GOOD-BYE SCYDMAENIDAE: OR WHY THE ANT-LIKE STONE BEETLES SHOULD BECOME STAPHYLINIDAE *SENSU LATISSIMO* (COLEOPTERA)

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Introduction

The beetle family Staphylinidae, or rove beetles, is one of the largest families of beetles and, indeed, of animals, passing the 50,000 described species mark in 2007. The monophyly of the family, and its internal phylogeny and classification, have been the subject of intensifying research in the past three decades. Lawrence & Newton (1982) summarized the classification at that time and proposed that the 22-odd staphylinid subfamilies recognized then could be organized into four main lineages or informal groups, with several small allied families being probably or possibly related to one or another of these lineages (making Staphylinidae paraphyletic with respect to these other families). The largest such lineage, termed by them the "Staphylinine Group", included the staphylinid subfamilies Oxyporinae, Megalopsidiinae, Steninae, Euaesthetinae, Leptotyphlinae, Paederinae, Staphylininae "and possibly Scydmaenidae and Silphidae". Subsequent phylogenetic studies by many authors (e.g., Hansen 1997; Beutel & Molenda 1997; Leschen & Newton 2003; Beutel & Leschen 2005; Caterino *et al.* 2005; Hunt *et al.* 2007), using adult, larval and/or molecular data, have tested and in some cases supported or refuted these suggestions (e.g., Silphidae have rarely been supported as a subgroup of Staphylinidae), but the relationship of Scydmaenidae to Staphylinidae has not been clearly resolved and previous results are widely divergent on this question.

The purpose of the current study (Grebennikov & Newton, submitted) is to provide a new phylogenetic analysis based on a more robust sample of all subfamily- and family-level taxa recently suggested as members of the Staphylinine Group, based mainly on adult and larval morphology but supplemented with inclusion of 18S rDNA molecular data available for a subset of taxa, with the intention of evaluating the monophyly of the Staphylinine Group and the relationships among the included groups, with special focus on the "scydmaenid question". The family Scydmaenidae, or ant-like stone beetles, is itself a large cosmopolitan group with more than 4,850 described species in about 90 genera, and has been consistently maintained as a separate family since 1815 (Newton & Thayer 1995, Newton & Franz 1998).

Palaeostigus bifoveolatus (Boheman), a "typical"-looking scydmaenid adult (above) and its larva (below)

Veraphis sp., a more staphylinid-looking scydmaenid with strongly truncate elytra

Analysis

Our analysis included 206 parsimoniously informative larval and adult morphological characters scored for 38 taxa, representing all groups currently placed in or associated with the Staphylinine Group of subfamilies as well as a broad set of outgroup taxa from other staphylinid subfamilies and from related families of Staphylinoidea:

Family/subfamily	Genus	Adult	Larva	Family/subfamily	Genus	Adult	Larva
LEIODIDAE	*Neopelatops* Jeannel, 1936	x	x	**STENINAE**	*Stenus* Latreille, 1797	x	x
AGYRTIDAE	*Necrophilus* Latreille, 1829	x	x	**STENINAE**	*Dianous* Leach, 1819	x	x
SILPHIDAE	*Thanatophilus* Leach, 1815	x	x	**EUAESTHETINAE**	*Euaesthetus* Gravenhorst, 1806	x	x
SILPHIDAE	*Necrodes* Leach, 1815	x	x	**EUAESTHETINAE**	*Edaphus* Motschulsky, 1857	x	x
SILPHIDAE	*Nicrophorus* Fabricius, 1775	x	x	**EUAESTHETINAE**	*Octavius* Fauvel, 1873	x	x
APATETICINAE	*Nodynus* Waterhous, 1876	x	x	**EUAESTHETINAE**	*Alzadaesthetus* Kistner, 1961	x	x
TRIGONURINAE	*Trigonurus* Mulsant, 1847	x	x	**LEPTOTYPHLINAE**	MexLeptotyphlinae	x	x
OMALIINAE	*Acrolocha* Thomson, 1858	x	x	**LEPTOTYPHLINAE**	ChiLeptotyphlinae	x	x
TACHYPORINAE	*Tachinus* Gravenhorst, 1802	x	x	**LEPTOTYPHLINAE**	AusLeptotyphlinae	x	x
PIESTINAE	*Siagonium* Kirby & Spence, 1815	x	x	**PSEUDOPSINAE**	*Zalobius* LeConte, 1874	x	x
OXYPORINAE	*Oxyporus* Fabriciaus, 1775	x	x	**PSEUDOPSINAE**	*Pseudopsis* Newman, 1839	x	x
MEGALOPSIDIINAE	*Megalopinus* Eichelbaum, 1915	x	x	**PSEUDOPSINAE**	*Nanobius* Herman, 1977	x	x
SOLIERIINAE	*Solierius* Bernhauer, 1921	x	-	**PAEDERINAE**	*Pinophilus* Gravenhorst, 1802	x	x
SCYDMAENINAE	*Scydmaenus* Latreille, 1802	x	x	**PAEDERINAE**	*Achenomorphus* Motsch., 1858	x	x
SCYDMAENINAE	*Veraphis* Casey, 1987	x	x	**PAEDERINAE**	*Hyperomma* Fauvel, 1878	x	x
SCYDMAENINAE	*Cephennodes* Reitter, 1884	x	x	**STAPHYLININAE**	*Arrowinus* Bernhauer, 1935	x	x
SCYDMAENINAE	*Palaeostigus* Newton, 1982	x	x	**STAPHYLININAE**	*Xanthopygus* Kraatz, 1857	x	x
SCYDMAENINAE	*Stenichnus* Thomson, 1859	x	x	**STAPHYLININAE**	*Nudobius* Thomson, 1860	x	x
SCYDMAENINAE	*Euconnus* Thomson, 1859	x	x	**STAPHYLININAE**	*Platydracus* Thomson, 1858	x	x

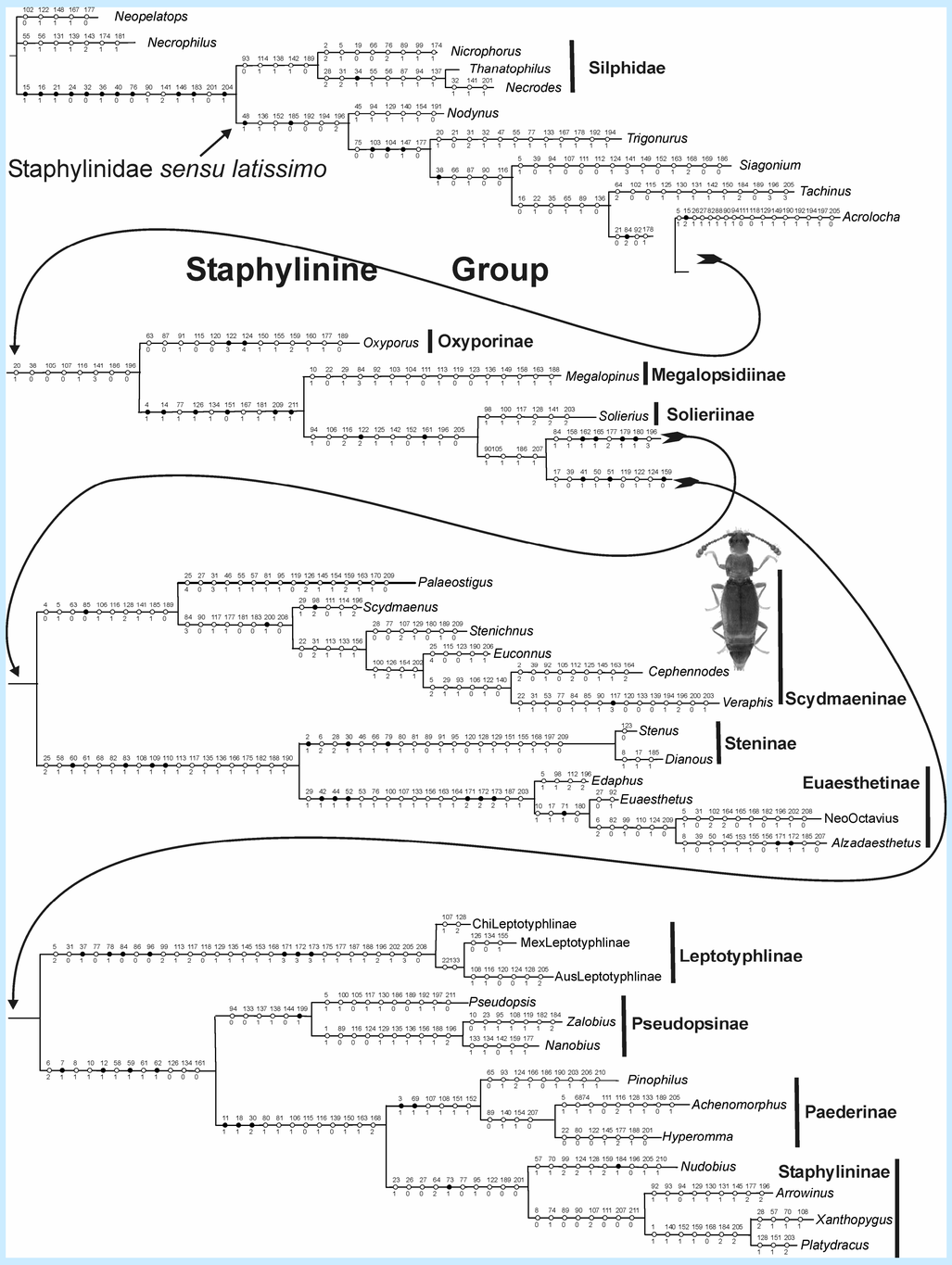
List of 38 terminals included in the phylogenetic analysis of the Staphylinine Group of subfamilies of Staphylinidae. The larva of *Solierius* is unknown. Subfamilies in **red** represent putative members of the Staphylinine Group; other subfamilies (Staphylinidae) and families represent outgroups.

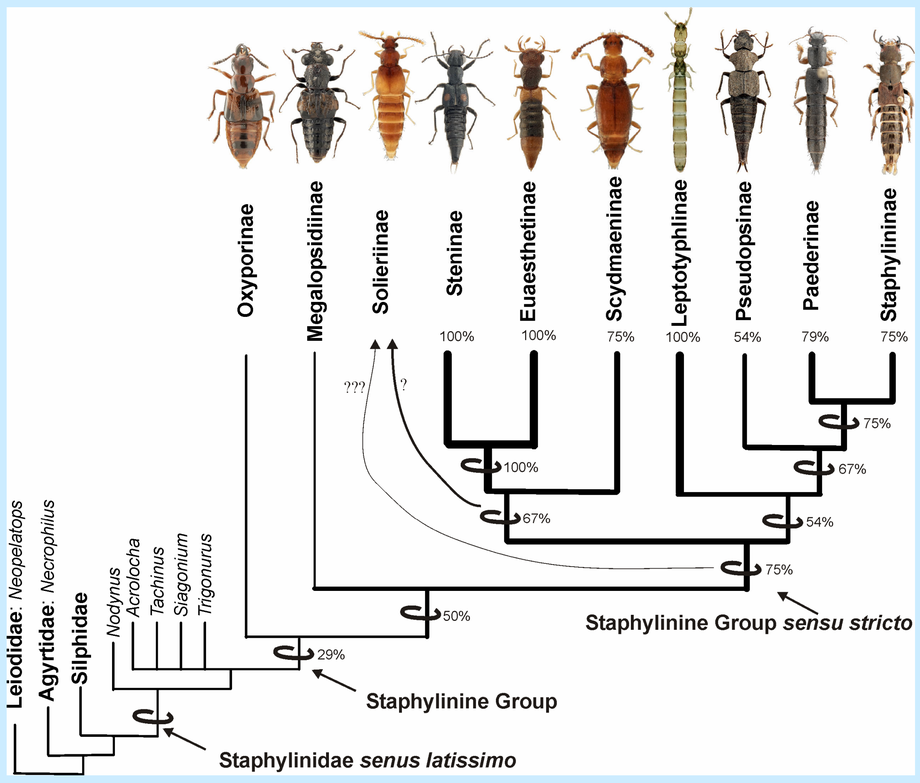
Twelve analyses utilised three datasets (larval, adult, and combined), each treated under four sets of assumptions (successively weighted/unweighted and multistate characters ordered/unordered). Strict consensus topologies from the shortest trees in all 12 analyses consistently placed Scydmaenidae as monophyletic and as sister to (Steninae + Euaesthetinae) in a monophyletic Staphylinine Group (with or without Oxyporinae).

At right as representative of these trees is the single most parsimonious tree from combined analyses of larval and adult morphological data with all characters unordered and not weighted (analysis 9) and with unambiguously optimized evolutionary events plotted along internodes. Character numbers are above circles; newly acquired character states are below circles. Black circles indicate unique evolutionary events; white circles indicate parallelisms or reversals.

Eight preliminary analyses of variably aligned 18S rDNA data for 93 members of Staphylinoidea under parsimony, neighbour-joining and Bayesian approaches were mainly inconsistent and inconclusive, although partly congruent with the Scydmaenidae + (Steninae + Euaesthetinae) hypothesis.

The single fully resolved and most consistently supported topology in our morphological trees is represented in the diagram at upper right. *Solierius* lacks larval data and is ambiguously placed within the Group.





Single fully resolved and most consistently supported topology of the Staphylinine Group of rove-beetle subfamilies. Width of internodes with plotted values of Relative Support Value is proportional to the degree of confidence to a hypothesis of monophyly of each clade. The phylogenetic position of *Solierius* is uncertain.

Conclusions

Our results strongly suggest that Scydmaenidae is a monophyletic group that is phylogenetically nested well within one subgroup (Staphylinine Group) of Staphylinidae, as a sister group to (Steninae + Euaesthetinae). This suggests that the relatively long elytra of most scydmaenids (e.g., *Palaeostigus* and *Veraphis* at left) are secondarily derived from the much shorter elytra of all other members of the subgroup (above) and most other Staphylinidae.

The family Staphylinidae thus becomes paraphyletic with respect to Scydmaenidae, a situation that is most easily rectified taxonomically (following the example of the former Pselaphidae) by demoting Scydmaenidae to a subfamily-ranked taxon, Scydmaeninae, within Staphylinidae, and demoting the three former subfamilies of Scydmaenidae to supertribes (a rank used in Staphylinidae but not previously in Scydmaenidae).

The classification above the generic level of the former "Scydmaenidae" can then be represented as follows, modified from the recent world classification of Newton & Franz (1998) and incorporating other recent changes and additions (most implemented in Newton & Thayer 2005):

STAPHYLINIDAE Latreille, 1802, ***sensu novo et latissimo***
- 31 Recent and 1 extinct subfamilies (Newton & Thayer 2005), **plus:**
- SCYDMAENINAE Leach, 1815, ***status novus***
  - SCYDMAENITAE Leach, 1815, ***status novus***
    - EUTHEIINI Casey, 1897
    - CEPHENNIINI Reitter, 1882
    - CYRTOSCYDMINI Schaufuss, 1889
    - PLAUMANNIOLINI Costa Lima, 1962
    - CHEVROLATIINI Reitter, 1882
    - LEPTOSCYDMINI Casey, 1897
    - SCYDMAENINI Leach, 1815
  - MASTIGITAE Fleming, 1821, ***status novus***
    - CLIDICINI Casey, 1897
    - LEPTOMASTACINI Casey, 1897
    - MASTIGINI Fleming, 1821
  - HAPSOMELITAE Poinar & Brown, 2004, ***status novus***

The family Staphylinidae, thus redefined, includes at least 55,440 species recognized as valid through 2007, making it the largest family of Coleoptera and one of the largest families of living organisms.

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Acknowledgements

We heartily thank the following colleagues for providing assistance of various kinds with our study: Rolf Beutel, Dave Clarke, Ignacio Ribera, Petr Janšta, Ainsley Seago, Aleš Smetana, Petr Švácha and Margaret Thayer, and Karen McLachlan Hamilton for reviewing the submitted manuscript. All photographs were prepared by José-Cristián Martínez as part of the Staphyliniformia TWiG of the US NSF-funded project "Assembling the Beetle Tree of Life" (grants EF-0531768, EF-0531754, EF-0531665) and used with permission of TWiG leader Margaret Thayer.