Morphology

The scarab-like beetles: Scarabaeoidea

The stag beetles, the Lucanidae, are a family within the superfamily Scarabaeoidea. Members of this superfamily generally have lamellate antennae. The terminal segments of this highly developed organ form a club, composed of plates known as lamellae. The typical scarab lamellae can be compressed into a ball or spread out in a fan-like manner. In the Lucanidae the antennal club is quite variable and is in some species flabellate rather than lamellate.

The main morphological characters of the Australian Lucanidae

Body elongate, some robust, 5–72 mm

Head prognathous, males often with prominent mandibles, some branched

Antennae with long scape, often geniculate, three to seven loose segmented club that cannot be completely closed

Eyes entire or with a partial or complete canthus

Labrum and clypeus usually fused to frons

Scutellum visible

Abdomen with five visible ventrites

Legs relatively long and slender, protibia well developed

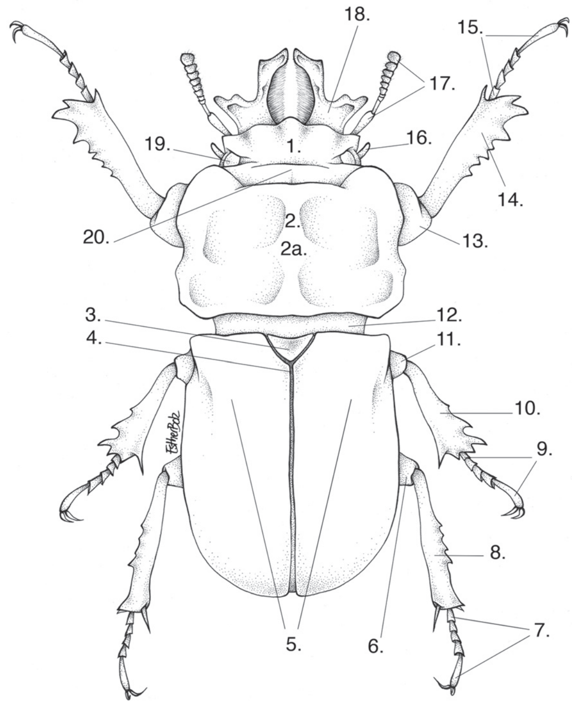
Tarsal formula 5–5–5

Usually brown or black, some species have lighter dorsal patterns, some vividly metallic.

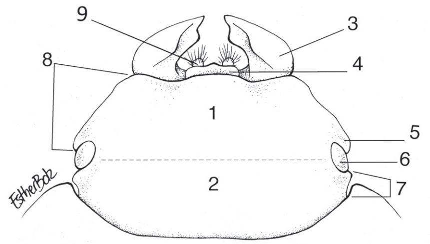
An important character that is used to differentiate lucanids from other scarabs is the number of segments in the club. In the Australian Lucanidae the antennal club is composed of three to seven segments and the antennae have 10 segments in total. The antennae vary from being geniculate (elbowed) to non-geniculate and have a relatively long scape (first segment of the antenna). The genus *Lissapterus* has at the most only a slightly pectinate antennal club whereas in the genus *Ceratognathus* the comb-like segments are quite long (especially in males) and movable, but cannot be closed fully into a compact club.

A very conspicuous character of these beetles is their sexual dimorphism. Males of many species have large, ornate mandibles, while females have smaller and very simple ones. The mandibles of male Lucanidae are often used in combat with rival males, especially when attempting to mate with a nearby female or in self-defence against would-be predators. Usually it is quite easy to distinguish the sexes through their mandibles, although in some cases the smallest males look very much like females and several species show only minimal sexual dimorphism. The sexes are indistinguishable externally in some genera (e.g. *Figulus*).

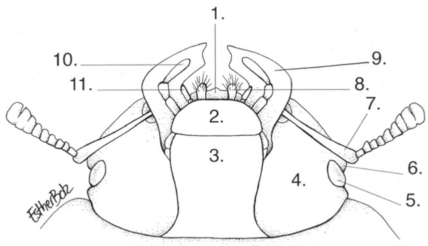
Another well-known character in this family is the allometric development



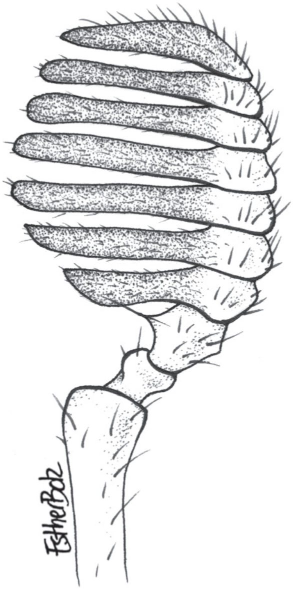
Schematic map of a non-specific stag beetle (based on *Ryssonotus nebulosus*), dorsal view. 1. Frons, 2. Pronotum, 2a. Disc, 3. Scutellum, 4. Suture, 5. Elytra, 6. Hind-or metafemur, 7. Hind- or metatarsus, 8. Hind- or metatibia, 9. Mesotarsus, 10. Mesotibia, 11. Mesofemur, 12. Mesothorax, 13. Fore- or profemur, 14. Fore- or protibia, 15. Fore- or protarsus, 16. Maxillary palp, 17. Antenna, 18. Mandible, 19. Eye, 20. Vertex. Drawing: Esther Bolz.



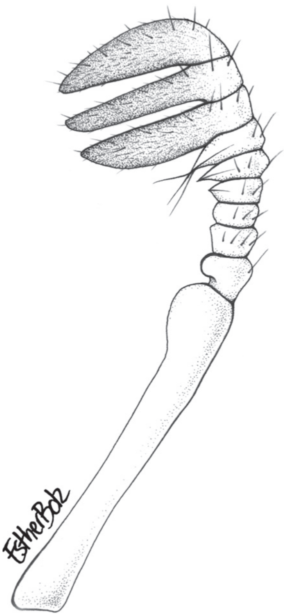
Schematic map of the head of a non-specific stag beetle (based on *Lucaninae female*), dorsal view. 1. Frons, 2. Vertex, 3. Mandible, 4. Labrum, 5. Canthus, 6. Eye, 7. Postocular margin, 8. Preocular margin, 9. Galea (outer lobe of the maxilla). Drawing: Esther Bolz, after Holloway.



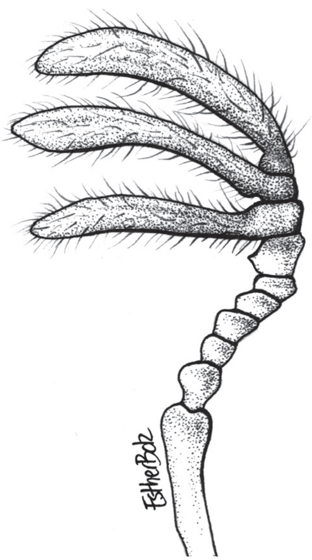
Schematic map of the head of a non-specific stag beetle (based on *Lucaninae female*), ventral view. 1. Labrum, 2. Mentum, 3. Gula (throat), 4. Gena (cheek), 5. Eye, 6. Canthus, 7. Antenna, 8. Galea (outer lobe of the maxilla), 9. Mandible, 10. Maxillary palp, 11. Labial palp. Drawing: Esther Bolz after Holloway.



Antenna of *Syndesus cornutus*. Drawing: Esther Bolz.



Antenna of a *Lamprima* sp. Drawing: Esther Bolz.



Antenna of a male *Ceratognathus* sp. Drawing: Esther Bolz.

of the male mandible (the size of the mandible is proportional to the size of the body), which has often confounded taxonomists. The marked differences in the teeth of the mandibles may depend on the overall body size of the male. In this book, where this occurs, we will simply refer to small males of a species as 'minor males' and large males as 'major males'.

Australian lucanids are mostly black, dark brown or, in the case of the subfamily Lampriminae, a vivid colour with a metallic lustre. The scutellum is always visible, although sometimes it may be rather small.

The Lucanidae

Stag beetles have always interested coleopterists, amateurs and professionals alike. Many of these beetles have spectacular shapes, their larvae lead cryptic lives and, in most species, people do not commonly encounter the adults in their habitats. The Lampriminae and many of the tropical Lucaninae are splendidly coloured while others show an amazing variety in the male mandibular size and structure – these are some of the outstanding characteristics of this family which made these beetles so popular. Their aesthetic appeal and the rarity of some species represent great value to collectors. In several cultures the stag beetle represents a mythical or mystical element and some important representations of it can be found already in Renaissance art (e.g. Dürer's famous drawing of the European stag beetle). Undoubtedly, the study of this beetle family has great scientific importance.

The family Lucanidae consists of scarab type beetles belonging to the superfamily Scarabaeoidea. In the past this family was considered to be the most primitive family within the Scarabaeoidea (Lawrence and Newton 1995). More recent research, however, proposes that the Glaresidae (glaresid beetles) are the most primitive family of scarabs and places the Lucanidae between Glaresidae and Trogidae (skin or hide beetles) and in the same clade with Passalidae (bess beetles) and Bolboceratinae (Geotrupidae, earth-boring dung beetles) (Smith *et al.* 2006). Glaresidae are small, 2.5–6.5 mm long beetles that don't occur in Australia and practically nothing is known about their biology.

Some lucanid beetles have secluded, long life cycles, spent mostly inside or under decaying, fungus-ridden logs or standing dead and rotting trees. Development from egg to adult can take several years, depending on the species and local circumstances. Lucanid larvae, like most other wood-eating insects, must employ the help of microorganisms to digest food with high cellulose content. Recent studies have shown that female lucanid beetles possess microbe-storing organs (mycangia) containing microorganisms closely related to xylose-fermenting yeasts (Tanahashi *et al.* 2010). After laying an egg, the female discharges some of these microorganisms on and around it, thus leaving a digestion aiding 'starter pack' for the offspring (Fremlin 2015). So far this research has focused only on European and Japanese lucanid species – the Australian lucanid fauna has yet to be investigated.

As the developing larva grows, it moults several times. The stages between moults are known as instars. Stag beetle larvae have three instars. Once the larva reaches its full size, it pupates. For pupation to happen, the larva must first make a cavity (pupal chamber) within the rotting wood or in the soil where it developed. Pupal duration is usually several weeks or a month depending on the species, and the newly emerged adult needs to harden and will remain in the pupal chamber for a similar amount of time or for many months if the time of year or conditions are not appropriate. Young beetles with unhardened exoskeletons and immature colouring are known as teneral adults.

The lucanid larva has typical scarabaeoid characteristics as it appears as the usual, whitish, C-shaped scarab 'curl grub'. The head is strongly sclerotised and the mandibles are stout and strong, adapted to feed on decaying wood.

Lucanid larvae can stridulate, although this may not be readily observed and is often not audible to the human ear. It is thought that stridulation helps to establish the presence of a larva to other larvae in a population and may help in promoting avoidance behaviour. Lucanid larvae can be distinguished from the larvae of other scarab families by the location of the stridulatory apparatus on the mid and hind coxae of the legs and by the large fleshy pads on either side of the vertical or Y-shaped anal opening.

Stag beetles have exarate pupae. The appendages are free and quite recognisable, but movement is limited to the abdominal segments. The pupa may wriggle a little when irritated, but otherwise remains inactive.

While larvae consume considerable amounts of rotten wood and have even been found in rotten structural timber (Lawrence 1981a), it is believed that adults of many species eat very little or don't eat at all. This assumption is based on the study of some species' reduced mouthparts and studies of their alimentary canal. Adults of some *Lamprima* species feed on plant secretions and possibly nectar and certainly do feed on soft fruit when kept in captivity. Other species (e.g. *Cacostomus squamosus*) are known to feed on the exuding sap of injured trees.

For a large percentage of Australian Lucanidae, nothing much is known about adult feeding nor breeding habits. The biology of the Australian stag beetles

A characteristic stag beetle larva. Photo: PZ.

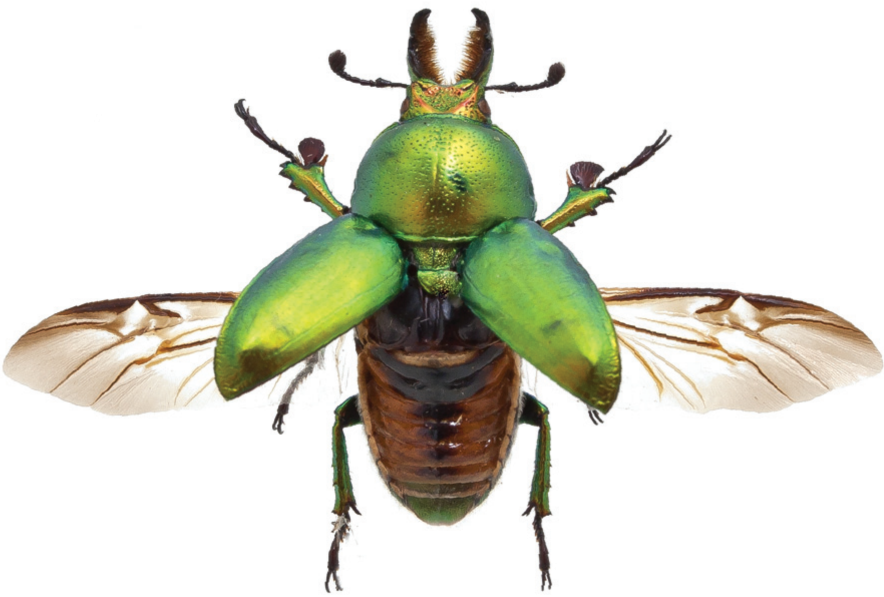
The sclerotised head of a stag beetle larva. Photo: PZ.

The large fleshy pads at the posterior of a stag beetle larva. Photo: GH.

is not thoroughly researched although some species are successfully bred in captivity. This topic is discussed with more details on pages 212–215.

Origins of the Australian stag beetle fauna

The Australian fauna shows definitive connections to the fauna of the ancient Gondwana and also to Asia. The adjective 'Gondwanan' is often used in biogeography, the study of the distribution of species and ecosystems in geographic space and through geological time. Gondwana, the ancient, enormous continent, included most of the landmasses in today's Southern Hemisphere, including Antarctica, South America, Australia and also some others that are now north of the Equator. This supercontinent started to break up in the early Jurassic, ~180 million years ago. The parts that separated moved apart, taking with them their flora and fauna, like travellers on gigantic rafts, dispersing over huge areas. Many aspects of Southern Hemisphere biogeography refer to patterns of distribution of living organisms, especially when these seem to be related and are restricted to two or more of the now discontinuous regions that were once part of Gondwana.



A stag beetle that can fly: *Lamprima latreillii* Macleay, 1819. Photo: PZ

The discovery of two extant species of *Sphaenognathus* (p. 72) and one extinct, fossil *Syndesus* (p. 67) species are perhaps the best examples (in Lucanidae) of our Gondwanan origins.

Biogeographic connections between Australia and Asia are still poorly understood, although the plate tectonics of the Indo-Pacific region is now well described. During the Pleistocene (2 588 000 to 11 700 years ago), extended periods of glaciation caused decreases of sea levels by more than 100 m in Australasia. During these periods, landbridges formed between South-East Asia and northern Australia. Migration of plants and animals was possible throughout the epoch.

Ancestors of some of our stag beetle species belonging to genera *Dorculus*, *Dorcus*, *Prosopocoilus* and *Figulus* could have arrived from Asia through the connecting expanses of dry land.

Some of our endemic species are good fliers but others, mainly those that exist in much more specialised habitats and lead cryptic lives, have lost the ability to fly; examples are *Lissapterus* and *Lissotes*, which live under or within decaying timber.

Kim and Farrell (2015) recently researched lucanid relationships and divergence time estimates and how Gondwanan break-up effected biogeographical developments.