

**ARBOREAL BEETLES OF NEOTROPICAL FORESTS: *AGRA* FABRICIUS,  
LARVAL DESCRIPTIONS WITH NOTES ON NATURAL HISTORY AND  
BEHAVIOUR (COLEOPTERA, CARABIDAE, LEBIINI, AGRINA)**

ERIK ARNDT

Anhalt University of Applied Sciences, Fachbereich LOEL  
Strenzfelder Allee 28  
D-06406 Bernburg, GERMANY

SUSAN KIRMSE

University of Leipzig, Institute of Botany  
Johannisallee 21  
D-04103 Leipzig, GERMANY

AND

TERRY L. ERWIN

Megadiversity Group, Department of Entomology  
Smithsonian Institution, Washington, D.C. 20560, U.S.A.

**Abstract**

Using a mobile crane system covering a canopy area of about 1.4 ha in a rain forest in southern Venezuela, adults of several species of *Agra* Fabricius were observed and captured. Adults of 17 species were kept in the laboratory. Movements and foraging behaviour in the forest canopy and in the laboratory are reported. Larvae of four *Agra* species are described. Larvae of all four species are highly modified. Short antennae, multiple setae FR8/9, elongate head capsule with enlarged frontale, trochanter and femoral spines or spin-like tubercles, absence of a lacinia, markedly long, multisetose and multisegmented urogomphi, a pygopod with two groups of hooks, as well as bifid-toothed tarsal claws are larval apomorphies of *Agra*. The enlarged pulvillus is shared with larvae of other genera in Lebiini that are regarded as related to *Agra* based on adult characters. Amongst themselves studied larvae show a number of differences. The larva of the *Agra cajennensis*-group has small abdominal egg bursters on terga I–VIII that were previously known only from coleopteran suborder Polyphaga; these are not present in the other first instars studied. From larval attributes, it is hypothesized that *Agra* larvae live under bark and are predatory.

---

Tropical rain forest canopies are “the last biotic frontier” (Erwin 1983). These biomes are extremely complex. Their ecological connections are poorly known beginning with their still very incompletely known faunas. Beetles of the family Carabidae represent one of the better-examined insect groups in rain forests; even so, there remain thousands of unnamed species. There are numerous arboreal ground beetle genera known which include high numbers of species, but often are represented by single specimens and many of those lack data regarding ecology and life history.

One of these mysterious ground beetle taxa is the genus *Agra* Fabricius described in 1801, thus knowledge of the life cycle comes some 200 years after discovery of the adults. *Agra* species are restricted to the Neotropical Region and subtropical edges of the Nearctic and Neoaustral Regions. One described and two undescribed species occur northwards as far as the southern

United States in Texas. There are 567 *Agra* species validly described in total, but more than 1500 more are in museums, yet to be described (Erwin: [http://entomology.si.edu: 591/entomology/carabids/search.html](http://entomology.si.edu:591/entomology/carabids/search.html)). Recent collections made with the insecticidal fogging technique indicate that many more species remain yet to be discovered. *Agra* individuals are strictly arboreal and collecting them seems to be mostly possible at light or with fogging techniques. Erwin (1979) and Erwin and Pogue (1988) demonstrated many arboreal adaptations, thus classifying *Agra* species as "leaf running." They assumed that *Agra* species occupy their habitat in a very fine-grained way that allows a high number of species to co-exist in a diverse forest. Details about their natural history are not known or have yet to be published; what is known is summarized by Erwin (1978a), who supposed that *Agra* adults might be snail predators because of the labial palpi resembling those of the snail-eating Cydrini. However, evidence of their foraging behaviour has not yet been published.

One of us (SK) observed several species of *Agra* in their natural habitat using canopy crane facilities in southern Venezuela. One aim of this paper is to report the ecological, behavioural and larval morphological data of two species representing different species groups of *Agra* observed, and secondly to present information on larvae of two additional *Agra* species from the western Amazon Basin collected by Erwin. This is a first attempt to understand the life history of these extraordinary insects that Erwin (1978a) called the "top predators among beetles in term of size" in rain forest canopies.

### Study Areas, Material, and Methods

**Study Areas.** The study site of S. Kirmse is located in the upper Orinoco region (Venezuela, state of Amazonas) close to the black water river Surumoni (3°10'N, 065°40'W; 105 m). A canopy crane system, 42 m in height, was installed at the study site and its swing covers an area of about 1.4 ha; its vegetation is completely accessible by means of the crane's gondola. The vegetation is that of a moist lowland tropical rain forest classified as terre firme (Prance 1979). The upper canopy ranges usually from 25 to 27 m in height. Only a few emergent trees rise to a height of 35 m. The forest here is frequently interrupted by light gaps, thus the canopy is not completely closed. The Surumoni canopy crane plot contains average tree species richness for the area. Frequent species in the tree fraction with a DBH of  $\geq 10$  cm are *Goupia glabra* (Celastraceae), *Oenocarpus bacaba* (Arecaceae), *Dialium guianense* (Caesalpiniaceae), *Ocotea amazonica* (Lauraceae) or *Ruizterania trichanthera* (Vochysiaceae) (Wesenberg *et al.* pers. comm.).

Anhuf *et al.* (1999) describe the weather pattern as a gross rainfall of about 3,100 mm (with year to year fluctuations of about 500 mm) with a strong peak in the annual precipitation from May to July, then a lower peak in September and October. The average annual temperature in the study area is *ca.* 26°C, usually with slight variations between the coolest month (25°C) and the warmest month (26.5°C), whereas a daily range of 5–10°C frequently occurs.

The study site of T. Erwin is at the border of Yasuni National Park in Ecuador (0°39'25.685"S 076°27'10.813"W; 216.3 m). The landscape consists of gently rolling hills covered by a rich hardwood rainforest moderately endowed with epiphytic growth, also classified as terra firme. Bamboo is rare and never forms dense stands locally. Small intermittent streams drain the area into the permanent and nearby Rio Piraña, a second order stream that drains

into the Rio Tiputini. The fogging plot contains average tree species richness for the area, 669 trees of 250 species identified; 40 trees are not yet identified. Frequent species in the tree fraction with a DBH of  $\geq 10$  cm are the palms, *Iriartea deltoidea* and *Oenocarpus bataua*. Abundant hardwoods are *Matisia malacocalyx*, *Eschweilera coriacea*, *Brownea grandiceps*, *Pourouma bicolor*, *Pseudolmedia laevis* and *Siparuna decipiens*.

Rainfall is just under 3,000 mm per year, with the rainy season arriving in April and persisting usually until early October.

**Observation, Collecting, and Warding of Live Adults.** Using the large tower crane, the crowns of all tree species were searched for species of the genus *Agra* with the aid of a lamp at night. Several specimens were observed at the study site between October 1997 and March 1999. *Agra* adults of different species were captured by hand collecting or with an entomological net.

Both males and females were kept separately or in pairs in plastic tubes with a height of about 12 cm and a diameter of about 15 cm filled with loam to a height of nearly 3 cm. The tubes were equipped with small twigs of the host tree and a fragment of wood with bark. The adults were kept under the natural temperature regime and natural day/night conditions for the area.

Different food items were offered and the beetles checked every second day. As food, Kirmse used 1–2 ml of viscose honey per individual. The honey was never devoured completely, but continually a sugary, somewhat watery solution remained at nearly two thirds of the quantity of honey. In some cases small living moths were offered; only in a few cases did *Agra* adults feed on these moths. The moths were not eaten completely; the beetles bit only a small gap in the abdomen of the moths and fed on the internal tissue. Fruits were also offered, but no beetle was observed feeding on them.

Altogether, across the study year, 54 individuals of *Agra* were kept, including 35 females of 17 species. The average life span in captivity of the females was 38 days. The longest kept adult female survived 78 days.

*Cajennensis* group (Erwin 1996): Two males and three females of one species of this group were captured between January and March, 1999. Two specimens were found on a flowering tree of *Peltogyne paniculata* (Caesalpiniaceae), another individual was found masticating the flowers of *Licania heteromorpha* and another on the liquid secreted from young leaves of *L. subarachnophylla*.

One of the females found gravid on January 22, 1999, was observed in the tubiform flowers of *P. paniculata*. One egg of longish form, soft condition, and white colour deposited by this female was found on the moist surface of loam in the cage on February 2. The egg was separated and a larva hatched after nine days. Larva and adult were preserved in ethanol.

*Peruana* group: Four adults representing a species of this group were captured, one in July, 1998, and three in January, 1999. One female was found on *R. trichanthera*, one male feeding on liquid secreted from a young shoot of *S. silvestris*, one female on *L. hebantha* and another male on *L. subarachnophylla*, both feeding on secreted liquid on the upper surface of young pubescent foliage.

The gravid female was captured on January 30, 1999, masticating newly emerged leaves of *L. hebantha*. It survived 31 days in captivity. An egg from this female was found on the vertical moist surface of the timber fragment two weeks later. The longish egg was of soft condition and slightly yellow coloured. The egg was separated as before and a larva hatched eight days later. It was highly active on the soil surface, sometimes creeping into the substrate.

The larva was offered fruits, earthworms, and small caterpillars, however it fed only on earthworms, one of which was completely devoured. A small caterpillar offered as a food item produced some silk. The *Agra* larva climbed this silk repeatedly, possibly trying to catch the caterpillar, but it was not successful even in reaching the caterpillar. Fruits were ignored by the *Agra* larva. The larva survived 41 days without moulting.

**Larval Specimens and Study Methods.** Material studied: *Agra* sp. (*cajenensis*-group): one first instar larva, reared *ex ovo* by S. Kirmse. *Agra* sp. (*peruana*-group): one first instar larva, reared *ex ovo* by S. Kirmse. An additional 12 larvae of both first and second instars were obtained by Erwin's insecticidal fogging program in Ecuador between 1994 and 1999. These "Lebiini" larvae were unidentifiable to genus until SK reared *Agra* larvae *ex ovo* and we learned their characteristics. All 12 larvae were associated with adults of the common *lycisa* group members in the fogging samples and likely belong to this group.

For comparative purpose, larvae of 41 carabid tribes including the following representatives of Lebiini were studied: *Calleida* Latreille and Dejean, *Cymindis* Latreille, *Syntomus* Hope, *Lionychus* Wissmann, *Microlestes* Schmidt-Göbel, *Paradromius* Fowler, *Dromius* Bonelli, *Philorhizus* Hope, *Demetrius* Bonelli, *Lebia* Latreille, and *Plochionus* Dejean. All compared larvae are deposited in the collection of E. Arndt, except that of *Plochionus*, which is in the collection of van Emden (Natural History Museum, London). In addition, Erwin examined numerous larvae of *Calleida* from the fogging samples; they are housed in the Smithsonian Institution, Washington, D.C. and in Politecnica Nacional University in Quito, Ecuador.

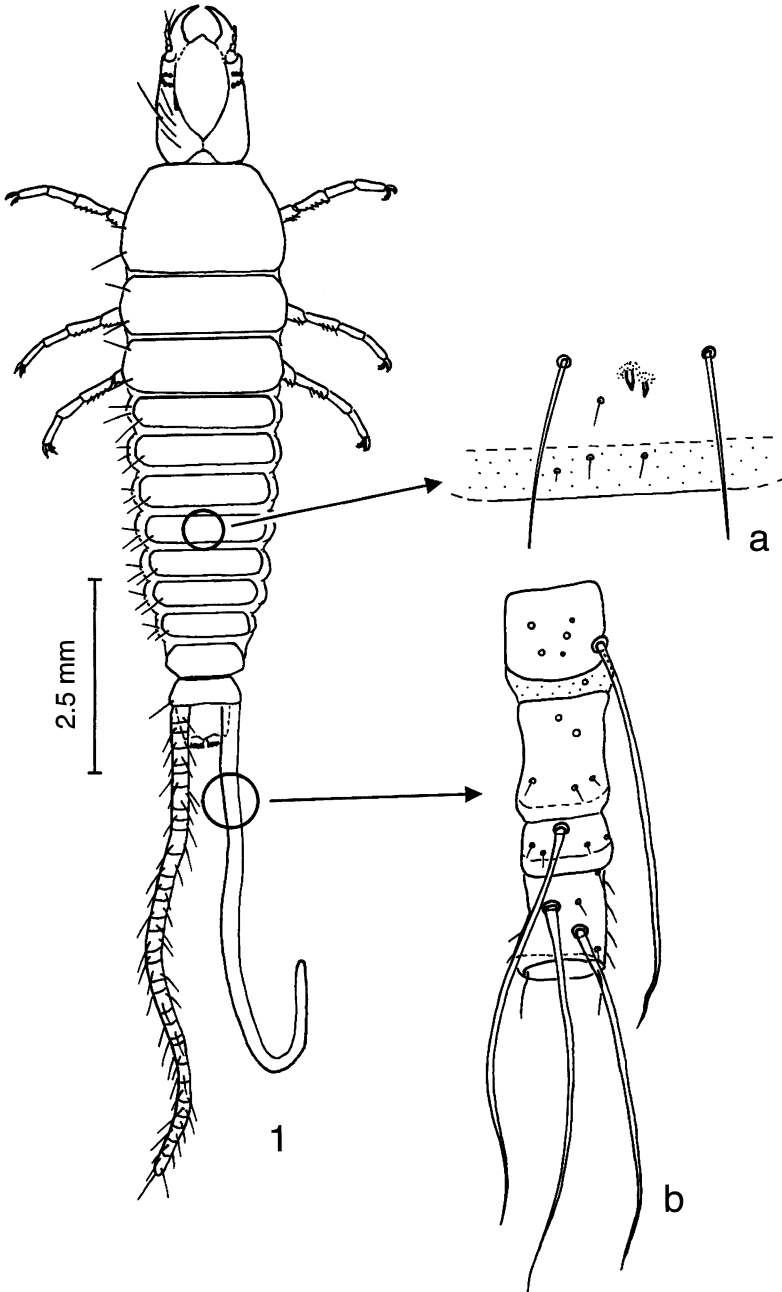
The *Agra* larvae from Venezuela were mounted in Canada balsam on microscope slides and studied at magnifications up to 400×. One Ecuadorian larva was mounted for SEM examination, the rest are stored in 80% ethanol. Body length is measured without urogomphi. Abbreviations of chaetotaxy follow Bousquet and Goulet (1984) and Arndt (1993). Terms of morphology follow Lawrence (1991).

### Behaviour and Foraging Activities of Adults

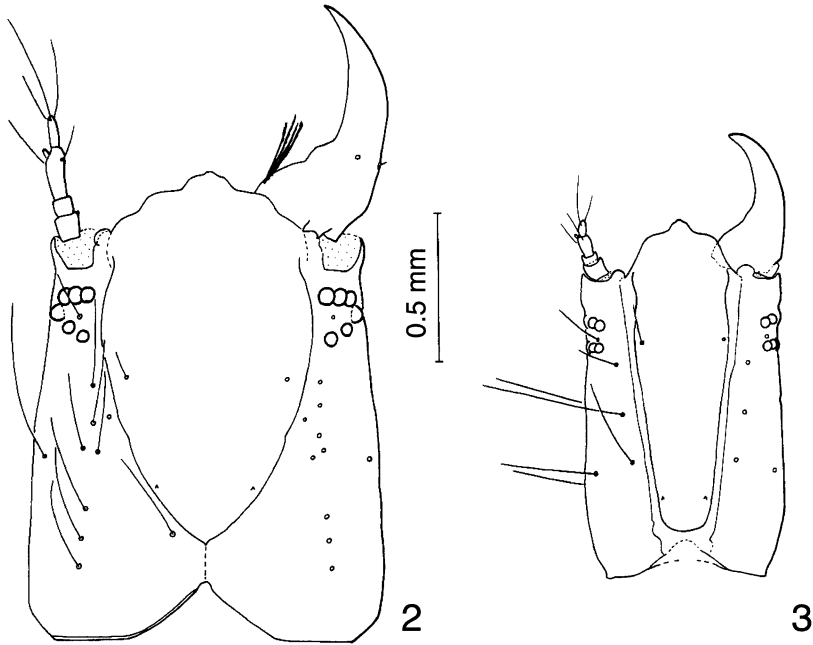
The adult beetles of several species show a strictly nocturnal activity in the canopy and could often be found perching on the surface of leaves. The movements of these beetles are swift, often running and changing their direction from leaf to leaf, across twigs and as a rule on the upper surfaces. Moving so, the adult *Agra* frequently were occupied with food intake. They were not observed on thick branches or trunks.

Most observed specimens did not fly within the tree crowns. One individual, observed on *R. trichanthera* in January 1999, did fly from leaf to leaf or twig, landing sometimes on the upper or the lower surfaces. Running periods interrupted the flights. The distance of a single flight or running movement did not exceed 0.5 m. When attempting to capture from above, the adult *Agra* would drop down about 20 to 30 cm and fly to a neighbouring twig. When shaking the branches, beetles would cling tight.

All specimens observed were foraging in the canopy taking liquid or masticating plant parts. Nutrient compounds are found in diverse parts of plants. Usually, the adult beetles masticated flowers (nectar, pollen and sometimes diverse components of the whole flower) or on extra floral nectaries. Liquid producing new leaf shoots of a few species of *Licania* (Chrysobalanaceae)



**Fig. 1.** Habitus, L1, *Agra* sp. (*cajennensis*-group), dorsal aspect. **1a)** Posteroventral part of an abdominal tergum VII with egg burster-like spines; **1b)** articles of urogomphus.



**Figs. 2–3.** Head capsule, L1, dorsal aspect. **2)** *Agrina* sp. (*cajennensis*-group). **3)** *Agrina* sp. (*peruana*-group).

seem to be of special interest for diverse species of *Agrina*. The immature leaves of these trees are densely covered with glandular hairs; the adults were observed grazing on the pubescent upper surfaces.

Copulation was observed in July 1998, between adults on *Senna silvestris* (Caesalpinaceae) at 8.30 pm. The pair perched on the surface of a leaf hidden from above by foliage. This female survived in captivity 78 days without oviposition. E.S. Ross (pers. comm.) and Erwin have observed adults “sleeping” on the bottom side of leaves aligned to the mid-vein and wholly cryptic in that position.

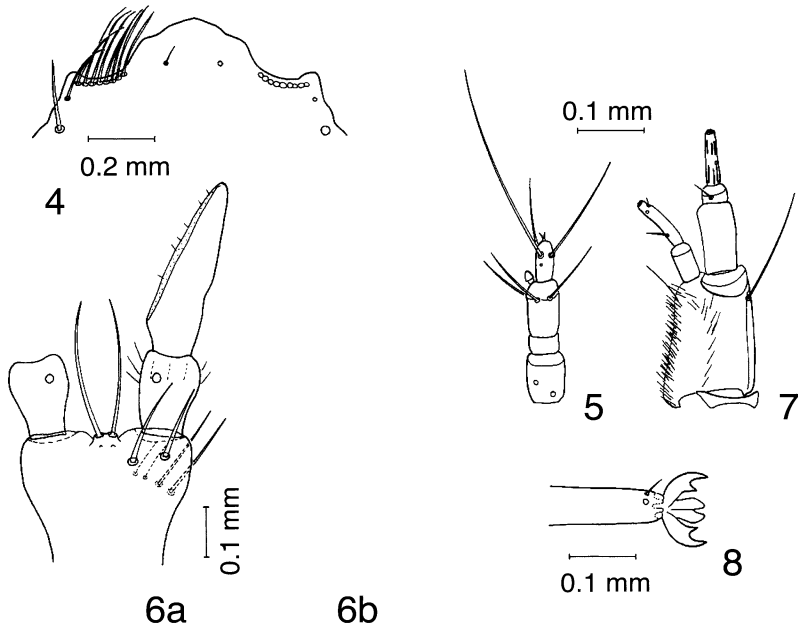
### Descriptions of Reared Larvae

*Agrina* sp. (*cajennensis*-group)

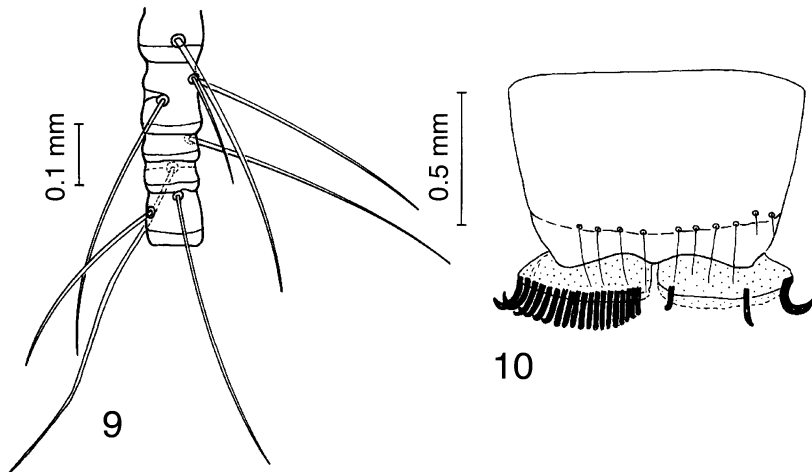
*Size.* Head width: 1.15 mm, length of body about 11 mm.

*Habitus and colouration.* Larva slender with markedly elongate head capsule and urogomphi; thorax widest part of body (Fig. 1). Head capsule reddish brown, other sclerites yellowish, abdomen and urogomphi weakly sclerotized.

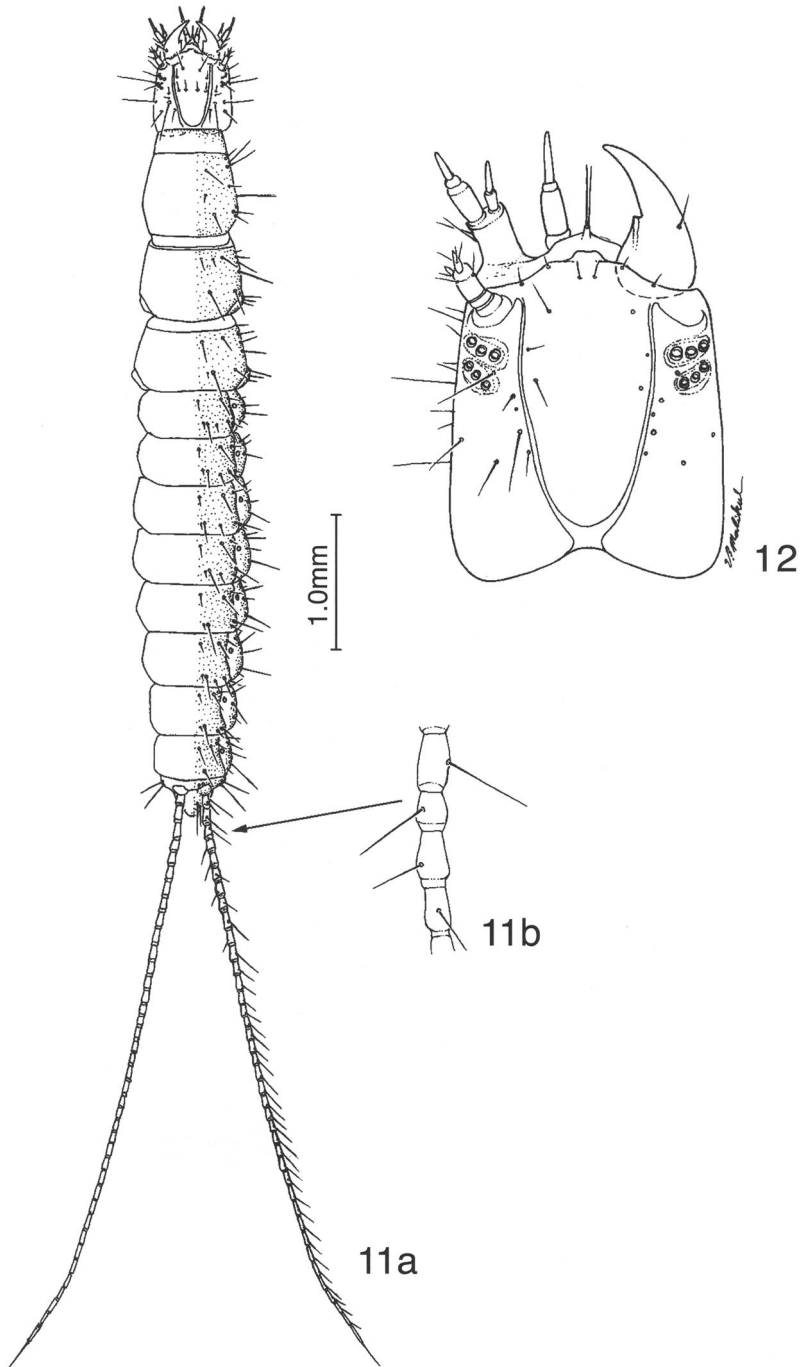
*Head.* Head capsule conical, widest near posterior margin, lateral margin not rounded, with 6 small stemmata present (Fig. 2). Frontale large with epicranial suture not curved, scutiform, small egg bursters in form of microspines paired on posterior part of frontale. Nasale protruding, without teeth (Fig. 4), FR10,11 absent, adnasale with multiplied setae FR8,9. Coronal suture slightly longer than antennomere IV, cervical and ocular groove lacking. Antenna 4-segmented, short, barely extending half-length of mandible; antennomeres I,



**Figs. 4–8.** 4) Nasale and adnasale, dorsal aspect, L1, *Agra* sp. (*cajennensis*-group); 5) antenna, left, dorsal aspect, L1, *Agra* sp. (*peruana*-group); 6) labial palpus, dorsal aspect, L1, *Agra* sp. (*cajennensis*-group); 7) maxilla, right, dorsal aspect, L1, *Agra* sp. (*peruana*-group); 8) claws and pulvillus, dorso-oblique aspect, L1, *Agra* sp. (*peruana*-group) (bifid tooth of claw not visible in dorso-oblique aspect).



**Figs. 9–10.** 9) Part of urogomphus, as indicated in Figure 1. of *Agra* sp. (*peruana*-group); 10) pygopod, dorsal aspect, L1, *Agra* sp. (*cajennensis*-group).





II wide, III and IV slender; antennomere II shortest, III longest; antennomere III with small subcylindrical sensorium. Mandible short, retinaculum lacking, penicillum present. Prementum (Fig. 6) wide, with several additional setae, short ligula with one pair of setae (LA6), LA7 pore like, labial palpus 2-segmented; ultimate segment enlarged, elongated and flattened medially with longish sensorial field at the inner margin,  $2.2 \times$  longer than penultimate (Fig. 6). Maxilla (cf. Fig. 7) with cardo slender, stipes about 1.8 longer than wide; galea 2-segmented, segments long and slender, ultimate segment  $1.3 \times$  longer than penultimate; lacinia lacking; palpifer short and wide, with microspines dorsally; maxillary palpus short, 3-segmented, slender, relation of segments from base 2.9:1:1.3. Stipes with extended setal field gMX dorsomedially and several microspines dorsolaterally. Hypopharynx large, bulging. Gular suture complete.

*Thorax.* Ecdysial line of thoracic nota present, anterior keel of meso- and metathorax present. Legs long and slender; relation of femur:tibia:tarsus about 1.2:1.1:1. Two claws present; claw with bifid basal tooth. Pulvillus (cf. Fig. 8) well developed.

*Abdomen.* Terga I–IX with anterior keel present, ecdysial line lacking; terga I–VIII with 1–3 egg bursters anteriorly at middle (Fig. 1A). Pygopod wide and short with two apical groups of hooks; each group comprising about 18–20 hooks (Fig. 10). Urogomphi moveably attached to abdominal tergum IX, markedly long, multisetose and multisegmented, comprising about 30 segments.

*Microsculpture.* Regular sculpture lacking, except pointed structures on dorsal side of stipes and maxillary palpomere I, as well as meshed microsculpture in apical half of tarsus.

*Chaetotaxy.* Irregular on most sclerites, with numerous additional setae (in the sense of Bousquet and Goulet 1984), e.g., on labial palpomere I, maxillary palpomeres I, II, antennomeres I–III in apical half; outer margin dorsally and laterally of mandible, prementum. Thorax with long primary setae and numerous minute additional setae. All segments of legs with additional setae, femur and trochanter with two rows of spines ventrally beside numerous minute additional setae. Minute additional setae on hypopleurite and epipleurite, sternites, and terga; long additional setae on parietale; numerous long and markedly short additional setae on urogomphi (Fig. 9). Setal field gMX with about 50 setae divided into a dorsal row and more extended field on inner (median) side.

*Agra* sp. (*peruana*-group)

Same character states as in larva of *Agra cajennensis*-group, except the following:

*Size.* Head width: 0.67 mm, length of body about 8 mm.

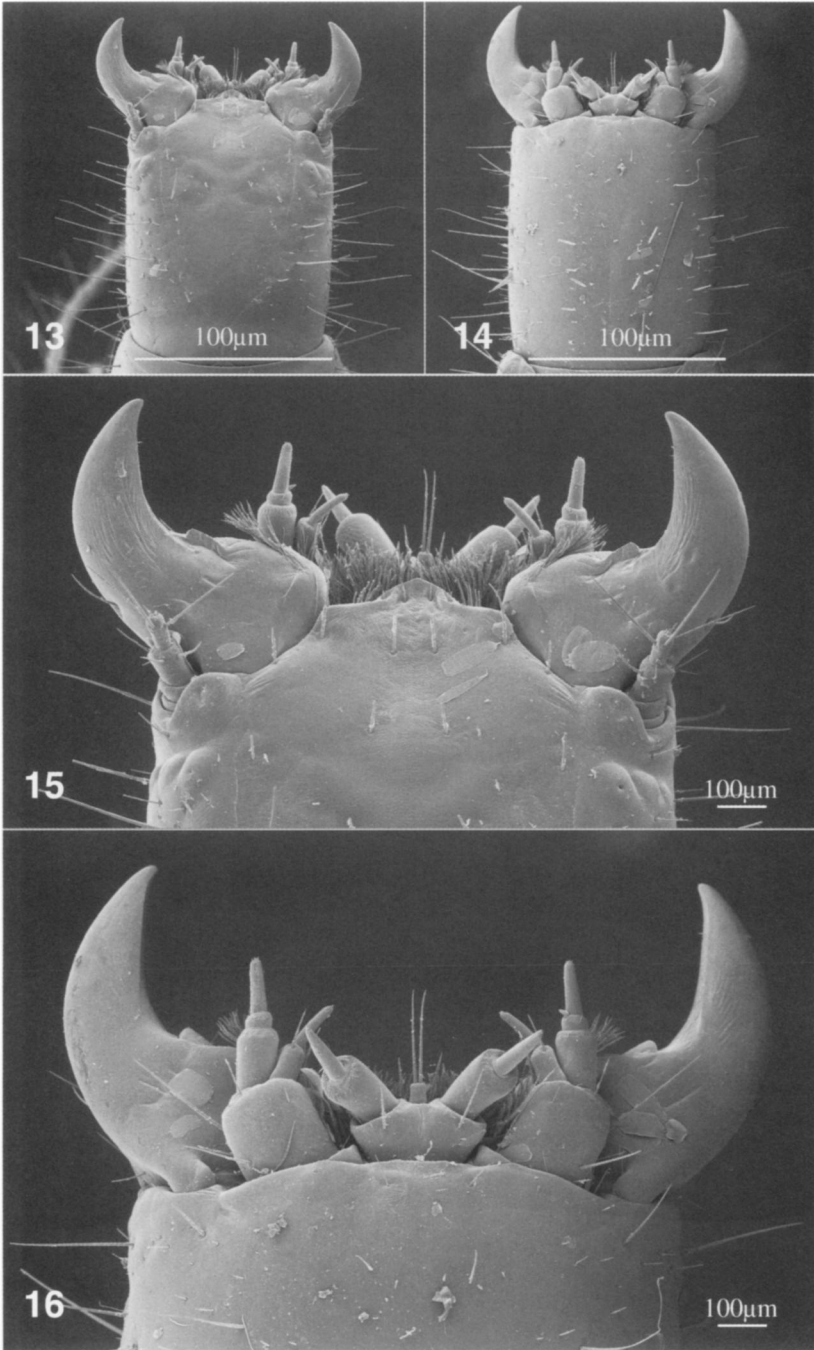
*Habitus and colouration.* Brown, markedly sclerotized.

*Head.* Head capsule slender and elongate (Fig. 3). Frontale longer, posteriorly truncate, separated from parietale by distinct membranous region. Coronal suture lacking. Mandible obtuse (Fig. 3). Antenna much shorter than half-length of mandible (Fig. 5). Maxillary palpomeres shorter. Ultimate segments

---

←

**Figs. 11–12.** **11a)** Habitus, L2, *Agra* sp. (*?lycisa*-group), dorsal aspect; **11b)** part of urogomphus indicated in Figure 11a; **12)** head, L2, *Agra* sp. (*?lycisa*-group), dorsal aspect.



of both labial and maxillary palps with numerous long and fine sensorial foveae.

*Abdomen.* Terga without egg bursters. Urogomphi with more than 35 segments.

*Microsculpture.* Dorsal side of stipes and maxillary palpomere I smooth. Urogomphi with transverse microsculpture.

*Chaetotaxy.* Additional setae mainly absent. Urogomphi with numerous long setae, short setae lacking.

### Descriptions of Fogged Larvae

*Agra* sp. (possibly *lycisa*-group)

1<sup>st</sup> Instar (one specimen from Erwin's site, Fig. 11a and 11b)

*Size.* Head width, 0.2 mm; body length, 3.0 mm. As in larva of *Agra peruana*-group, except the following: head capsule quadrate, nasale truncate with two small teeth, mandible (Fig. 12.) with retinaculum and lateral seta MN1, maxilla without fine setae on inner margin.

2<sup>nd</sup> Instar (one specimen from Erwin's site. Possibly not the same species as the 1<sup>st</sup> instar.)

*Size:* Head width, 0.6 mm; body length, 6.0 mm; same character states as in 1<sup>st</sup> instar larva of *Agra lycisa*-group except the following: nasale prolonged, slightly emarginated apically, head capsule slightly tapered anteriorly, frontale wide and rounded posteriorly (Fig. 12).

*Agra* sp. (unknown group)

(one specimen from Erwin's site, Figs. 16–18)

*Size:* Head width, 1.0 mm; body length, 8.0 mm. Mandibles markedly exceed in length maxillary and labial palpi, retinaculum markedly developed (Fig. 13), lateral seta present, nasale prolonged and broadly produced, head capsule perfectly quadrate and arrangement of setae different from other larvae (Figs. 13–14), and trochanters and coxae armed with numerous tubercle-like spines (Fig. 19).

*Note:* This specimen is either a large second instar or small third instar. Its attributes, somewhat different than the other three species above, are described and illustrated here to demonstrate the variability to be expected in this very large and diverse genus of carabid beetles.

### Discussion of Larval Morphology

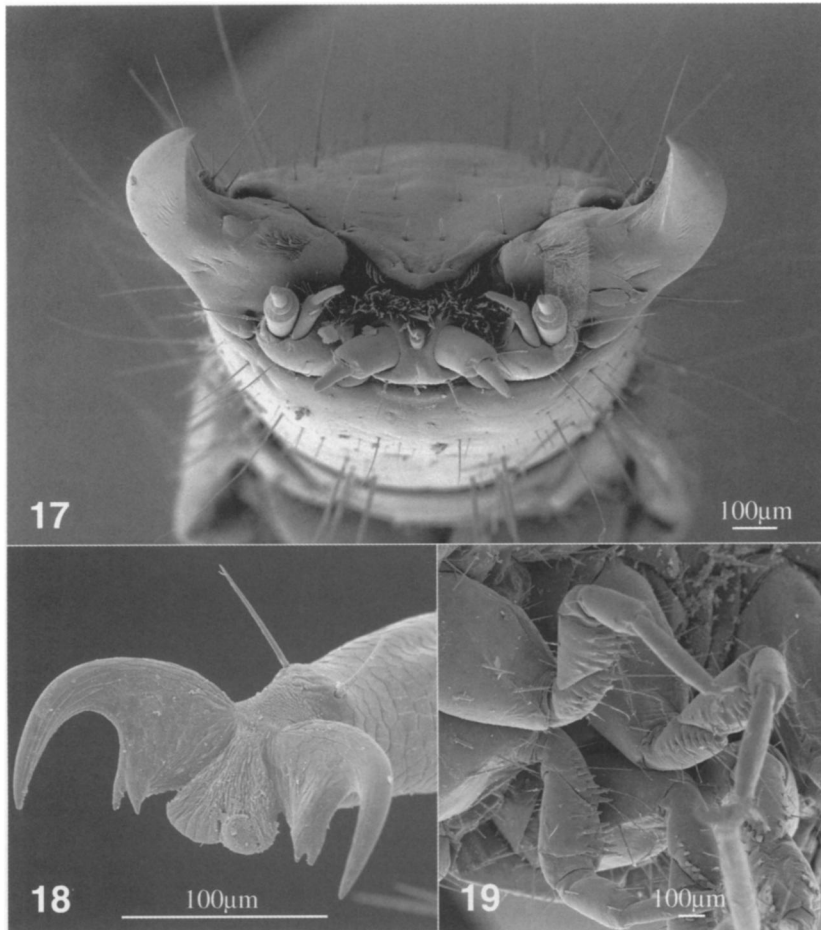
The *peruana* and *cajennensis* group larvae are very large compared with size of the adults, although adults of these groups are among the largest in the genus. A reduced number of larval instars seem possible compared with the normal three instars of Carabidae. However, the *lycisa*-group larvae do not appear to be out of proportion to the adults, the latter of which are among the smallest of the genus.

**Larval Characters of *Agra* in Comparison with Other Lebiini.** Short antennae, multiple setae FR8/9, elongate head capsule with enlarged frontale, trochanter and femoral spines or spin-like tubercles, absence of a lacinia, mark-

---

←

**Figs. 13–16.** 13) Head, L?, *Agra* sp. (unknown group), dorsal aspect; 14) head, L?, *Agra* sp. (unknown group), ventral aspect; 15) mouthparts, L?, *Agra* sp. (unknown group), dorsal aspect; 16) mouthparts, L?, *Agra* sp. (unknown group), ventral aspect.



**Figs. 17–19.** 17) Mouthparts, L?, *Agra* sp. (unknown group), frontal aspect; 18) claws and pulvillus, lateral frontal aspect, L?, *Agra* sp. (unknown group); 19) trochanters and coxae, ventral aspect, L?, *Agra* sp. (unknown group).

edly long, multisetose and multi-segmented urogomphi, a pygopod with two groups of hooks, as well as bifid-toothed tarsal claws are larval apomorphies of *Agra*.

The larvae of *Agra* share a number of derived character states with those of other Lebiini. Apomorphic characters of Lebiini are lacinia absent and cervical groove lacking. However, these characters also occur in other tribes (e.g., Odacanthini, Dryptini, Zuphiini, Perigonini, Masoreini), thus do not represent synapomorphies (see also Arndt, 1993). Other apomorphic characters of *Agra* larvae are found in single genera or subgroups of Lebiini.

Membranous attached, segmented urogomphi, a pulvillus and basal tooth on claw, and two groups of sclerotized hooks on the pygopod are shared by larvae of *Agra* with those of the genus *Plochionus*, a representative of Calleidina

(=Agrina, Lorenz, 1998), the hypothesized adelphotaxon of *Agra* (Erwin 1982). Segmented urogomphi, pulvillus and sclerotized hooks were already mentioned by van Emden (1942) as attributes of larval Calleidina. According to van Emden, these characters occur in the calleidine genera, *Calleida* (in widest sense), *Onota* Chaudoir, and *Parena* Motschulsky as well as *Euproctinus* Leng and Mutchler (cited as *Andrewesella* Csiki) which were transferred to the new subtribe Metallicina (Basilewsky 1984; Lorenz 1998). Hooks on the pygopod in both *Agra* and *Plochionus* are shared; furthermore, with *Dromius* (in widest sense) and *Cymindis*, both with fused urogomphi. The urogomphi of *Demetrias* are segmented like those of *Plochionus*, but *Demetrias* lack the hooks of pygopod and have one claw with pulvillus instead of two claws each with one pulvillus as in *Agra*. Markedly elongate urogomphi are found in larvae of *Syntomus* Hope, which belongs to another subgroup of Lebiini than *Agra* and the other taxa discussed here.

We can conclude that a suite of derived characters evolved convergently in several genera of the large tribe Lebiini. The particular incomplete knowledge of juvenile stages in this tribe does not allow us to examine relationships based on larval characters in more detail at present. Out of the proposed relatives of *Agra* (with genus *Callidiola* Jeannel or other genera in the subtribe Calleidina), we know only the larva of *Plochionus*. Our knowledge of larval Lebiini is nearly limited to the few taxa in the boreal Holarctic Region. The great majority of Lebiini, however, is distributed pantropically.

**Markedly Modified Characters.** Many larval attributes of the four known species are markedly modified relative to other lebiines. An elongate labial palpomere II and microspines on abdominal terga, in the first instar, as in the larva of the *Agra cajennensis*-group are unique characters among known larval Carabidae. It is not possible to explain the function of these attributes at this time. However, information from the canopy foggings suggests that *Agra* larvae do not expose themselves on outer surfaces often, as do *Calleida* larvae which are common to almost every fogging event and likely forage openly on leaves or twigs. Also, *Agra* larvae have a thick, highly sclerotized cuticle in the second instar, particularly the head. This attribute is common in many larvae found under bark. *Calleida* larvae are much softer and somewhat more long-legged. They are surface gleaners and very common. However, *Agra* adults are more common than *Calleida* adults in the very same samples.

The markedly long and moveable urogomphi are found elsewhere in the larvae of species of *Chlaenius* Bonelli, *Siagona* Latreille and *Enceladus* Bonelli (Erwin 1978b; Arndt 1991:131; Grebennikov 1999). The first named genus has larvae, which live in clefts of parchy and loamy soil quite unlike tree surfaces, while the latter has larvae living under bark; the exact habitat of *Siagona* larvae is unknown. The abdominal micro-spines in *Agra* larvae may also function as support during movement in narrow spaces, e.g., under bark, nevertheless, they have the same apparent structure as true egg bursters. Cavities under bark are the supposed microhabitats of these species, though both females laid eggs on the soil or bark surface. This egg laying behaviour could be an artefact due to the laboratory conditions.

A simple mandible lacking a retinaculum, like that in the two *Agra* from Venezuela, was observed in some ectoparasitic carabid taxa. But, an ectoparasitic life habit is unlikely for *Agra*, as we now know that the second and first instars larvae are fully campodeiform. The mandible of *Agra* is comparably blunt in contrast to that of ectoparasitic larvae. On the other hand, the larvae of *Agra* fed on earthworms in the laboratory. *Agra* produce comparably large

eggs from which hatch very large first instar larvae. Therefore, females produce only few eggs probably, which is very unlikely for parasitic species. In dissected adults, Erwin found fragments of termites.

#### Acknowledgments

S. Kirmse gratefully thanks W. Morawetz (University of Leipzig) for his support and for the possibility of joining the Surumoni project. The fieldwork was supported by a grant for a travel of ESF Tropical Canopy Programme and a grant of the Stiftung der Deutschen Wirtschaft. All of us thank the Department of Entomology of the Smithsonian Institution for funding the publication of this article. Warren Steiner, Department of Entomology of the Smithsonian Institution, provided the SEM photos and Vichai Malikul, Department of Entomology of the Smithsonian Institution, provided the drawings of the *lycisa*-group larva.

#### Literature Cited

- Anhuf, D., T. Motzer, R. Rollenbeck, B. Schröder, and J. Scarzynski. 1999. Water budget of the Surumoni crane site (Venezuela). *Selbyana* 20(1):179–185.
- Arndt, E. 1991. Carabidae [pp. 45–141]. *In: Die Larven der Käfer Mitteleuropas*, Bd. 1 (B. Klausnitzer, editor). Goecke and Evers, Krefeld. 273 pp.
- Arndt, E. 1993. Phylogenetische Untersuchungen larvalmorphologischer Merkmale der Carabidae (Insecta: Coleoptera). *Stuttgarter Beiträge zur Naturkunde, Serie A*, 488:1–56.
- Basilewsky, P. 1984. Essai d'une classification supragénérique naturelle des Carabides Lébiens d'Afrique et de Madagascar (Coleoptera Carabidae Lebiinae). *Revue de Zoologie Africaine* 98:525–559.
- Bousquet, Y., and H. Goulet. 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). *Canadian Journal of Zoology* 62:573–588.
- Emden, F. I. van. 1942. A key to the genera of larval Carabidae (Col.). *Transactions of the Royal Entomological Society, London* 92:1–99.
- Erwin, T. L. 1978a. Systematic, natural history, and zoogeographic notes on the genus *Agra* Fabricius, with a description of a new species from Panama (Coleoptera: Carabidae: Lebiini). *Coleopterists Bulletin* 32:261–267.
- Erwin, T. L. 1978b. The larva of Neotropical *Enceladus gigas* Bonelli (Coleoptera: Carabidae: Siagoninae: Enceladini) with notes on the phylogeny and classification of some of the more primitive tribes of ground beetles. *Coleopterists Bulletin* 32: 99–106.
- Erwin, T. L. 1979. Thoughts on the evolutionary history of ground beetles: Hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions [pp. 539–592]. *In: Carabid beetles: their evolution, natural history, and classification* (T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern, editors). *Proceedings of the First International Symposium of Carabidology*. Dr. W. Junk b.v. Publishers, The Hague.
- Erwin, T. L. 1982. *Agra*, arboreal beetles of neotropical forests: *erythropus* group systematics (Carabidae). *Systematic Entomology* 7:39–71.
- Erwin, T. L. 1983. Tropical forest canopies, the last biotic frontier. *Bulletin of the Entomological Society of America* 29(1):14–19.
- Erwin, T. L. 1996. Arboreal beetles of neotropical forests: *Agra* Fabricius, the *cayennensis* complex (Coleoptera: Carabidae: Lebiini: Calleidina). *Annales Zoologici Fennici* 33:17–21.
- Erwin, T. L., and M. G. Pogue. 1988. *Agra*, arboreal beetles of Neotropical forests: Biogeography and the forest refugium hypothesis (Carabidae) [pp. 161–188]. *In: Neotropical Distribution Patterns: proceedings of a 1987 Workshop* (W. R. Heyer and P. E. Vanzolini, editors). *Academia Brasileira de Ciências*.
- Grebennikov, V. 1999. Larvae of the supertribe Siagonitae: genera *Siagona* Latreille

and *Enceladus* Bonelli (Coleoptera: Carabidae). Koleopterologische Rundschau 69:1–10.

**Lawrence, J. L. 1991.** Order Coleoptera [pp.144–658]. *In*: Immature insects (F.W. Stehr, editor). Vol. 2. Dubuque.

**Lorenz, W. 1998.** Systematic list of extant ground beetles of the world. Tutzing. 503 pp.

**Prance, G. T. 1979.** Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31(1):26–38.

(Received 28 November 2000; accepted 14 May 2001. Full page charges borne by the authors.)

### Erratum

Richard Leschen's review of **Coleopteros de Chile, Chilean Beetles** in the previous issue (Coleopterists Bulletin 55: 218) erroneously gave the author's name as E. A. Tobar. It should have been cited as E. T. Arias. The author and editor apologize for the reversal and any resulting confusion.