Grebennikov and Newton 2009; Clarke and Grebennikov 2009: figs. 7C–F, 8; Clarke 2011: figs. 41 and 44). Traditionally, larvae of Euaesthetinae and Steninae have also been distinguished from each other by the structure of the head capsule and ligula (with distinct neck and nuchal carina and narrow, acute, or finger-like ligula in Euaesthetinae; no neck or nuchal carina, and distinctly broad and bilobed ligula in Steninae; e.g., Kasule 1966; Newton 1990; Frank 1991; Leschen and Newton 2003). However, known *Edaphus* larvae lack a distinct neck and nuchal carina, and only *Euaesthetus* Gravenhorst, 1806, larvae actually have a somewhat developed neck (Newton 1990; Clarke and Grebennikov 2009: fig. 5C). Moreover, an undescribed litter-dwelling stenine genus endemic to southeastern Australia also has a distinct neck and nuchal carina (and short antennae), unlike the known larvae of other stenines (Clarke et al., in prep.), and it is now known that the structure of the ligula in both subfamilies is more variable than previously thought (see also Welch 1966: 250). Euaesthetine larvae are also very similar to those of the related subfamilies Staphylininae, Paederinae, Pseudopsinae, and Leptotyphlinae. From the first three of these, Euaesthetinae can be most easily distinguished by the lack of a

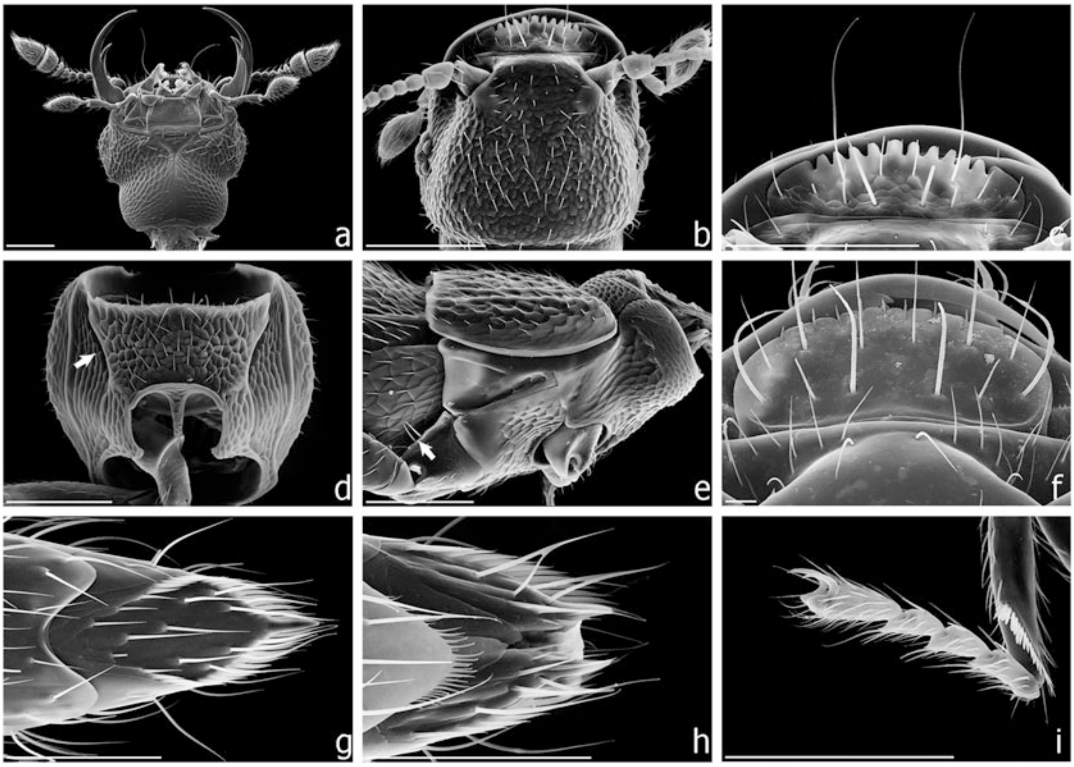

Fig. 6.2 Euaesthetinae, details of morphology (**a**) head (ventral), (**b**) head (dorsal), (**c**) labrum (dorsal), (**d**) prothorax (ventral), (**e**) pterothorax (right lateral), (**f**) labrum (dorsal), (**g**) male abdominal apex (ventral), (**h**) female abdominal apex (ventral), (**i**) metatarsus (lateral). (**a**) *Austroesthetus* sp., (**b–e**, **g–h**) *Chilioesthetus* sp., (**f**, **i**) *Edaphus* sp. Scale bars = 100 µm. See text for discussion of structures identified by arrows

distinct neck constriction, the presence of only one pair of parasclerites per abdominal segment, and the mesially open maxillary foramen (Grebennikov 2005). From leptotyphline larvae, Euaesthetinae can be distinguished by the lack of a subapical tooth along the inner mandibular margin, a dorsally instead of mesially projecting maxillary mala, and abdominal spiracles placed in membrane and not embedded in the terga (Grebennikov and Newton 2008).

6.2 Biodiversity and Systematics

6.2.1 Species Richness and Taxonomy

Although a small subfamily, the rate of species description for Euaesthetinae shows no sign of leveling off (Fig. 6.3) and demonstrates how much basic taxonomic work still remains in this group. The lower rate of taxonomic description for Euaesthetinae compared to that for its putative sister group Steninae reflects both the astonishing diversity in the genus *Stenus* Latreille, 1797, and also the greater taxonomic effort expended on that subfamily. Nearly 89% of the 1155 nominal species of Euaesthetinae are in the mainly pantropical genera *Edaphus* (593 spp.), *Octavius* (260 spp.), and *Stenaesthetus* (110 spp.), and the mainly Holarctic genus *Euaesthetus* (55 spp.). For these genera the rate of new species descriptions has generally been high and continues to be so (e.g., *Edaphus*: Puthz 2006a, b; *Octavius*: Puthz 2006c; *Stenaesthetus*: Puthz 2013a; *Euaesthetus*: Puthz 2014a). The rest of the 137 nominal species in the subfamily are scattered among the numerous species-poor and more or less geographically restricted genera

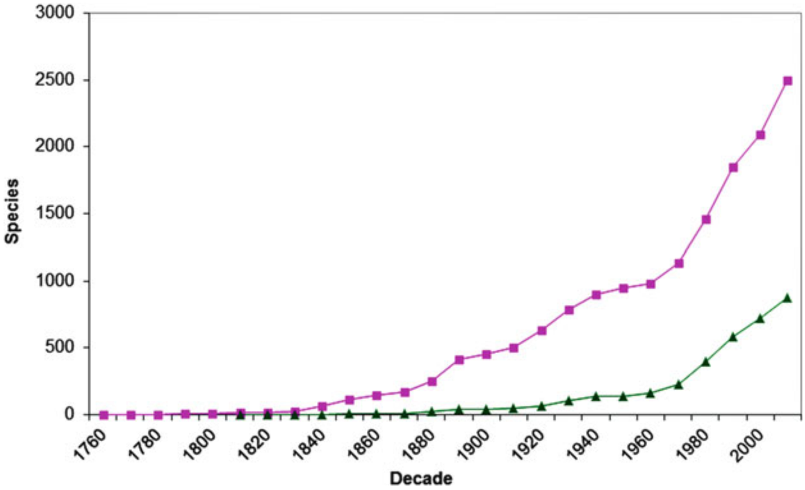

Fig. 6.3 Rate of species description for subfamilies Euaesthetinae (triangles) and Steninae (squares)

occurring primarily in temperate regions (Fig. 6.4). Similar diversity increases for these faunas have been slower, with most notable increases reported only recently and for only a few genera [e.g., South African *Octavius*, from 15 to 53 spp. (Puthz 2006c; Janák 2014); New Zealand *Agnosthaetus*, from 6 to 34 spp. (Clarke 2011); Chinese *Edaphosoma*, from 6 to 22 spp. (Puthz 2010a, b)]. The numbers of undescribed species reported in Fig. 6.4 are the result of my own in-progress surveys of the austral euaesthetine fauna (with substantial help from V. Puthz), and these further emphasize that the rate of species description for this subfamily will continue to increase. The difficulty with collecting euaesthetines (mostly via Berlese/Winkler extraction from sifted plant material) in combination with the still vast and ecologically diverse areas of unsurveyed habitat in just the austral areas alone helps to explain the trend in Fig. 6.3 and strongly suggests that the real diversity in any region is much greater than what is currently known (e.g., Puthz 1978). For example, in a review of Neotropical *Edaphus*, Puthz (2014b) indicates >240 new species of *Edaphus* known to him (most of these from the Oriental Region). In Chile, just one euaesthetine species has been described from the large and southernmost Magellanic Province of Chile (*Nothoesthetus australis* Sáiz, 1970), and the published figures of this species and also *N. obesus* Sáiz, 1970 (both known only from females), suggest that neither species are even congeneric with *N. coiffaiti* Sáiz, 1970, the type species. In Australia the lack of collecting effort is more pronounced. For example, fewer than 40 total specimens representing at least a dozen species in three genera have been collected from the cool temperate forests of Western Australia. These include the two most unusual Australian species of Austroesthetini (the only fully winged species of an austral-endemic genus—an undescribed species of *Austroesthetus* Oke, 1933; the only blind, flightless, and soil-dwelling species of *Chilioesthetus* Sáiz, 1968; see below).

As typical for Staphylinidae, alpha taxonomy of Euaesthetinae has historically been (and continues to be) entirely based on morphological characters, with differences between species largely anchored on male genital structures. It is common in this group for the only illustrations accompanying descriptions to be of the aedeagus, secondary sexual structures, and (less frequently) female genitalia (spermatheca). For some genera there are not yet any published habitus images, and much imaging work remains to help increase the profile of this interesting subfamily. Important aspects of future taxonomic work will include the development of electronic identification guides with comprehensive image documentation for all genera and major species

				Biogeographic Regions												
	Des. sp.	Und. sp.	Lar.	WP	EP	NA	AF	OR	NE	PA	MA	SA	AU	NZ	CH	Wid. sp.
NORTHERN																
Nordenskioldiini																
Edaphosoma	22	?						22								0
Nordenskioldia	2	?			1	1										0
Stictocraniini																
Fenderia	6	?	D			6										0
Stictocranius	5	?				2		3								0
Euaesthetini																
Euaesthetus	55	?	D	2[5]	5[7]	21[6]		3[2]	12[5]							12
Ctenomastax	7	?		4[2]	1[1]		[1]									2
Euaesthetotyphlus	1	?		1												0
TROPICAL																
Stenaesthetini																
Stenaesthetus	110	?	U		[2]		19[2]	35[2]	22	[1]	28	2[2]				4
Euaesthetini																
Edaphus	593	~75	D	1	29	4	82	299	104	46	7	2	12		1	6
				[1]	[2]	[1]	[1]	[5]		[1]	[2]	[1]	[1]	i[1]		
Octavius	260	?	D	59	[1]		37	16[2]	26	9[1]	58	53	**(1)**			2
Tamotus	11	~1						**(1)**	11							0
Schatzmayrina	3	~1					1[1]	[1]	1		**(1)**	[1]				1
[Macroturellus]	1	-					1									0
{Phaenoctavius}	1	-							1							0

Fig. 6.4 Biodiversity and biogeographic data for Euaesthetinae

AUSTRAL																
Alzadaesthetini																
Alzadaesthetus	2	1	D												3	0
Austroesthetini																
Austroesthetus	4	13	D										17			0
Chilioesthetus	6	10	D										6		10	0
Kiwiaesthetus	7	5												12		0
Mesoaesthetus	2	17											19			0
Nothoesthetus	10	4	D												14	0
Tasmanosthetus	1	2											3			0
Gen1_CHI	-	2													2	0
Gen2_CHI	-	1	U												1	0
Euaesthetini																
{Coiffaitia}	6	~2									8					0
{Neocoiffaitia}	1	~1									2					0
Protopristus	3	~120	D										22	101		0
Gen1_SAF	{1}	4	U?									5				0
Gen2_SAF	{1}	1										2				0
Gen3_TAS	-	1											1			0
Stenaesthetini																
Agnosthaetus	34	0	D											34		0
[Tyrannomastax]	2	-									2					0
EuaAUS	-	2											2			0
TOTALS	1155	263	13	67	36	34	140	378	177	55	105	64	157	147	31	27

The 32 described and undescribed genera of Euaesthetinae are divided into a northern fauna, a tropical fauna, and an austral fauna. Numbers of described and known undescribed species are shown in their respective regions; total numbers of widespread species (two or more regions; right column) are shown inside square brackets within regions. *Euaesthetus:* 12 species in WP/EP (4 spp.), EP/OR (2 spp.), NA/NE (5 spp.), and NA/WP/EP (1 sp.); *Ctenomastax*: 2 species in WP/EP (1 sp.) and WP/AF (1 sp.); *Stenaesthetus:* 4 species in AF/SA (2 spp.), EP/OR (1 sp.), and EP/OR/PA (1 sp.); *Edaphus:* 6 species in EP/OR (2 spp.), OR/MA (1 sp.), OR/PA (1 sp.), AF/MA/AU (1 sp.), and WP/NE/OR/AU/NZ (1 sp.); *Octavius:* 2 species in EP/OR (1 sp.) and OR/PA (1 sp.). Column totals exclude bracketed numbers; the total for AU includes the ~75 undescribed Australian *Edaphus* omitted from that cell due to space. *Des. sp.* Described species, *Und. sp.* known undescribed species (~ estimated; others confirmed by dissection), *Lar.* larval records for genera (D = described; U = undescribed; U? = uncertain larval association), *WP* Western Palearctic, *EP* Eastern Palearctic, *NA* North America, *AF* Afrotropical, *OR* Oriental, *NE* Neotropical, *PA* Pacific, *MA* Madagascar region, *SA* Southern Africa, *AU* Australia, *NZ* New Zealand, *CH* Chile and Argentina, *Wid. sp.* widespread species, *i* introduced species, [*Genus*] likely a synonym of another genus, {*Genus*} belongs in another subfamily, **(1)** new records for that region, {1} described species currently misplaced in another genus, numbers in square brackets, e.g., [1], are the total number of widespread species in the region

Fig. 6.4 (continued)

groups. At present, no molecular taxonomic or phylogeographic studies have been performed, but these would likely reveal many more species than are currently known from morphology alone. Figure 6.4 summarizes current estimates of known undescribed species for the austral fauna, details of which are discussed later in this section.

The generic-level taxonomy of extant Euaesthetinae is still in flux (Fig. 6.4), with three included genera misplaced in Euaesthetinae (*Coiffaitia* Kistner and Shower, 1965, and *Neocoiffaitia* Orousset, 1988 probably belonging in Solieriinae; and *Phaenoctavius* Pace, 1986 in Oxytelinae, this genus likely being a synonym of *Carpelimus* Leach, 1819) and at least two currently valid genera that should probably be placed in synonymy with others, pending detailed study of type material. For example, the genus *Tyrannomastax* Orousset, 1988 has derived mouthparts similar to those of *Stenus* (as discussed by Leschen and Newton 2003) but in nearly all important respects has the characters of *Stenaesthetus* including several unique or diagnostic characters such as the filamentous antennal structure, prothoracic structures, form of the elytral epipleural carina, ventral abdominal carinae, and genital structure. From the figures in the original description, the African monotypic genus *Macroturellus* Orousset, 1987 is clearly a highly derived member of a primarily African and Oriental group of *Octavius* species comprising distinctive forms like *O. batesi* (Sharp, 1876) and *O. bicolor* (Cameron, 1938), both originally described in the separate genera *Turellus* Sharp, 1876 and *Doletica* Cameron, 1938, respectively, reflecting the shared unique form of these species. Most notably, *M. pulcher* Orousset, 1987, *O. bicolor*, and several related species share among other characters a unique pronounced lateral flanging of the prothorax and strongly tapering abdomen as well as longitudinally carinate elytra (e.g., Orousset 1987: fig. 11; Kistner 1961a: figs. 9–16), similar to those of Pseudopsinae. The current taxonomic status of World Euaesthetinae, as summarized in Fig. 6.4, reveals that a significant number of new but as yet undescribed genera are known in the austral region but none are known for other regions. This perhaps reflects the well-known bias toward northern hemisphere faunas in both collecting and taxonomic effort but may also reflect different evolutionary histories for austral and other regions. Six putative new genera in three tribes are known for the austral region and await description and proper phylogenetic study. Two undescribed genera have been identified among minute South African species described in *Octavius* (Puthz 2006c; “Gen1_SAF” for *O. angusticollis* Puthz, 2006, and four undescribed species; “Gen2_SAF” for *O. bacillus* Puthz, 1986, and one undescribed species) that may actually be closely related to *Protopristus* of Australia and New Zealand. Five more species described in the same paper (*O. caecigenus* Puthz, 2006; *O. longesulcatus* Puthz, 2006; *O. unocellus* Puthz, 2006; *O. brevisulcatus* Puthz, 2006; and *O. inoptatus* Puthz, 2006) plus one other (*O. atomus* Puthz, 1986) and at least three more undescribed ones belong in either *Tasmanosthetus* Puthz, 1978 or a new genus placed near *Tasmanosthetus* and *Nothoesthetus* Sáiz, 1970, in Austroesthetini; unlike *Tasmanosthetus*, these species have abdominal parasclerites (hence their inclusion here within Euaesthetini in Fig. 6.4). At least one Tasmanian species and possibly others from the Australian mainland are probably related to *Protopristus* but may require a new genus (“Gen3_TAS”) because they lack the key character of that genus, the derived ligula tooth (Puthz 1978; Newton 1985), as well as having differently structured pharyngeal characters (Clarke, in prep.). Two other new genera from Chile are more enigmatic because of their unusual combinations of seemingly primitive and derived characters. A new genus of Stenaesthetini in Australia has been previously reported in the literature (Puthz 1978) and has been since referred to by the tag name “EuaAUS” (Clarke and Grebennikov 2009), which hereafter is used to refer this genus. The phylogenetic placement of all these species within the context of a global phylogenetic analysis of Euaesthetinae is a fundamental goal of future phylogenetic work on Euaesthetinae, especially since the South African taxa imply new Gondwanan area connections that, as far as I am aware, have not been previously recognized for this subfamily. Ongoing morphological phylogenetic studies by the author are addressing the generic-level classification of Euaesthetinae with future taxonomic changes likely resulting in a reduction in the number of currently valid described genera in the subfamily, with an eventual total of ~30 genera for Euaesthetinae when all new genera are described and other taxonomic actions implemented.

6.2.2 Phylogeny and Suprageneric Classification

Euaesthetinae, Steninae, and Megalopsidiinae have been placed together in the "stenine group" (Hansen 1997; Leschen and Newton 2003) within the "staphylinine group" of subfamilies (Lawrence and Newton 1982). Monophyly of Euaesthetinae has been previously questioned on account of there being no clear ubiquitous synapomorphies for the group (e.g., Thayer 2005) and only weak support for it in the first phylogenetic analysis of the stenine group (Leschen and Newton 2003). In a later much-expanded analysis of adult and larval characters, Clarke and Grebennikov (2009) recovered the first strong support for monophyly of Euaesthetinae, including 19 hypothesized adult and larval synapomorphies. In an analysis of the staphylinine group of subfamilies, Grebennikov and Newton (2009) also consistently recovered Euaesthetinae as a monophyletic group in analyses based on adult morphology, larval morphology, and 18S rDNA data, as did McKenna et al. (2015) in a phylogenetic analysis of Staphyliniformia using 28S rDNA and *CAD* sequences. However, none of these studies included all genera, nor representatives from all tribes of Euaesthetinae, and likely did not include the most basal lineages within the "euaesthetine subgroup" (Clarke and Chatzimanolis 2009: Euaesthetinae + Steninae), such as the enigmatic northern temperate genera *Nordenskioldia* and *Ctenomastax* Kraatz, 1870, or the now much better known Oriental genus *Edaphosoma* (Puthz 2010a). As well as including such taxa, future and more rigorous tests of euaesthetine monophyly will also need to be based on analyses that include multiple diverse species sampled from each genus (especially *Octavius*, *Edaphus*, and *Stenaesthetus*) as well as molecular data sampled for a wider range of genera and genes (Clarke in prep.). Only few molecular phylogenetic studies have included Euaesthetinae, and most of these included too few genera to draw any suitable conclusions; a clear priority for future phylogenetics within this group will be to expand the taxon sampling of molecular phylogenies. Previous morphological phylogenies (Clarke and Grebennikov 2009; Grebennikov and Newton 2009), augmented by ongoing surveys of character diversity within Euaesthetinae and Steninae (Clarke unpublished), indicate that the most promising synapomorphies for the subfamily include:

In adults:

(1) The presence of differentiated setae at the apex of antennomere X
(2) The denticulate apical margin of the labrum (though this is not uniform within the subfamily)
(3) A line of macrosetae on the posterolateral margin of the metacoxa
(4) The mesal edge of the gonocoxite and apex of male sternite IX produced into a spine

In larvae:

(5) The markedly reduced or apparently absent maxillary mala
(6) The dorsad (rather than mesad) orientation of the mala
(7) The reduced cardo, which is much narrower than the base of the stipes [though a more significant feature of the euaesthetine larval cardo, including *Euaesthetus* (Newton 1990: fig. 38B.4) is the postero-oblique displacement of its apical edge from the basal edge of the stipes; see also illustrations in Clarke and Grebennikov 2009]
(8) The stipes markedly narrowed distad
(9) The longest leg seta located on the tibia

Only the adult labrum and larval cardo characters might be restricted to Euaesthetinae (some Paederinae and Leptotyphlinae adults have teeth along the labral edge, but these apparently do not form a serrated edge as they do in Euaesthetinae), but few possible synapomorphies are likely uniform within the subfamily, and several of them occur in other subfamilies.

The current suprageneric classification of Euaesthetinae consists of a system of six tribes (Scheerpeltz 1974) and has been recognized as in need of critical phylogenetic review (Newton 1985; Clarke and Grebennikov 2009). An overview of the salient historical milestones in the development of the higher classification of Euaesthetinae, as well as the problems with it, was given by Clarke and Grebennikov (2009). The six tribes represent artificial groupings based on just a few superficial but commonly used characters (Newton 1985) including tarsal formula, presence/absence of wings, and abdominal "margination" (presence/absence of parasclerites), which vary both within and among genera. Clarke and Grebennikov (2009) recovered only weak support for the monophyly of one of these tribes (Stenaesthetini) and discussed the problems associated with using tarsal formula and abdominal margination as characters for distinguishing suprageneric taxa: the tarsal formula 4-4-4, for example, likely represents independent and often only partial instances of basal tarsomere fusion, whereas abdominal "margination" obfuscates several different character states (e.g., one vs. two pairs of parasclerites per segment; parasclerites on some segments but not others), an issue that is further complicated by the uncertain morphological origin and therefore homology of the individual lateral sclerites (see Naomi 2014). The extent of the evolutionary lability of "margination" within Euaesthetinae is therefore not yet certain; in Steninae this issue is clearer, with margination varying not only within *Stenus* (e.g., within the Australian fauna; within even individual species elsewhere) but also within a new genus of only three species (Clarke et al., in prep.)! In addition, the current system of tribes did not include all the known genera when originally proposed and until recently was not widely adopted nor critically evaluated by others (Newton and Thayer 1992). Although it is maintained here for organizational reasons, the numerous exceptions to the character combinations used to define the tribes make the system not particularly useful for either identification or for drawing general biological or ecological conclusions. A major goal of the author's ongoing phylogenetic work is to establish a new, holistic suprageneric classification system for Euaesthetinae based on a robust phylogenetic hypothesis for the euaesthetine subgroup.

6.2.2.1 Austroesthetini

In Australia, this tribe includes species generally lacking abdominal parasclerites, though there is considerable variability in the precise lateral structure of the abdomen in different genera: parasclerites are completely absent in *Mesoaesthetus*, but the terga and sterna are separated by a fine suture; there is a single parasclerite on segment III only in *Austroesthetus* and *Chilioesthetus*, with segments IV–VI tubular; and parasclerites are absent entirely in *Tasmanosthetus*, with each tergum and sternum of segments III–VI fused into a solid ring. In New Zealand, this tribe is represented by the single genus *Kiwiaesthetus*, and in Chile/Argentina the genera *Chilioesthetus* and *Nothoesthetus* (see also Fig. 6.4)—all three genera have different states for abdominal margination. Until recently, the tribe was thought to comprise only wingless—or at least flightless—species (Scheerpeltz 1974), but at least the female of one undescribed *Austroesthetus* species (from Western Australia) has abbreviated wings beneath full-length elytra (the species is possibly sexually wing dimorphic or sexually flight dimorphic), and other species are now known to be micropterous or variously brachypterous instead of wingless (Clarke, unpublished). Recent phylogenetic work on Euaesthetinae included all the then-known genera of Austroesthetini and concluded that the tribe is most likely polyphyletic (Clarke and Grebennikov 2009).

6.2.2.2 Euaesthetini

This tribe consists of a morphologically heterogeneous assemblage of species ranging from fully winged robust species of *Ctenomastax* and *Edaphus* to the minute elongate-slender, eyeless, and wingless species of *Octavius* and *Protopristus*. The tribe is widely understood to be non-monophyletic (e.g., Clarke and Grebennikov 2009) and includes genera with quite different structural features, including degree of metacoxal separation, type of abdominal margination (number, form, and presence of parasclerites), and presence and form of various head, antennal, and mouthpart structures. Ongoing comparative morphological studies of particularly internal head and mouthpart characters (but also others) indicate the group is more than likely polyphyletic, with groups of genera dispersed throughout the phylogeny of the group.

6.2.2.3 Stenaesthetini

Of the six tribes recognized in the current higher classification of Euaesthetinae, Stenaesthetini is the only one that may be monophyletic. Clarke and Grebennikov (2009) recovered a weakly supported clade comprising EuaAUS, *Stenaesthetus* (including *Gerhardia* Kistner, 1960, now a synonym), and *Agnosthaetus* based on an analysis of adult morphological characters. This clade was suggested to be supported by a single uniquely optimized synapomorphy—a carinate groove on the basomesal surface of the mesocoxa that receives the intermesocoxal process. Subsequent extensive dissection efforts, however, indicate instead that this character may be too variable within genera, and similar conditions are seen elsewhere in the subfamily (casting doubt on its phylogenetic value). The main character tying these genera together is the 5-5-4 tarsal formula (unique within Euaesthetinae), and although a classic composite character ("tarsal formula") in beetle classification at all taxonomic levels, proper phylogenetic treatment of it would preclude interpreting the state "5-5-4" as a unique synapomorphy for Stenaesthetini (see discussion of characters 93–95 in Clarke and Grebennikov 2009: 393), at least when considering it as the numeric character "number of tarsomeres". Further comparative study of this character could, however, shed light on whether this reduction in metatarsomere number may be different from that seen in Euaesthetini and Austroesthetini, since the arrangement of "landmark" setae on the basal metatarsomere in Stenaesthetini is dissimilar from that in these other tribes (and differs within it). If Stenaesthetini does represent a monophyletic group, its presence in Australia—represented only by EuaAUS, a species-poor and range-restricted taxon—seems anomalous. It may be relictual, considering the widespread occurrence of *Stenaesthetus* in the tropics (but its apparent absence from Australia and New Guinea), as well as the occurrence of the relatively diverse genus *Agnosthaetus* (34 spp.) in neighboring New Zealand (Clarke 2011).

6.2.2.4 Alzadaesthetini, Stictocraniini, and Nordenskioldiini

Of the three remaining tribes, Alzadaesthetini is monotypic, comprising only the genus *Alzadaesthetus* Kistner, 1961, with two species, and both Stictocraniini (=Fenderiini) and Nordenskioldiini each have two genera. Neither *Alzadaesthetus* nor Stictocraniini were found to be monophyletic by Clarke and Grebennikov (2009), and the two genera in the latter tribe (*Edaphosoma* and *Nordenskioldia*) have not yet been studied phylogenetically.

6.3 Ecology and Biology

Information on the ecology and biology of Euaesthetinae is largely buried in the primary taxonomic literature. The following review gathers much of this and summarizes unpublished label data for thousands of specimen-level collection records held in a database, most of which at the time of writing are for southern hemisphere taxa. Although *Edaphus* is arguably the most diverse genus of Euaesthetinae, space prevents a complete synthesis of its ecology and biology here.

6.3.1 General Ecological Patterns

Euaesthetinae are broadly characterized as litter- or soil-dwelling rove beetles that occur worldwide from near polar environments to the tropics, where they are most diverse, and from sea level to high-elevation mountains. They are primarily found in forested regions in all major biomes but may also be found in other diverse vegetation types. Predominant ecological communities include tropical rainforest, boreal and temperate forests, montane and alpine habitats, shrublands, and wetlands. In Australia, where Euaesthetinae are generically most diverse, they are mainly found in cool temperate rainforest dominated by *Nothofagus* Blume, 1851 and *Eucalyptus* L'Heritier, 1879 species but can also be found in savannah, dry sclerophyll forest and scrubland, as well as alpine grasslands and meadows; in New Zealand they are found in all forest types as well as indigenous alpine grasslands (Clarke 2011); in South Africa they are most diverse in podocarp and Afromontane forests; and in Chile they are more or less restricted to cool temperate rainforests.

At the global/regional scale, the elevational distribution of many genera changes with decreasing latitude. In the Holarctic, the genus *Euaesthetus* extends south into both the Oriental Region and the Neotropical Region, but in these regions species are seemingly restricted to high-elevation mountains. Several southern hemisphere genera show this pattern also (e.g., *Austroesthetus*, *Kiwiaesthetus*, *Mesoaesthetus*), becoming increasingly restricted to alpine or high-elevation habitats from southern to northern limits of their ranges. This suggests that many of the genera are cold-tolerant and well-adapted to high altitude environments.

The general ground-dwelling Euaesthetinae can be divided into different "ecological groups" of genera that have microscale distributions extending beyond the general leaf litter and into either above- or belowground microhabitats (with little overlap). The first group comprises genera that are also found in aboveground situations on tree trunks, large boulders, and fallen logs, in association with bryophyte communities that grow on these substrates (e.g., *Austroesthetus*, *Mesoaesthetus*, *Tasmanosthetus*, EuaAUS, *Alzadaesthetus*, *Stenaesthetus* in part). A second group comprises genera that are also found, perhaps even more abundantly than in litter, in the soil beneath the surface litter (e.g., *Chilioesthetus*, *Euaesthetotyphlus*, *Octavius*, *Protopristus*, *Tasmanosthetus*, *Stenaesthetus* in part), and this group could be considered a truly endogeous fauna. Results of recent soil sampling by entomologists and collectors working in Australia and New Zealand suggest that soil may be the preferred microhabitat of the immature stages of at least some genera. This hypothesis may help explain the comparative rarity of euaesthetine larvae in collections and the still unknown larvae of several otherwise well-collected genera.

Another useful ecological group of genera can be recognized, though not comprising a set of genera mutually exclusive from the first two. Some genera can be identified as having a stronger association with riparian and general wetland-type habitats than others (*Euaesthetus*, *Nordenskioldia*, *Schatzmayrina*, possibly *Ctenomastax*). This periaquatic group contrasts with the remaining genera of the subfamily that are found in more diverse (but also generally moist) habitats, though some of the genera in this third group likely also occur in both above- and below-ground microhabitats. Yet another ecological group could recognize "surface runners," those genera that, based on ecomorphological criteria, are thought to be primarily found, or have been collected, in open situations such as on river banks (e.g., *Ctenomastax*, *Schatzmayrina*, some *Octavius*) versus those cryptic taxa that usually remain hidden within the litter or soil. A subset of these "surface runners" might also be recognized as a distinct group that may be arboreal, walking on exposed plant surfaces. This subset probably would include genera like *Tamotus* Schaufuss, 1872, some species of *Stenaesthetus* and *Octavius* (e.g., Puthz 1977: *O. dybasi* Puthz, 1977; Palau), and likely some species of *Edaphus*.

6.3.2 Tribe Nordenskioldiini

6.3.2.1 *Edaphosoma* (India, Nepal, China)

The genus *Edaphosoma* is evidently a specialist alpine genus found nearly exclusively in high mountainous areas (Puthz 2010a). The Nepalese species *E. janetscheki* Scheerpeltz, 1976 is recorded from 4800 to 5250 m (Scheerpeltz 1976) and *E. nepalensis* Puthz, 1979 from 5000 m. Chinese species are known from 650 to 4350 m, with nearly all collections occurring over 2000 m. Specimens have been collected from *Salix* L., *Rhododendron* L., oak and alder scrub and woodland, from bamboo and generally subalpine to alpine habitats dominated by grass heath and moss. Most collections have come from sifted debris, including grass, dead wood, mushrooms, and pine needles.

6.3.2.2 *Nordenskioldia* (Siberia, Russia; British Columbia, Canada)

This genus, known only from type material, seems to be a cold-tolerant, subarctic group and one of the most northerly distributed taxa in Euaesthetinae. The three known specimens of *N. glacialis* Sahlberg, 1880 were collected under or among stream-edge stones (an unusual collecting situation for Euaesthetinae); those of *N. columbiana* Puthz, 1974 from among stream-edge *Salix* litter at ~1600 m. *Nordenskioldia* may prefer wet riparian microhabitats. Fieldwork in Yoho National Park in 2008 by the author failed to recollect *N. columbiana* from the type locality as well as numerous other sites throughout Yoho National Park, Banff National Park, and Kootenay National Park. The habitat at the type locality is coniferous forest with sparse shrubby understory but with thicker broadleaf growth near streams. Leaf litter is rare, with dense and thick moss mats forming a uniform and predominant ground cover. Future collecting efforts should more deliberately target riparian areas and, especially, should include Berlese processing of partly submerged moss and other semiaquatic debris (A. Newton, pers. comm.) and should also focus on direct searching of stream-edge gravels.

6.3.3 *Tribe Stictocraniini* (=*Fenderiini*[1])

6.3.3.1 *Fenderia* (USA) and *Stictocranius* (USA, China)

Fenderia is a locally endemic genus restricted to the Pacific North West states (California, Oregon, Washington), occurring mainly in coastal areas (Puthz 2003). Most collections have been from old-growth coniferous or mixed conifer-hardwood forest from low to mid elevations, 40–1234 m, where species are commonly collected by Berlese-processing leaf litter samples; most published collection records are from Douglas fir and redwood duff. Larvae are known, also from leaf litter samples; at Mary's Peak (Oregon), a long series of both adults and larvae have been collected from around a huge decaying stump in old-growth *Abies procera* Rehder forest.

Stictocranius is commonly found in montane Appalachian forests of eastern North America (*Stictocranius puncticeps* LeConte, 1866) with a second species, *S. mariae* (Hatch, 1957), found in montane areas of the western USA (where the types were collected from grass sod) and British Columbia, Canada. Originally thought to be primarily found in the Appalachian Mountains (Puthz 1974), *S. puncticeps* is now known to be

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[1] This name has now been placed in synonymy with Stictocraniini, a previously overlooked but now resurrected valid name for this tribe (see Newton 2017).

widespread in forested areas of the eastern USA and Canada (Ontario), where most collections have been from Berlese-processed leaf litter samples. This species seems to be commonly collected from deep litter deposits and occurs in both hardwood and coniferous forests. In China, the three species have been found from 1600 to 2000 m, with one collection from a mixed deciduous forest with bamboo and small meadows. Larvae are unknown.

6.3.4 Tribe Alzadaesthetini

6.3.4.1 *Alzadaesthetus* (Chile/Argentina)

Comparatively little material with collecting data is available for *Alzadaesthetus*. Specimens have been collected at low to mid elevations (10–1300 m) in mixed *Nothofagus*-conifer forest and *Saxegothaea* Lindley, 1851-dominated Valdivian rainforest with dense *Chusquea* Kunth, 1822 (bamboo) understory, with most taken in leaf litter samples or by pyrethrum knockdown. A few series of several specimens have also been collected from processed aboveground moss samples, suggesting this genus may be common outside of the general leaf litter. Larvae have been collected in Berlese-processed leaf litter samples. No ecological differences between the two described species are evident, but the different morphologies of *A. chilensis* Kistner, 1961 and *A. furcillatus* Sáiz, 1972 suggest they may be distinct (see Sect. 6.3.8.2). For example, *Alzadaesthetus* is one of the few euaesthetine genera with species differing in abdominal margination, and the lack of shared derived characters suggests included species may not be congeneric (Clarke and Grebennikov 2009). Also, a unique feature of *A. furcillatus* (and a related undescribed species) is the densely papillate underside of the elytra; these species are (almost) wingless, and these structures have no obvious function, but the morphological differences between *A. furcillatus* and *A. chilensis* suggest that ecological differences exist.

6.3.5 Tribe Austroesthetini

6.3.5.1 *Austroesthetus* (Australia)

This genus is found primarily in cool temperate rainforest dominated by *Nothofagus* and *Eucalyptus* species but can also be found in both wet and dry sclerophyll forests, in coastal scrub and sand heath communities, in forest of all successional stages, and in both riparian and ridge-top communities. The genus occurs from sea level to >1600 m; most of the lowland records are from Victoria and Tasmania, whereas nearly all of the higher elevation collections (>1300 m) are from mountains in Queensland and New South Wales. Species are most commonly collected from general forest litter but are also frequently found in moss growing on a variety of substrates (living trees, old logs, rocks, and ground). Common collections from moss strongly indicate that at the microhabitat scale the most important environmental variable is high moisture content, since most of these collections were from aboveground mosses. One collection from wet moss at a seepage area near the crest of a mountain indicates that mossy microhabitats allow species to exist in drier, more exposed areas, including outside the general forest floor environment. Specimens have also been commonly collected from old logs (with or without fungi, via pyrethrum knockdown), from under bark of *Nothofagus* and *Eucalyptus* logs, and (rarely) from sifted woody materials. One collection from moss with ants is probably an incidental, rather than a myrmecophilous, association. Larvae have been taken from both litter and under bark, so there is some evidence that the life cycle can be completed in both aboveground microhabitats and the general ground litter.

6.3.5.2 *Chilioesthetus* (Australia, Chile)

Chilioesthetus is relatively rare in Australia, known from less than 50 specimens. Species are found primarily in cool temperate *Eucalyptus*-dominated rainforest and sclerophyll forest in Western Australia or subtropical montane rainforest in Queensland. In Western Australia, species have been found from near sea level in

Walpole National Park to 783 m in Stirling Range National Park. In contrast, nearly all Queensland collections have been from elevations above 1000 m (up to 1260 m). Collection records indicate a more restricted range of microhabitats for Australian *Chilioesthetus* than the related *Austroesthetus*. Most specimens have been collected via Berlese processing of general leaf and log litter, and unlike *Austroesthetus*, no specimens have been taken from moss nor via pyrethrum knockdown, whereas soil washing has produced several specimens (soil samples; 18 cm depth). This suggests a generic difference in microhabitat preference in Australia, with *Chilioesthetus* species possibly preferring soil microhabitats rather than surface leaf litter. The generally smaller size and reduced eyes of Australian *Chilioesthetus* species (compared to *Austroesthetus* and Chilean *Chilioesthetus*; completely blind in an undescribed Western Australian species) may support this inference.

Chilean *Chilioesthetus* are more common and have been collected from near sea level to 1250 m in mixed *Nothofagus*-conifer forest and Valdivian rainforest, often with *Chusquea*-dominant understory. Most specimens have been collected by Berlese-processing mixed *Nothofagus*-podocarp leaf litter samples. However, several collecting events from fungi (bracket fungi and soft fungi; fogging fungusy logs), from debris under logs, and from fine debris under bark of *Nothofagus* logs (Puthz 2008a) are unusual and suggest a broader range of microhabitats for this genus in Chile; larvae were also associated with these specimens collected from logs, as well as others from leaf litter. Adults of most species of *Chilioesthetus* are characterized by coarse, imbricate surface sculpturing with prominent lateral pronotal and elytral grooves, and many species (mostly Chilean, but also some Australian) are commonly observed to have a waxy encrustation on especially the dorsal surfaces (does not completely dissolve in KOH), and it is possible that this is secreted from foveae or pores near the grooves (see also *Octavius*) and may be related to their preference for moist habitats.

6.3.5.3 *Kiwiaesthetus* (New Zealand)

Kiwiaesthetus species are primarily found in all cool temperate forest types in New Zealand, including *Nothofagus* and podocarp-broadleaf forest, but also occur in subtropical kauri (*Agathis* Salisbury, 1807)-dominated forest in the far north of the country (Puthz 2008b). However, several species are also common in tussock grassland communities and in alpine areas above the tree line. Although species can be found from near sea level to ~1900 m, the genus seems to be most common at high elevations, with nearly all records from North Island [*K. whitehorni* (Puthz, 2008); one undescribed species] found in high montane forest and alpine scrub and tussock communities. The majority of collections have been nearly equally from moss and diverse types of forest and ground litter. Specimens have been hand collected from among the bases of tussock grasses and from under plant mats. Like other genera, the association of *Kiwiaesthetus* with moss indicates moisture is the most important microhabitat variable, which may also explain the ease of collecting specimens from the bases of alpine grasses. Only few specimens have been taken via pyrethrum knockdown (from old logs) and from soil. Larvae are unknown, and given how common this genus is in collections (and its apparent abundance), the immatures must have unusual seasonality or else occur in an as-yet unknown habitat, possibly deep in the soil.

6.3.5.4 *Mesoaesthetus* (Australia)

Mesoaesthetus species are found primarily in cool temperate rainforest dominated by *Eucalyptus* and *Nothofagus* species but can also be found in wet sclerophyll forest, scrub, and open woodlands. Species have been found from near sea level to ~1500 m; in Tasmania species are found primarily in lowland to montane habitats (~50–1100 m), whereas in the northern mainland part of their range (Victoria), they have been found almost exclusively above 1200 m. The majority of collections have been from diverse leaf litter types, including fern, woody, and fungusy debris. Species are also commonly found in moss growing on a variety of substrates (living trees, old logs, ground). Like

Austroesthetus and *Kiwiaesthetus*, the association of *Mesoaesthetus* with moss indicates moisture as the most important microhabitat variable. Only few specimens have been taken via pyrethrum knockdown (from old logs) and from soil. As one of the most abundant genera in collections, it is unusual that larvae have not yet been found, indicating an unusual microhabitat for the immatures (probably soil).

6.3.5.5 *Nothoesthetus* and Undescribed Genera (Chile)

The relatively few available *Nothoesthetus* specimens with ecological data have been taken largely from *Nothofagus* and mixed evergreen-conifer forest, Valdivian rainforest, and scattered forest remnants from 500 to 1080 m. This genus also occurs in forests with dense *Chusquea* understory, and all specimens, including larvae, have been taken from Berlese-processed leaf litter samples. The species of *Nothoesthetus* are generally distinguishable only by their genitalia, and these are remarkably diverse (e.g., Puthz 2012a: figs. 2 and 4). The undescribed genus “Gen1_CHI” is known from two undescribed species, one from a series collected in the Aysen Province from sifted moss growing on logs and the other from litter. “Gen2_CHI,” perhaps the most morphologically isolated euaesthetine taxon, has been collected in litter from *Cupressus* L.-*Eucalyptus* forest in Arauco Province.

6.3.5.6 *Tasmanosthetus* (Tasmania, Australia)

Tasmanosthetus species are found primarily in cool temperate *Nothofagus* rainforest, as well as *Eucalyptus* and wet sclerophyll forest, and scrubland. The genus occurs from near sea level to montane habitats (>950 m). Species have been commonly collected from forest litter of diverse types (fern, broadleaf, pine) but are also frequently found in moss growing on a variety of substrates (living trees, logs, ground, and rocks). Although common collections from moss (including one from wet *Sphagnum* Linnaeus, 1753 moss at a forest seep) indicate that *Tasmanosthetus* species prefer moist microhabitats, they evidently occur only at ground level. A few specimens have also been collected from soil suggesting that, like *Chilioesthetus* and *Protopristus*, this genus also occupies both the litter layer and the edaphic zone. The minute size and reduced eyes (blind in some) of all *Tasmanosthetus* species are consistent with a soil-dwelling lifestyle.

6.3.6 Tribe Euaesthetini

6.3.6.1 The Rare Genera (*Ctenomastax, Euaesthetotyphlus, Tamotus, Macroturellus*)

Several Euaesthetini genera are poorly known, collected only once or very rarely (and most not recently) such that little about their biology can be confirmed. An exception is *Euaesthetotyphlus*, known only from type material of the only known species, *E. almajensis* Coiffait and Decu, 1970. The series of 29 specimens (most of which are now presumed lost) were found at 200 m elevation at the base of a slope near a river in the limestone region of western Almajului Mountains, Romania, and collected by washing a sample of calcareous soil—described as being relatively cool (15°) at 5–15 cm depth and moist despite a prevailing drought (Coiffait and Decu 1970). Genera like *Protopristus* (Australia, New Zealand) and many *Octavius* species (e.g., from the Western Palearctic, South Africa, and Madagascar) are also collected in this way and are similarly adapted to subterranean life, being minute, flightless, and (many of them) nearly eyeless.

The holotype and only known specimen of *Macroturellus* (Cameroon) was probably collected at light (Orousset 1987), and there are no other hints about its biology, except that published figures suggest that it must be unusual given the highly modified structure of the labrum and front of the head (including the subgeniculate antennae) combined with the unusual combination of reduced eyes but presumably functional wings (Orousset 1987: figs. 1–3, 6, and 12).

The odd genus *Ctenomastax* is the only one largely restricted to the Mediterranean Region (North Africa, southern Europe) and is among the most distinctive genera of Euaesthetinae (e.g., Orousset 1990a: 131)—in several respects resembling *Stenus* (Steninae). Puthz (1988a) lists an elevation range of 1000–1500 m for *C. kiesenwetteri* Kraatz, 1870 (no other data are published), and compiled the ecological information then known: specimens have been found at the edges of a pond and collected from shoreline wrack (of fresh and salt waters, the latter unusual for Euaesthetinae) and under stones on clay soil. These records suggest that *Ctenomastax* species (like most Steninae) should be found most commonly in riparian habitats and immediately adjacent to bodies of water. As typical for riparian insects, specimens have also come to light and have been captured in flight, and it has been suggested that on clay-limestone plains they can be found in cracks in the ground (see Puthz 1988a). Orousset (1990a) describes the sand dune desert habitat (with palms) in the vicinity of where *C. mirei* Orousset, 1990 was collected, which demonstrates *Ctenomastax* can survive in arid regions, likely doing so by dispersing between localized bodies of water (species are winged); he also notes a corollary to this in that the holotype and paratype showed no detectable variation despite the great distance separating their respective localities.

The genus *Tamotus* is widespread throughout Central America, South America, and the Caribbean but relatively rarely collected. Most collections are singletons or small series from flight traps set in lowland tropical rainforest. Apart from *T. similis* Puthz, 2002, with the broadest elevational range of 200–1400 m, the other 10 species for which data are available seem to occur in lowland forest (100–400 m). A few records are from Berlese-processed forest litter, and Puthz (2007b) reports one record of *T. cariniceps* (*lapsus* for *T. carinifrons* Puthz, 1986) from an emergence trap with floats on aquatic macrophytes. With the frequency of flight trap records and paucity of litter records, these observations are notable since they suggest an arboreal habitat for *Tamotus* (see below, Sect. 6.3.8.4).

6.3.6.2 *Edaphus* (Summarized Mainly for the Australian Fauna)

The genus *Edaphus* is incredibly speciose, morphologically diverse, and likely more ecologically diverse than presently understood. A comprehensive overview of the ecological knowledge of this genus will be provided elsewhere, though information for the Australian fauna is provided here since this has recently been compiled in connection with an in progress revision of the fauna. Australian *Edaphus* species can be found in a diversity of vegetation types. Most collections have been from *Nothofagus* and *Eucalyptus* rainforest and others from subtropical forest, wet sclerophyll forest, and scrubland and woodland habitats. Species can be found from near sea level to ~1600 m. Most collections have been from various Berlese-processed forest litter and other substrates, but, unlike Austroesthetini and Stenaesthetini: EuaAUS, Australian *Edaphus* seem to avoid moss; no specimens have yet been collected from that microhabitat, except for the syntypes of *E. melculus* (Oke, 1933) that were collected “in moss with ants on stone” (Puthz 1978). In this case, the occurrence in moss was probably incidental to the association with ants: Oke (1933) reports finding on several occasions specimens of *E. melculus* var. *camponoti* (Oke, 1933) (=*E. termitophilus* Bernhauer, 1916: Puthz 1978) in nests of *Camponotus* Mayr, 1861 ants, including an instance of more than 50 specimens in one nest. Puthz (1978) reports a female of *E. termitophilus* collected with an *Aphaenogaster longiceps* (Smith, 1858) host and notes the very close resemblance shared by *E. melculus* and *E. termitophilus*—which also suggests the biology of these species is similar. Both are probably myrmecophilous, and, though not verified, the name of the latter species suggests that the type series was associated with termites. If an association of *Edaphus* with ants and/or termites could be confirmed, it would be a novel biological discovery for Euaesthetinae (not recorded for Euaesthetinae according to a recent review of myrmecophily in Staphylinidae by Parker 2016), though not unprecedented for the larger euaesthetine subgroup (Euaesthetinae + Steninae: some species of *Stenus*). *Edaphus* specimens have also been collected from old logs with fungi (via pyrethrum knockdown) and directly from fungi, rotting fruit, stream-edge flood debris, and under the bark of rotting logs. Most Australian species are fully winged, and many specimens have therefore also been taken in flight intercept traps. Larvae have been collected from Berlese-processed leaf, bark, and log litter samples.

Within *Edaphus*, there is a wide range of morphological variation in both overall body form and in the appearance and modification of specific structures, with many species groups being characterized by unique morphological characters. Among the more enigmatic of these characters and warranting special mention are the so-called "atrium pockets" of the Neotropical *ventralis* species group (Puthz 2006a: figs. 15–18). In several species of this group, these pockets comprise a cuticular shield that apparently encloses each of the spiracles of the first one to few abdominal segments in both sexes. It is as yet unclear what the function of these unique structures could be, but it is possible they function as some kind of regulatory structure, perhaps related to an unusual ecological association or microhabitat for these beetles. While many unique structures in *Edaphus* and other genera seem to be related to sexual selection, structures such as the atrial pockets have no obvious function and seem to indicate the evolution of unusual, but as-yet undiscovered biologies for many groups.

6.3.6.3 *Euaesthetus* (Holarctic)

This genus, the most northerly distributed of all Euaesthetinae, occurs into the far north of Europe, Russia, and Canada and as far south as Thailand in the Old World (Puthz 1994) and Panama in the New World (Puthz 2001a). At these southern range extremes, *Euaesthetus* beetles are restricted to high mountains (1500 m in the former, 1127–2900 m in the latter) and found in elfin cloud forest, grassland (large tussocks), montane mesophilous forest (with *Quercus* L., *Cupressus*), cloud forest, and mixed conifer-hardwood forest. Specimens have been sifted from tussock bases, extracted from Berlese-processed leaf and log litter, root mats, and flood debris. Most *Euaesthetus* species are found in North America, with many species distributed widely throughout. Puthz (2014a) provided collection data for the North American species, detailing the wide collecting circumstances (low and high elevation) in which these beetles have been found. In general they are mainly in wetland ecosystems (marshes, bogs, swamps) and riparian vegetation. They can be collected most abundantly from wet debris, moss, reeds, and litter in close proximity to streams and in dried river beds and ponds. Species have also been frequently found from litter sifted from the nests of various mammal species.

6.3.6.4 *Octavius* (Europe, Africa, Madagascar, Oriental and Neotropical Regions, Australia)

The genus *Octavius* comprises at least three or four morphological species groups (Clarke in prep.). The group for which there is by far the most available information includes flightless and frequently blind species from Europe, Madagascar, and South Africa (note, other species groups also have blind and/or flightless species). Orousset (2012) has written extensively about the ecology and biology of the French fauna and notes that although the environments of the Mediterranean and more northern mainland parts of France are quite different, the wingless *Octavius* there show great ecological tolerance, being broadly distributed in different habitats and elevations in both areas. In this region, this group of *Octavius* is mainly collected by soil washing and litter sifting. As similarly summarized for the Madagascan fauna by Orousset (1988), this group divides into those that live primarily in the soil (minute, all anophthalmous) and those in the surface leaf litter (larger, microphthalmous). They are found there primarily in dense mountain forests, from 900 to 2650 m, being most abundant from 1000 to 2000 m. In addition to different montane forest types, many species also occur at very high-elevation habitats, in various types of mountain scrub, and extending near to summits in turf-like communities where specimens have been sifted from dense mats of herbs and grasses growing on rocks. They have also been collected by Berlese-processing plant debris and soil samples taken from 0 to 10 cm depths. A few species there have been found in the litter accumulations of epiphytes. In South Africa the rich fauna of this group is found in similarly diverse habitats and collecting situations, similar as well to the austral euaesthetine fauna in general. They have been found from 10 to 1800 m (most records from above ~1100 m), mostly from podocarp and Afromontane forest, but they are also commonly collected from other forest types including coastal forest, various degraded forests, and mountain/alpine marshes and fynbos. Specimens have been collected from diverse litter types and also frequently from bryophytes. South African *Octavius* are generally very coarsely sculptured, and a waxy encrustation covering specimens is frequently observed (see also *Chilioesthetus*). This may be excreted from cuticular pores, which are sometimes visible in clean specimens under SEM examination. This possible excretion is yet to be studied and may relate to the prevalence of these beetles in moist habitats.

The Neotropical *Octavius* fauna comprises only ~27 species (e.g., Puthz 2001b), most of which form part of a distinctive group of minute, slender species, usually winged and with large eyes (also found throughout the Oriental and African tropics). This group is common at high elevations (>2000 m) but can be found throughout tropical lowlands, and specimens have been collected from all types of litter and in flight traps and associated with rotten wood. The species *O. panamensis* has been collected from the rubbish heaps of *Atta* ant nests and from thatch from a snapping ant nest, though it is unclear whether this is merely a facultative association. In Australia, this species group is so far known only from a single species from Christmas Island and from four localities on mainland Australia (*O. biroi* Puthz, 1977). Specimens have been found near sea level on Christmas Island, in rainforest near Mt. Tozer and on the Iron Range (Queensland), and in open *Eucalyptus* forest at 1490 m in Kosciusko National Park (New South Wales). Most collection records are from Berlese-processed forest litter, but specimens have also been found in flood debris, under bark, in fungi, and by malaise trapping.

By far the most enigmatic *Octavius* species belong to a group comprising species resembling *O. bicolor* and *O. flavescens* (Kistner, 1961). Several of these species are so unusual in their morphology that they were described in separate genera by different authors, some being placed in different staphylinid subfamilies (e.g., Piestinae: *Doletica bicolor* Cameron, 1938; Micropeplinae: *Nepalopeplus himalayicus* Coiffait, 1982). Sharp (1876), in describing his new genus *Turellus* (in Piestini), states of *T. batesi* Sharp, 1876 that it is "perhaps the most interesting of the Staphylinidae discovered by Mr. Bates, and ... the insect is one of the most anomalous of the Staphylinidae..." This group is comprised of mainly winged but also some flightless and blind species (e.g., *O. anophthalmus* Puthz, 1991) and is found throughout Africa and the Oriental Region (including in the high mountains of Africa and Nepal); only a single species (*O. batesi*) has so far been described from the Neotropical Region. Although found in largely similar collecting situations as other *Octavius* (including records from mammalian nests; e.g., Kistner 1961a), the peculiar morphology of species in this group, including the evolution of several novel structures and unusual character combinations, strongly suggests an as-yet unknown and possibly unique biology for these species.

6.3.6.5 *Protopristus* (Australia, New Zealand, Subantarctic Islands)

In Australia, *Protopristus* species are found in cool temperate rainforest dominated by *Nothofagus* and *Eucalyptus* species but can also be found in a variety of other habitat types (see *Austroesthetus*) from near sea level to 1650 m. Nearly all of the available Australian *Protopristus* material has been collected by Berlese processing of forest leaf litter samples, though recent soil sampling has also proven to be productive (in both Australia and New Zealand) and strongly indicates that this genus is common in both surface litter and subterranean microhabitats. However, the maximum depth below surface that this genus (and other soil-dwelling genera) might be found is not known. Some specimens (including larvae) have been taken from moss in Tasmania, but this is an otherwise rare microhabitat for Australian *Protopristus*. Larvae have also been collected from leaf litter; however, much more soil sampling has occurred in New Zealand than Australia, and this method has produced nearly all of the numerous larval specimens known from there (Clarke in prep.). New Zealand *Protopristus* have been collected from sea level to 1700 m, in litter from diverse forest types and also from alpine tussock grasslands and coastal megaherb communities on the Subantarctic Islands. In contrast to the Australian fauna, much New Zealand material has been collected from both moss and by soil washing, the latter likely reflecting greater soil sampling effort in New Zealand.

6.3.6.6 *Schatzmayrina* (Africa, Asia, South America)

Schatzmayrina is a small genus of only three species. One of these, *S. oxyclypea* Koch, 1934, is among the most widely distributed of euaesthetines; it occurs throughout Africa and Asia (Puthz 2007b) but it is unclear whether this distribution is entirely natural or partly human-assisted. The genus has been recorded from low to high elevations (150–1660 m in Southeast Asia; 800 m in Congo; 500–1240 m in South Africa) in diverse vegetation types. According to Kistner's (1961a: 30) translation of C. Koch's original description, Egyptian *S. oxyclypea* records were "in fields under stones," and the species "swarms over dirt on the shores of the Nile." Although stream-edge associations are known or suspected for other genera, it would be highly unusual to observe both large numbers of any Euaesthetinae at one time but also that they would be actively moving on open ground (such as can be observed for many *Stenus* species). *Schatzmayrina* does seem to prefer riparian habitats or otherwise high-moisture microhabitats away from rivers. Since species are fully winged, specimens have been collected at light and in flight intercept traps. Most records have been from forest (e.g., dense gallery forest) or from generally wet places including swamps and bogs. In Brazil, *S. braziliana* Puthz, 2007 has been found in white-water inundated forest where it was collected with an arboreal "photo eclector" during rising waters (Puthz 2007b). Other *Schatzmayrina* records are from Afromontane forest, from mixed exotic plantings, and from open, highly disturbed, and drier habitats such as dry forest, recently burned vegetation, forest edge or ecotones, savannah, and grasslands (Kistner 1961a, 1962). Specimens have been collected by sifting plant debris near watercourses, from diverse debris under *Cyperus auricomus* Clarke, and by Berlese-processed general litter. However, the genus has also been commonly collected under stones and from soil (including deep soil), and from samples taken from the base of hollow trees. In South Africa, the author has collected an unidentified *Schatzmayrina* species (likely *S. oxyclypea*) together with *Edaphus* sp. and *Octavius* sp. from fungi [probably *Lenzites elegans* (Spreng.)] growing prolifically on the stumps of recently felled trees, and this fits with the seemingly moisture-loving habits of this group. Of further potential interest are the several records suggesting *Schatzmayrina* may be a loosely associated nest inhabitant of small African mammals (Kistner 1961a). Specimens have been sifted from debris from several different rodent nests, but the association may be merely incidental since these nests were also in areas otherwise frequented by the beetles (from burrows in grasses; nests made of grasses on swampy soil).

6.3.7 Tribe Stenaesthetini

6.3.7.1 "EuaAUS" (Australia: Victoria)

This undescribed genus is found in cool temperate *Nothofagus* and *Eucalyptus* rainforest and wet sclerophyll forest from ~250 to 560 m elevation. The more common of the two known species has been collected primarily from Berlese-processed leaf litter but has also been found abundantly (via Berlese processing and pyrethrum fogging) in moss growing on the ground, on trees, and on old logs both in contact with the ground and not. It would seem that this taxon, like several other austral genera, is also able to exist outside the general forest floor by utilizing the high-moisture microhabitats provided by dense bryophyte growth. The other species is known from a single specimen collected much further north in the Grampian Ranges. This region is much drier than southern Victoria, and so a collection from there is unusual. Larvae remain unknown despite much collecting in relevant areas but will most likely be found in the soil, a microhabitat that has not yet been extensively targeted where this genus occurs.

6.3.7.2 *Agnosthaetus* (New Zealand)

A recent revision of this genus (Clarke 2011) included compilations of detailed ecological data gathered entirely from specimen labels. This information demonstrates a number of key ecological characteristics of the fauna: (1) several species seem to be "alpine specialists" (e.g., *A. lanceolatus* Clarke, 2011; *A. ecarinatus* Clarke, 2011; and other species found primarily in the Southern Alps). (2) Most species appear not to be restricted to specific forest types (e.g., *Nothofagus* versus podocarp-broadleaf forest, early succession versus mature old-growth forest, etc.). For many species, the distribution data suggest that they can be found in a wide range of general vegetation types ranging from forest through shrubland and tussock grassland (the three major vegetation types in New Zealand). (3) With the exception of primarily alpine species, other well-sampled species appear to be broadly distributed with respect to elevation; as a whole, *Agnosthaetus* beetles have been collected from sea level to >1600 m in the mountains. (4) Within major vegetation types, individual species are associated with a broad spectrum of different but related microhabitats, including general forest leaf litter, moss, wet debris, decaying vegetation, dead wood, and rarely soil and fungi. The general habitat requirement seems to be moist litter or vegetation, rather than a specific vegetation type—such habitats, e.g., moss, can be found both in "sheltered" forested environments through more open early successional forest, and in scrubland and even highly "exposed" grassland communities, such as high-elevation tussock grasslands. Similar to several other genera, some species have been collected via pyrethrum fogging of old logs and substrates with bryophytes, indicating that these beetles can also extend beyond the ground layer. Larvae have been collected from litter, moss, and soil (Clarke 2011).

6.3.7.3 *Stenaesthetus* (Africa, Madagascar, Oriental Region, Neotropical Region)

The genus *Stenaesthetus* is distributed in tropical areas of Africa, Asia, and South and Central America, with extensions into temperate areas of South Africa and mountainous areas of northern India, Nepal, and China. Although this broad distribution entails that *Stenaesthetus* species are found in diverse environments and habitat types, the group appears to be generally orophilic—preferring high-elevation montane and alpine habitats. The majority (~3/4) of species are flightless (brachypterous or apterous), showing morphological features typically correlated with the loss of flight and adaptation to endogeous life (e.g., eye reduction, depigmentation, increasing fusion of thoracic sclerites); nearly all of them are also restricted in distribution (most are likely narrow-range endemics). Flightless *Stenaesthetus* species occur in sheltered, mainly ground-layer microhabitats; as an ecomorphological group, they therefore seem to form a tropical ecological analog of the austral fauna. Although ecological data are otherwise scant for *Stenaesthetus*, several papers treating the faunas of the Oriental Region (Puthz 2013a), Madagascar (Orousset 1988), Africa (Puthz 2011), and the Neotropical Region (Orousset 1990b) were important in their compilation of basic ecological data for a broad cross section of *Stenaesthetus* diversity.

Approximately one third of described *Stenaesthetus* species are Oriental wingless species in the *quadrisulcatus* species group (Puthz 2013a). This group comprises distinctly orophilic species, almost all of them having been collected from mountain ranges, most from elevations exceeding 1400 m, and up to 4150 m in Nepal (*S. quadrisulcatus* Cameron, 1930). Most species from this group have been collected in general forest litter (leaf litter, grasses, ferns, and dead wood) from diverse forest types dominated by *Quercus*, *Rhododendron* L., *Abies* Miller, *Tsuga* Carrière, bamboo, or pine and from riparian and non-riparian habitats. Numerous collections from outside of the general forest litter suggest that these flightless species are also common in a broad range of other microhabitats, including in dead wood, under bark, on fungi, and under stones and logs. Although available data demonstrate that species from the *quadrisulcatus* group can occur in aboveground microhabitats (in dead logs not entirely contacting the ground, in aboveground bryophytes), none have been collected from the soil, and so the only indications that this group may also be soil-dwelling are from specimens taken under stones and logs.

Madagascan *Stenaesthetus* are also flightless and so far as known occur only in forested and alpine habitats on the eastern (wetter) side of the island (Orousset 1988). Species in the *rugosus* species group were reported as restricted to the northern part of the island and at low to mid elevations, from 80 to 1200 m; in contrast to the *quadrisulcatus* group, nearly all specimens were collected by soil washing and from sifted moss growing on soil. The *vadoni* species group, seemingly more orophilic and widespread, was recorded from 110 to 2000 m (most records from >1000 m), with species also collected by soil washing and from sifted moss (and general litter). Some species in this group therefore extend above the tree line and have been collected from moss growing on rocks. The species *S. haribe* Janák, 1996 and *S. miskovai* Janák, 1996 (*vadoni* group) were collected from thick moss growth and humus accumulations from around tree roots in a wet forest, 1150–1300 m. Janák (1996) also described *S. dunayi* (*rugosus* group) from a disparate locality in central Madagascar, collected at >1800 m from moss and litter on an old stump. This validates Orousset's (1988) caution that apparent ecological differences between species groups may only reflect collecting effort, and it seems likely that species in the *quadrisulcatus* species group may yet be found in soil samples.

In eastern Africa (Ethiopia, Kenya, Tanzania) a group of wingless species superficially similar to the abovementioned species groups has also been collected so far only at high-elevation sites. Three described species are known from mountains in Ethiopia, 2100–3230 m, where they were collected from soil under embedded stones near a stream and under embedded rocks and roots of ferns and grass mats (Puthz 1988b). Two similar species from Tanzania (Puthz 2012b) and one from Kenya (Puthz 1986) were found from 1050 to 1350 m by sifting forest litter. The species *S. leleupi* (Kistner, 1967), collected in forest litter from sites at 300 to 800 m elevation, also morphologically related to these species, is seemingly anomalous in its distribution; it is currently the only known species of this wingless "type" (e.g., a group of several wingless species, many originally described in the now-sunk genus *Aulacosthaetus* Bernhauer, 1939) from South Africa and is seemingly closely related (morphologically) to Madagascan and possibly Brazilian wingless species in the *mrazi* species group (see below). This is also the only *Stenaesthetus* species for which larvae have been collected (a single specimen, associated with a large series of adults, awaits description by the author).

The *mrazi* species group includes ten described wingless South American species collected in forests (e.g., Atlantic forest) south of the Brazilian Plateau, from 50 to 1100 m (Orousset 1990b). Although ecological/collection data are unavailable for most of these, the collection of *S. carinipennis* Puthz, 2011 from an abandoned cocoa plantation (Puthz 2011) suggests that at least some species may be able to withstand major disturbance (deforestation etc.) or at least retain a stronghold for some time following deforestation.

Nearly one quarter of described *Stenaesthetus* species are winged and fully flight capable, and most of these belong to either the "*Gerhardia*" species group (e.g., see Puthz 2011) in Africa and the Oriental Region or the *illatus* species group (Orousset 1988) in the Neotropical Region. The former group mostly consists of species sharing similar derived male genital segment and aedeagal characters (see below, Sect. 6.3.8.3), and several of these species also have broad distributions within the regions they occur in. For example, *S. sunioides* Sharp, 1874, the type species, extends from Pakistan east through Asia to Japan and Indonesia (Puthz 2013a) and from 200 to 2400 m; it has been suggested that the current range of this species (among the largest of Euaesthetinae) has been facilitated by human transport and disturbance since it is found frequently in rice fields and other disturbed habitats (Kistner 1962; Puthz 2013a), and it is clearly able to tolerate a wide range of environmental conditions. The three other Oriental species of this group have been found in mid- to high-elevation sites, from 200 to 1800 m. Most specimens have been collected from sifted litter from a variety of vegetation types (e.g., teak forest, bamboo, and grasslands) with some records of *S. conflictatus* Puthz, 1995 from elephant dung likely being incidental. African species of the *Gerhardia* species group have been collected from primarily high-elevation sites, from 150 to 2850 m (most with elevation data from above ~1300 m). Specimens have been collected from diverse vegetation types, mainly wet or humid habitats including rainforest, forest remnants, secondary and plantation forests, bamboo forest, gallery forest, general periaquatic and riparian habitats, and wetlands, but also in semi-arid habitats including sclerophyllous forest and savanna. These species have also been frequently collected from sifted litter of various types, as well as from soil and rotten wood, but have also been found in microhabitats more unusual for Euaesthetinae [under bark, from dead and live flowers, on mushrooms, and from the nests of a few different mammals, also at light (Kistner 1962; Puthz 2013a)].

The *illatus* group in the Neotropical Region is known from throughout the Amazonian basin and the Brazilian Plateau, reaching as far as the Andes in the northwest and occurring from 200 to 1630 m (though elevation data is scant for the known species). All species for which ecological data are available have been collected from rainforests, though *S. castaneus* Orousset, 1990 has been collected from a diverse range of wet and dry habitats including gallery forest (with bamboo), *Eucalyptus* plantation forest, bromeliad groves, Cactaceae scrub, and dry forest. Most *illatus*-group specimens have been collected by sifting leaf litter and dead wood, but some have also been found in rotten palm flowers, beaten from foliage (see below, Sect. 6.3.8.4), and taken at light (Orousset 1990b).

6.3.7.4 *Tyrannomastax* (Madagascar)

The genus *Tyrannomastax* is known only from the type series of the two described species (Orousset 1988), both of which were collected in sifted forest litter from southeastern Madagascar. The genus differs from *Stenaesthetus* only in the remarkably derived labial apparatus, in which several structures are modified or somewhat exaggerated compared to *Stenaesthetus*, and the two species are overall morphologically close to the *vadoni* species group. The labium appears to be modified to function as a prehensile prey-capture apparatus, and it has been suggested that if not homologous to the apparatus found in Steninae: *Stenus* (Leschen and Newton 2003; Betz and Kölsch 2004), then it is at least similar in its function. The anatomy and morphology of the labium are certainly different from that of *Stenus* (Clarke in prep.) and are fundamentally identical to that in *Stenaesthetus*. The modified labial palps are rigid, elongated, subconnate, and laterally extended, with the apical palpomere directed ventrad. This modification, combined with the ventrally curving, elongated, and subsclerotized (yet flexible) "paraglossae," seems to combine to form a claw-like apparatus (e.g., see Orousset 1988: fig. 415) that may serve to restrain captured prey (perhaps by pinning it to the ground) in order to draw it closer to the mouthparts. It is notable as well that the mentum is equipped with a pair of long ventrally projecting spines that may also assist in this function. Moreover, detailed examination of numerous *Stenaesthetus* species by the author has revealed a range of similar yet clearly nonhomologous modifications of the mouthparts, suggesting different morphological solutions to the functional problems associated with prey capture and/or feeding strategies within this group.

6.3.8 Biology and Morphology

In contrast to the wealth of biological information that has accumulated for Steninae (Chap. 11, this book), no studies of the biology or life history of any euaesthetine species have yet been made. The generalized falcate structure of the mandibles of Euaesthetinae suggests they are predators of other micro-arthropods, as in most other subfamilies placed in the "staphylinine group," whose included taxa are characterized by extraoral digestion (Lawrence and Newton 1982; Grebennikov and Newton 2009). Predation and preferred prey have not yet been directly observed for Euaesthetinae—though both predatory behavior and prey are well-studied for Steninae (e.g., Betz 1998b; Leschen and Newton 2003) and they have similarly structured mandibles and maxillae. The one exception may be a report by Remillet (1969), who kept a specimen of *Octavius massatensis* Coiffait, 1959 alive for a month feeding it diplurans. Notable intergeneric differences in the mandibles as well as other mouthpart structures further suggest either different predatory strategies or different prey in the different genera, perhaps partly resulting from ecological partitioning of, or adaptation to, alternative prey resources.

It is typical to find Euaesthetinae as singletons or small series in samples. However, the occasional finds of large numbers in litter samples might indicate a general (and possibly temporary) clustering within populations. Clusters of individuals on suitable microhabitats or substrates would be consistent with sexual selection and sexual conflict-type behaviors occurring in those species. This may be a general explanation for the morphologies discussed below. There is otherwise no other available information on the life history or biology of Euaesthetinae; only morphological variation allows for some inference. For genera in which larvae are known, they seem to occur in the same microhabitats as adults; however, this might not be true for common genera like *Kiwiaesthetus* and *Mesoaesthetus*, whose larvae remain unknown despite the abundance of adults in collections, and which thus likely occur in different habitats from the adults.

6.3.8.1 Morphological Traits Linked with Subterranean Life

In describing the high degree of adaptation of French *Octavius* to a subsurface soil-dwelling lifestyle, Orousset (2012) describes all stages of these beetles as developing in the soil, where they migrate throughout the rhizosphere depending on temperature and humidity. It is unclear whether his comments are based on observation or inference from field experience, but he describes excessive moisture as likely promoting vertical movement toward the surface and drought or freezing temperatures promoting movement in the other direction, where they likely would take refuge in deep crevices and pockets or partly decomposing roots and other plant structures.

Various morphological characters seem to be linked to the association with soil habitats and likely other aspects of their as-yet unknown biologies as well. Wing loss or reduction, generally associated with reduced pterothoracic volume, fusions of the elytra with each other and with the pterothorax (and to varying degrees), and other changes, is nearly ubiquitous in the austral-endemic genera and many other flightless groups, with many species also being blind (or with a reduced number of ommatidia) and showing varying degrees of depigmentation. These species also tend to have shorter, more robust legs. The association with leaf litter and soil habitats is therefore strongly reflected in several aspects of the morphology of numerous unrelated groups of Euaesthetinae and represents a major example of convergence involving a syndrome of interrelated and likely non-independent morphological changes.

6.3.8.2 Dimorphism Linked to Mating and Sexual Selection?

Sexual dimorphism involving nongenital or genital segment characters is a significant feature of many Euaesthetinae and suggests general behaviors and life history traits correlated with these characters. The most prominent category of dimorphic morphologies includes (usually male-specific) secondary sexual characters of the abdomen. Interspecifically variable modifications of the male abdominal sternites are known for many genera of Euaesthetinae. For example, males of most or all species of *Agnosthaetus*, *Alzadaesthetus*, *Edaphosoma*, *Kiwiaesthetus*, and *Mesoaesthetus* and some *Tamotus* and *Edaphus* species show varying degrees of (always) species-specific modification of one or more abdominal sternites (cuticular structures or modifications; often with modified setae). The degree of modification is typically highly interspecifically variable, but qualitative patterns of correlated variation (with other structures) among genera are perplexingly inconsistent and lead to interesting functional questions. For example, in *Agnosthaetus* and *Edaphosoma*, there are abdominal dimorphisms as well as strong interspecific differences in both the median lobe shape and internal sac structures (Puthz 2010a; Clarke 2011). But male sternites modified to a similar degree in *Mesoaesthetus* and *Kiwiaesthetus* species are not matched by such divergent median lobe shapes and internal sac structures (e.g., Puthz 2008b). The reverse pattern is seen in other groups. For example, the male abdomen of EuaAUS species is not modified, but the aedeagus is a highly modified lanceolate structure with reduced parameres and elaborate internal sac structures, while the female gonocoxites are characterized by strong secondary sclerotization. *Nothoesthetus* and *Protopristus* species show a similar pattern. Males of *Protopristus* species almost never exhibit secondary sexual abdominal modifications but likewise have complicated aedeagal morphology, including particularly complex internal sac structures, and the females likewise have heavily sclerotized internal vaginal structures (possibly related to, or in place of, the spermatheca). Puthz (2010a, 2013b) illustrates for males of several *Edaphosoma* species extraordinary forked processes arising from the apex of sternite VI, as well as substantial genitalic differences between species. Males of both described *Alzadaesthetus* species have secondary sexual characters on the abdomen, but these are completely different in each species: *A. furcillatus* and one new species both have an exaggerated explanate protuberance on the ventral posterior margin of segment VI (Sáiz 1972: fig. 8). Curiously, this structure is apically concave and lined with appressed, sub-tuberculate, and transversely ribbed spines. The function of this structure must presumably relate to mating, but the apical tuberculate surface also resembles a stridulatory file (though there is no obvious plectrum-like structure; this could be the hind legs). *Alzadaesthetus chilensis* males have instead a seemingly only minor modification, and to the apex of sternite IV (Kistner 1961b: fig. L), and the two species have dissimilar male genitalia. Secondary sexual abdominal modifications are not limited to the ventral side: Puthz (1990: figs. 3 and 11) illustrates remarkable modifications to the male tergites of *Edaphus nitidifrons* Puthz, 1990 and *E. sumatrensis* Schaufuss, 1887, which involve cuticular and setal developments.

Further notable examples of sexual dimorphism involve other structures or body regions, including the antennae, mouthparts, and legs. In *Edaphus*, males often have exaggerated (usually elongate) apical antennomeres compared to females (e.g., *E. ventralis* Puthz, 2006, *E. ventricula* Puthz, 2006; see Puthz 2006a), and males of other species show a modified eighth antennomere. The Australian taxon EuaAUS is notable for pronounced sexual labrum (and to a lesser degree, mandibular) dimorphism that may relate to intersexual dietary specialization. Similar modifications have been described for *Agnosthaetus* also, including perhaps the only examples of Euaesthetinae (*A. newtoni* Clarke, 2011 and *A. thayerae* Clarke, 2011) with more than one tooth along the inner mandibular edge and only in males (Clarke 2011). These derived labral morphologies are notable in providing examples of dimorphisms in which both sexes have a modified structure, rather than simply the male possessing some structure, or exaggerated structure, that is lacking or poorly developed in the female. Sexually dimorphic characters of the legs are common. Males of several *Octavius* and *Protopristus* species have modified metafemora (swollen and occasionally with a tooth on the inner face), and in many species, also in *Fenderia*, males have tenent setae on the ventral side of the tarsi (e.g., Orousset 2012: fig. 20; Clarke and Grebennikov 2009: fig. 13K), possibly used to grasp the female during mating.

Female-specific dimorphic characters not related to genitalia or the genital segment are extremely rare in Euaesthetinae and are perhaps the most interesting examples of sexual dimorphism. One locally endemic undescribed species of *Kiwiaesthetus* in northwest Nelson, New Zealand, is notable for an enlarged mesothoracic process in the females. This structure, with a concavity on each side resembling a socket, is unique to this species, and nothing like it is known anywhere else in Euaesthetinae suggesting it is involved in some novel biological function. Other examples of female dimorphisms include apparent sexual wing dimorphism and associated sexual eye dimorphism in some undescribed Australian *Edaphus* (and possibly some *Austroesthetus*) species that indicate sedentary females and dispersive males.

These and many other modifications in Euaesthetinae likely relate to mating and have different sensory and mechanical functions. The very different morphologies and locations involved in dimorphism suggest a diverse set of life history attributes and mating strategies within Euaesthetinae that are yet to be studied. Together these intergeneric morphological patterns indicate that biological differences likely exist between genera (or groups of genera) as well.

6.3.8.3 Complex Genital Structures

Complex genital structures (usually only of males) occur in most species of Euaesthetinae, suggesting that mating is characterized by sexual selection or sexual conflict-type behaviors (Eberhard 1985). Two categories of male sexual structures in Euaesthetinae are most important to emphasize. The first consists of male aedeagus structures that interact with the female during copulation (mainly elaborate internal sac structures) and are the most pronounced and widespread examples of genital complexity in Euaesthetinae. Nearly all genera show diverse internal sac structures, but both the presence and absence of derived internal sac structures likely indicate biological differences among taxa. The wide range of structural diversity seen in the internal sac suggests highly nuanced biological functions likely associated with sexual competition or sexual selection and suggests that these latter two mechanisms are prevalent in the mating biology of many Euaesthetinae. An unusual example of complex genital morphology is seen in several African *Stenaesthetus* species (Puthz 1995). These species have an extremely elongate flagellum that in repose is coiled within the median lobe. During mating, presumably this structure engages with the comparably elongate spermatheca in the female, as has been described for an aleocharine staphylinid with similar structures (Gack and Peschke 2005). Interestingly, the novel internal modifications of the ninth tergite and sternite in these *Stenaesthetus* species may be used analogously to how the elytra is used in the aleocharine—a behavior termed “shouldering” by those authors is used to ensure retraction of the flagellum without entanglement, and presumably a similar biomechanical problem occurs in these *Stenaesthetus* species.

The second category of male genital characters includes two internal structures that do not physically interact with the female during copulation and are found in males of many species of *Edaphus*, *Schatzmayrina*, *Stenaesthetus*, and *Tamotus*. Puthz (1973: figs. 24, 28–29) has described two internal structures, which he named the “double-trumpet” and “vesica seminalis.” These are best developed in *Tamotus*, where they can occupy a substantial space in the abdomen. The “double-trumpet" structure is seen in scattered species in the aforementioned genera and is thought to represent a sperm pump or be otherwise involved in sperm transfer. Weakly coiled longitudinal muscles surrounding this structure (and resembling an extended corkscrew) have been observed and support the notion that the two "trumpet" ends of the structure can contract toward each other. The "vesica seminalis" is found mainly in *Tamotus* but also in *Edaphus* (e.g., Puthz 2010b) and may function as a temporary sperm reservoir. Ultimately, the functions of these remarkable structures in Euaesthetinae remain unknown, and detailed studies are required; there may be, for example, as-yet unrecognized correlations between the differential presence, form, or size of these internal structures and that of other genitalic or apparently morphologically unlinked structures.

6.3.8.4 Arboreal Habitats for Some Euaesthetinae?

Several collections of South American *Stenaesthetus* have been directly from foliage. This ecological association is apparently unusual for Euaesthetinae but may be more widespread than currently appreciated, at least for the winged fauna. The tarsi of these and related *Stenaesthetus* species are clothed with explanate setae, including several elongate spatulate setae near the apices of the tarsomeres, which is consistent with the idea that these beetles walk on flat surfaces. Other cases of this ecomorphological pattern are known: the tarsal morphology of *Tamotus*, combined with collection records (see above), suggests this genus may be primarily an arboreal one—*Tamotus* is unique within Euaesthetinae in having strongly bilobed penultimate tarsomeres (Puthz 1973: figs. 18–20) with dense tenent setae, features again typical of beetles that crawl on smooth plant surfaces.

6.4 The Fossil Record and Evolution of Euaesthetinae

6.4.1 Cenozoic Fossil Record

The fossil record for Euaesthetinae is scant compared with other staphylinid subfamilies and is represented by only six described amber specimens in four nominal genera from three tribes and an additional unassigned compression fossil (reviewed in Clarke and Chatzimanolis 2009; Chap. 3 of this book). Considering the extraordinary diversity of extant *Edaphus*, it is notable that no fossil species of that genus has yet been discovered. One silicified fossil extracted from calcareous nodules from the Barstow Formation, California (~middle Miocene), and now preserved in the US National Museum (USNM-MO 561993), was recently identified as potentially belonging to this genus or to Pselaphinae (A. Newton pers. comm.; Fig. 6.5a, b). Although the author's preliminary study of this specimen in situ could not improve the confidence in the identification (originally described as *Carpelimus* sp.; Palmer 1957), the observable details of the dorsal side are consistent with *Edaphus* but are insufficiently preserved to allow conclusive determination. The form of the abdomen is reminiscent of *Edaphus* (Fig. 6.5a), and Palmer's description of the ventral characters is also largely consistent with this genus. But the "many closely spaced spines" on the posterior face of the mesocoxa would be unusual for *Edaphus*, and further study using sophisticated imaging may be necessary to confirm its placement.

The genera in Baltic amber (Eocene; ~44 Ma) include *Euaesthetus*, *Octavius* (Euaesthetini), and *Stenaesthetus* (Stenaesthetini), but the specimens were not sufficiently well preserved to allow formal naming (Puthz 2006d, 2008c). Only the first two generic records are from within the current distributional limits of these genera; *Stenaesthetus* is now largely restricted to the tropics. However, although all of the recorded species show clear affinities with extant species, they also either belong to species groups not now known from the Western Palearctic or comparable temperate regions elsewhere or are most similar to species far disjunct from the Palearctic. Being similar to *O. securifer* Puthz, 2006 (Puthz 2008c), the Baltic amber *Octavius* specimen seems to belong in a species group now largely restricted to (or at least with greatest diversity in) South Africa, rather than that in which the European species belong. Moreover, the same is true for another recently discovered undescribed *Octavius* species from Baltic amber (Fig. 6.5c). This specimen, while having a seemingly more primitive antennal

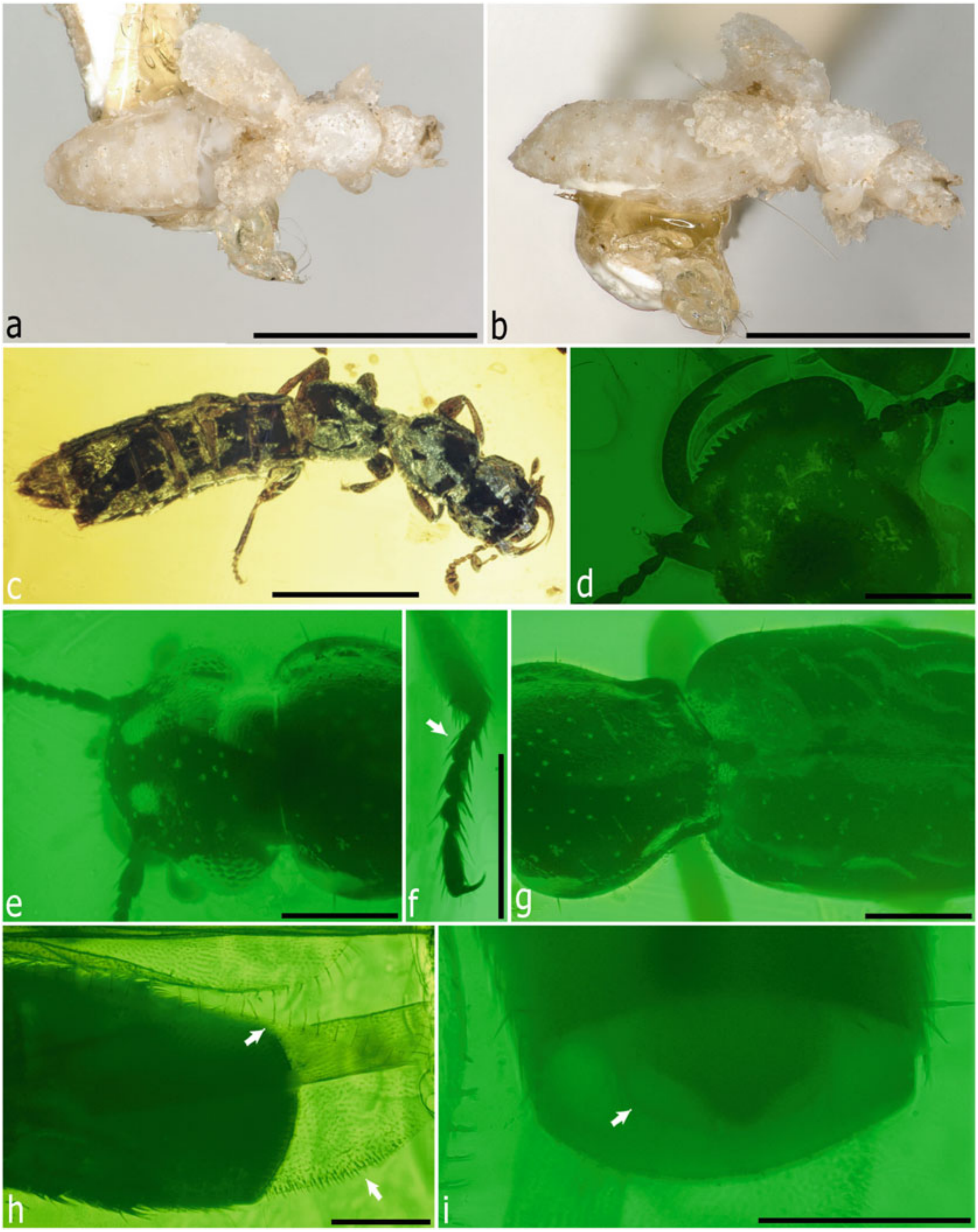

Fig. 6.5 Some fossil Euaesthetinae: (**a**) specimen #USNM-MO 561993 ("*Carpelimus* sp." = ?*Edaphus*; dorsal); (**b**) same (dorsolateral); (**c**) *Octavius* sp. (Baltic amber); (**d**) Euaesthetinae, gen. nov. (Cretaceous Burmese amber); (**e–i**) holotype of *Nordenskioldia pentatarsus* (Lefebvre et al., 2005); (**e**) head and front of prothorax (dorsal); (**f**) right metatarsus (dorsal oblique); (**g**) pronotum and elytra; (**h**) detail of wings; (**i**) telescoped abdominal apex. Scale bars in (**a–b**) = 1000 μm, (**c–i**) = 15 μm. See text for discussion of structures identified by arrows

club that is rare within the genus, belongs to a largely pantropical species group along with species like *O. neotropicus* Puthz, 1977 and *O. biroi*. This new fossil does not "fit" with most of the rest of the blind or nearly blind Palearctic *Octavius* fauna (belonging in a different species group). It has relatively large eyes typical of the tropical species group in which it likely belongs and may provide further indication of the paleoclimate of the Baltic region during the Eocene (Grimaldi and Engel 2005).

6.4.2 Cretaceous Fossil Record

Mesozoic fossils substantiate the view that crown-group Euaesthetinae—those having the putative synapomorphies listed above, notably the serrate labral edge—appeared as early as the Early Cretaceous, 125–135 Ma (e.g., Fig. 6.5d) and that these fossils reflect a pattern of scattered extant higher taxa in Staphylinoidea occurring already by the early Mesozoic (Lefebvre et al. 2005). The first and oldest recorded species, described from Lebanese amber in the extinct genus *Libanoeuaesthetus* Lefebvre et al., 2005 was subsequently transferred to the extant genus *Nordenskioldia* (Puthz 2008c). A detailed comparative morphological study of this fossil is currently under way, and although Puthz (2008c) correctly pointed out the superficial (albeit fairly extensive) original description of this species, it can now be confirmed that it does not belong in *Nordenskioldia*. It lacks the diagnostic characters of that genus: deep dorsal tentorial pits on the vertex, median pronotal impressions, and basal arcuate abdominal ridges (Fig. 6.5e, g; Clarke, in prep.). New fluorescent confocal imaging of this fossil has also revealed other characters potentially informative for its eventual phylogenetic placement. For example, among other details not previously studied or in need or re-evaluation, the tarsal formula may be 4-4-4, not 5-5-5 as in *Nordenskioldia* (e.g., see Lefebvre et al. 2005: fig. 3C, who illustrated a distinct tarsomere articulation at the position of the arrow in Fig. 6.5f but also illustrated only a line bisecting the basal pro- and mesotarsomere—i.e., no clear articulation). The pronotum also has basolateral impressions and a basal line of foveae and the pterothorax an elongate scutellum (Fig. 6.5g). Fossils with visible wings can be particularly valuable since characters from this structure may be visible. Although the original description of *Nordenskioldia pentatarsus* (Lefebvre et al., 2005) illustrated elongate setulae along the trailing wing edge, Fig. 6.5h also documents the presence of short setulae along the leading edge (Fig. 6.5h, top and bottom arrows, respectively), and the configuration of these and other wing structures varies among winged euaesthetine genera. The apical abdominal structure identifies the holotype as female based on the visible angulate eighth sternite, which has the form characteristic of females of at least Austroesthetini, Stenaesthetini, and Alzadaesthetini, and a few genera from other tribes, and protrudes slightly apicad from tergite VIII (marked by the arrow in Fig. 6.5i). It is notable that the type of antennal club of *N. pentatarsus* is most similar to that of *Austroesthetus*; indeed this specimen bears a strong overall resemblance to the only winged (currently undescribed) species of *Austroesthetus* from Western Australia, though unlike that genus it has a completely margined abdomen.

The description of *Octavius electrospinosus* Clarke and Chatzimanolis, 2009, introduced the second oldest euaesthetine from Burmese amber (~100 Ma), and based on observable characters that fossil seemed to be best placed in the extant genus *Octavius*. This conclusion has subsequently been "corroborated" by a recent phylogenetic analysis of Euaesthetinae and Steninae that placed this species as the sister group of a Neotropical *Octavius* species (Zyla et al. 2017). With this and the Baltic amber fossils discussed above, the *Octavius* lineage now has a confirmed paleontological record spanning ~50 Ma. Another undescribed euaesthetine fossil from Burmese amber either is an additional fossil species of this genus or is morphologically close (Clarke et al. unpub.).

6.4.3 Extinction Resilience and the "Environmental Buffer Effect"

It is becoming increasingly clear that Cretaceous "euaesthetine subgroup" diversity comprised a mix of both extinct and extant lineages. Recently discovered Burmese amber fossils are proving to be diverse, with at least three new genera of Euaesthetinae (e.g., Fig. 6.5d) and one of Steninae now known (Zyla et al. 2017; Clarke et al. in prep.). The hypothesized existence of crown-group Euaesthetinae and still-extant euaesthetine genera in the Lower Cretaceous is significant for at least two reasons. First, it demonstrates the great antiquity of these derived lineages, highlighting the long-term persistence of morphological taxa. Second, it places their minimum age, and by extension all other basally subtending nodes, into deep geological time. The existence of "cloistered habitats" (Stanley 1984), such as the consistently mesic habitats where euaesthetines occur (Sect. 6.3, above), led Clarke and Chatzimanolis (2009) to propose the hypothesis that the continuous presence of mesic habitats over geological time may explain the apparent morphological stasis in these lineages, but likely also other lineages as well (e.g., Cai et al. 2014: Olisthaerinae, Jurassic; Clarke et al. in prep.: ?*Stenus*, Burmese amber). Generally, this hypothesis can be labeled the "environmental buffer effect."

Assuming that observable ecological associations were similar in the Cretaceous ("uniformitarianism"; e.g., Gould 1965), it is straightforward to understand how Euaesthetinae and other groups may have been buffered from extinction through geological time. Using the New Zealand fauna as an example, within genera the distributions of individual species collectively span diverse geological settings, climatic regimes, and vegetation types (Clarke 2011). If these lineages are "paleoaustral" (sensu Fleming 1963), having drifted with New Zealand since the breakup of Gondwana, it is likely that they were little affected by the extreme and cyclical climatic/environmental changes of the Tertiary period and particularly those of the Pliocene and Pleistocene periods that resulted in widespread extinction of many plant and animal groups and drastic changes in composition of the regional biota in New Zealand (see Mildenhall 1980; McGlone 1985; McGlone et al. 2001; Worthy et al. 2007). This resilience to extinction may be a virtue of Euaesthetinae and other litter-dwelling staphylinids when considering target groups for biogeographic analysis.

6.5 Conclusions

Taxonomic work on the saw-lipped rove beetles has revealed a great diversity at the species level, but distinct lineages also still remain to be further described and explored. More collecting in association with monographic work on the austral fauna in particular is needed to better understand this fauna and its connection to northern temperate and tropical faunas, as well as the biogeographic structure of individual groups. Most genera in the austral region are relatively species-poor, but the genus *Protopristus* has radiated into a diverse group, likely comparable in richness to some of the tropical and northern genera, which include most of the diversity of Euaesthetinae. An increasing database of specimen-level collection data is beginning to reveal much new insight into the biological and ecological diversity of Euaesthetinae. This information suggests that there are distinct differences among genera and groups of taxa in microhabitat preferences but that the larger habitat within which many species and genera occur is free to vary considerably. Moreover, ecological data associated with specimen records indicates that general collection methods used to find Euaesthetinae may not be able to provide sufficiently resolved information on the biologies and ecological requirements of most taxa, suggesting new efforts to directly locate in the field and rear specimens in captivity could provide critical and novel data on the natural history of Euaesthetinae. The increasingly better known fossil record and future dedicated ecomorphological and biological studies will eventually expand the kinds of evolutionary inferences that can be made about the group, offering insight into general phylogenetic and biogeographic problems. The Cretaceous fauna from Myanmar was diverse, comprising both extant and extinct genera, while the Tertiary record preserves fossils so far assignable only to extant taxa.

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