The family Scarabaeidae is one of several families included in the superfamily Scarabaeoidea, a large distinct group of quite highly specialized beetles most easily recognized by their lamellate antennae. Various authors have proposed raising certain subfamilies to family rank such as the Geotrupidae [Paulian (117)], Hybosoridae [Gardner (52)], Pleocomidae [Paulian (118)], Acanthoceridae [BÖVING & CRAIGHEAD (10)] and Trogidae [Leng (89)]. Crowson (26) recognizes six families in the Scarabaeoidea, the Lucanidae, Passalidae, Trogidae, Acanthoceridae, Geotrupidae and Scarabaeidae. Brues, Melander & Carpenter (16), however, divide the Scarabaeoidea into 22 families. They have even made families of such commonly accepted subfamilies as the Aphodiinae, Cetoniinae and Rutelinae and raised several tribes to family status.

Detailed studies of scarabaeid larvae, many of which were unknown to earlier workers, make it difficult to define as families such groups as the Geotrupinae. For this reason, such workers as van Emden (39) and the writer prefer to recognize only three families in the superorder, Lucanidae, Passalidae and Scarabaeidae. This is in accord with the classification followed by Blackwelder (8) in his checklist of coleopterous insects of Mexico, Central America, the West Indies, and South America.

The family Scarabaeidae according to Leng (89) includes 14 commonly recognized subfamilies, namely the Coprinae, Aegialiinae, Aphodiinae, Ochodaeinae, Hybosorinae, Geotrupinae, Pleocominae, Glaphyrinae, Acanthocerinae, Troginae, Melolonthinae, Rutelinae, Dynastinae, and Cetoniinae arranged as far as possible in phylogenetic sequence. My comments on the biology of the group will follow this order.

Published information on scarabaeid biology is exceedingly voluminous because of the world-wide distribution of the group and its diverse habits and because of the importance of many genera as crop pests. As in so many other fields, information on noneconomic forms is apt to be scanty and there is still much to be learned about such subfamilies as the Coprinae, Aphodiinae, and Troginae. Little is known about the biology of the Aegialiinae and Ochodaeinae. Habits of Coprinae, Geotrupinae, and Dynastinae are discussed by Arrow (3) who gives an interesting account of the habits of horned beetles but many of his conclusions are based largely on inferences from their morphology. Howden (75) presents an excellent summary covering the biology and taxonomy of Geotrupinae from the world standpoint.

1 The survey of the literature pertaining to this review was completed in May, 1957.
Leng (89) has suggested that food is the chief environmental factor affecting beetles and that this factor is correlated with profound structural modifications. Certain it is that food is one of the most important considerations in the biology of scarabaeids both for larva and adult, and the structure of both is adapted for particular feeding functions.

Food of adults.—In Table I may be found some general conclusions about the food preferences of adult scarabaeids. It will be noted that the subfamilies fall into two main groups, one group including such subfamilies as the Coprinae, Aphodiinae, Geotrupinae, and Troginae which are either saprophagous or fungus feeders and a second including the subfamilies Melolonthinae, Rutelinae, Dynastinae, and Cetoniinae which are strictly phytophagous. This diversity of habit has been long recognized and the family has often been divided into the so-called lamellicorn scavengers and the lamellicorn leaf chafer [Comstock (23)]. This also corresponds in general to the division into the groups Laparosticti and Pleurosticti based on the position of the spiracles [Blatchley (9); Hayes (66)].

**TABLE I**

**FOOD HABITS OF SCARABAEIDS**

A = Adults    L = Larvae

<table>
<thead>
<tr>
<th>SUBFAMILY</th>
<th>Carrion</th>
<th>Dung</th>
<th>Humus</th>
<th>Decay-Ing Veg. Matter</th>
<th>Duff</th>
<th>Litter</th>
<th>Wood</th>
<th>Fungi</th>
<th>Seed Plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coprinae</td>
<td>A</td>
<td>L</td>
<td>L</td>
<td>A</td>
<td>A</td>
<td>L</td>
<td></td>
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<tr>
<td>Aphodiinae</td>
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<td>A</td>
<td>L</td>
<td>A</td>
<td>L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geotrupinae</td>
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<td>A</td>
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<td>L</td>
<td>L</td>
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<td>L</td>
<td>A</td>
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</tr>
<tr>
<td>Acanthocerinae</td>
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<td>L</td>
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<td>L</td>
<td>A</td>
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</tr>
<tr>
<td>Pleocominae</td>
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<tr>
<td>Glaphyrinae</td>
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<tr>
<td>Troginae</td>
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<tr>
<td>Melolonthinae</td>
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<tr>
<td>Rutelinae</td>
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</tr>
<tr>
<td>Dynastinae</td>
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<td>L</td>
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<td>L</td>
<td>L</td>
<td>L</td>
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<td>A</td>
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<tr>
<td>Cetoniinae</td>
<td>A</td>
<td>L</td>
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<td>L</td>
<td>L</td>
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<td>L</td>
<td>A</td>
<td></td>
</tr>
</tbody>
</table>

According to Leng (89), feeding upon decaying substances is a primitive food habit for Coleoptera, while the habit of feeding on living plant tissue is found in more specialized forms. For this reason Leng and many others have considered the lamellicorn scavengers the more primitive of the groups.

Adults of the Coprinae and Aphodiinae are known to feed on carrion, dung, decaying vegetable matter, and fungi (56, 76, 99, 141). Pessoa & Lane (124) have mentioned some of the food habits of Coprinae found in Brazil. Pereira (121) describes the unusual case of the coprine beetle *Zonocopris gibbicollis* (Harold), which feeds on the slime of snails. The various species of *Aphodius* feed commonly in dung or decaying organic matter. In England,
BIOLOGY OF SCARABAEIDAE

adults of *Aphodius fimetarius* Linnaeus and *Aphodius subterraneus* Linnaeus, which are common in horse manure, also injure mushrooms by devouring portions of the caps (2).

There is now a considerable body of literature on the food habits of Geotrupinae (1, 73, 75, 87, 116, 143, 152, 155, 167, 174). Adults of some species of *Geotrupes* feed only on dung while others feed either on dung or on fungi [Howden (75)]. The same writer observed adults of *Bolboceras* (formerly *Odontaeus*) *darlingtoni* (Wallis) feeding on fungi. According to Fabre (44), adults of *Bolbolasmus* (formerly *Bolboceras*) *gallicus* (Mulsant) also feed on fungi.

Adults belonging to the Pleocominae (genus *Pleocoma*) never feed. The same is also true for adults of the Glaphyrinae (genus *Lichnanthe*) [Franklin (49)].

Although the lamellicorn leaf chafers may be placed in one general group on the basis of their feeding on living tissue, there is in reality a great diversity in their food habits. Adults of Melolonthinae and Rutelinae devour plant tissues, especially leaves, flowers or young fruits. In contrast, adults of Dynastinae usually attack stems or roots of plants in their search for liquid nourishment, often feeding underground. Adults of the Cetoniinae are also largely liquid feeders, but feed above ground, preferring nectar or sap or the juices of ripening fruits and vegetables. Some species feed on pollen. There are species in each of the subfamilies Melolonthinae, Rutelinae, and Dynastinae which do not feed at all in the adult stage.

Adults of many species of Melolonthinae are voracious feeders on the leaves of various plants, particularly those of shrubs and trees. Thus beetles of several species of *Melolontha* often defoliate trees in many parts of Europe (86, 130). Many species of *Phyllophaga* frequently defoliate trees in the United States and Canada (19, 100, 136, 145). Adults of both genera are crepuscular or nocturnal.

In Malaya, adults of *Apogonia cribricollis* Burmeister and *Apogonia expeditionis* Ritsema attack the leaves of cacao [Lever (91)]. In the Sudan, adults of *Schizonycha* feed on the leaves of *Dolichos* [Pollard (128)]. Johnson (80), in the United States, found adults of *Polyphylla decemlineata* feeding on the needles of ponderosa pine. According to Dumbleton (33) adults of the grass grub *Castelytra (Odontria) zealandica* (White), occurring in New Zealand, prefer foliage of rosaceous plants, sometimes causing severe defoliation of fruit and ornamental trees. The same species has also been responsible for severe damage by defoliating cruciferous seedlings.

Other melolonthine adults feed either on blossoms or young fruits. In the United States, adults of *Macroductylus subspinosus* (Fabricius) often injure young fruit of grapes, apples, and peaches (144). Adults of *Hoplia callipryge* Leconte devour the blossoms, young leaves, and fruit of many different plants along the Sierra foothills of California [Essig (43)].

Adults of *Amphimallon majalis* Razoumowsky do not feed, according to Gyriscot et al. (60). This also holds true for adults of *Cochliotis melolonthoides* (Gerstaecker) in Tanganyika [Jepson (78)].
Adults of ruteline leaf chafer feed commonly on leaves, fruits, and blossoms. In the United States, the introduced Japanese beetle, *Popillia japonica* Newman, has been found feeding on over 275 species of plants including tree and bush fruits, shade trees, corn, soybeans, and many ornamentals [Hawley & Metzger (62)]. In feeding on foliage small portions of the leaf surface are consumed resulting in a skeletonized appearance.

Many species of *Anomala* have similar habits [Hayes & McColloch (67); Lupo (98)] but a few species feed little or not at all. Laughlin (88) reports that adults of *Anomala horticola* (Linnaeus) do not need to feed for mating and egg laying to occur. Friend (51) found that the adults of *Anomala orientalis* Waterhouse feed very little and concluded that they fed only to obtain moisture. According to Bradford (13), adults of *Anomala vetula* Weidemann, occurring in Africa, have not been observed to feed.

In Malaya, adults of *Chaetadoretus cribratus* (White) and *Adoretus compressus* (Weber) feed on the leaves of cacao [Lever (91)]. In southern Chile, the adults of *Hylamorpha elegans* (Burmeister) feed on the leaves of *Nothofagus obliqua* and *Prunus avium* [Duran (35)].

The main food of dynastine beetles is the juice of living plants obtained most often from the underground stems, shoots, or tap roots. Thus adults of *Strategus quadrifoveatus* (Palisot de Beauvois) attack the base of coconut sprouts underground and may even feed on the juices of older coconut palms [Plank (126)]. Adults of several species of *Euetheola (Dyscinetus)* are pests of rice, maize, and sugar cane in various parts of the world, working underground where they gnaw into the heart of the plants or cut the young shoots [Baerg (4); Kern (81); Phillips & Fox (125)]. In the United States adults of *Ligyrus gibbosus* DeGeer feed on the underground parts of carrots, sunflowers, celery, sugar beets, and potatoes [Hayes (63)].

Adults of *Heteronychus licas* Klug, in Mozambique, damage young maize, rice, and sugar cane [del Valley y March (162)]. In Kenya, Le Pelley & Goddard (119) found that adults of *Heteronychus consimilis* Kolbe feed extensively on the young shoots of wheat, just below the surface. In Australia, adults of the introduced species *Heteronychus sanctae-helenae* feed on a wide variety of field, vegetable, and fruit crops and on ornamentals [Wallace (166)]. Depending on the crop, damage is caused by underground feeding on the tap roots, on stem bases, in tubers (potatoes), on cuttings (sugar cane, grape vines), or on suckers (bananas). Fruits resting on the ground are also injured.

In northern Venezuela, Box (11) and Guagliumi (59) report adults of *Podischnus agenor* (Olivier) damage sugar cane by boring into the stalks. The same species damages young bamboo plantations in Central America and is an important pest in sugar cane in Guatemala and Colombia [Box (12)].

Adults of *Oryctes rhinoceros* (Linnaeus), widely distributed in southern Asia and the East Indies, have different habits from the above species in that they work in the tops of coconut and other palms [Gressitt (58); Nirula,
Antony, & Menon (111)]. This results in damage to the growing point and destruction of leaf tissue. According to Gressitt (58) the beetle does not ingest solid plant material, but sucks the juices from the macerated tissue.

Adults of some species do not feed. This is true of *Cyclocephala immaculata* Olivier and *C. borealis* Arrow, commonly found in eastern United States [Ritcher (138); Johnson (79)].

Adults of many species of Cetoniinae feed on plant juices, either sap or juices of ripening or overripe fruit. Other species are common on flowers where they feed on pollen or nectar. Most species are diurnal in habit.

Adults of *Cotinis nitida* (Linnaeus) occurring in eastern United States, feed on ripening fruits, on tomatoes, corn in the milk stage, and the sap of oak and other trees (140). Adults of *Cotinis texana* Casey have similar habits and also feed on pollens of sorghum, corn, cotton and other plants [Nichol (110)]. Adults of several species of *Euphoria* have similar habits and in addition frequent flowers where they secure nectar or pollen (140). Hoffman (70) in his monograph on *Trichiotinus* states that beetles of this genus feed on pollen.

According to Korschefsky (84) adults of *Cetonia aurata* Linnaeus damage blossoms and fruits in Germany. He reports that adults of *Potosia aeruginosa* Drury are found on flowers and at tree sap and adults of *Potosia cuprea* Fabricius damage blossoms and occasionally bore into ripe fruits. Adults of *Valgus canaliculatus* (Fabricius), common in eastern United States, feed on the nectar of flowers [Ritcher (140)].

**Food of Larvae.**—The food habits of scarabaeid larvae do not lend themselves to easy division into a few distinct groups (Table I). There are some plant feeders among the larvae of the lamellicorn scavengers and dung feeders among the larvae of the lamellicorn leaf chafer. It is true, however, that the majority of the dung and carrion feeding forms belong to the lamellicorn scavengers (Laparosticti) and the majority of the root feeding forms belong to the lamellicorn leaf chafer (Pleurosticti). Unlike adult scarabaeids, no scarabaeid larvae are definitely known to feed on fungi, although this habit has been suspected by various writers.

The food of coprine larvae is provided by the adults and is discussed in a later section on nidification. Dung is the larval food of most species; others feed on carrion [Pessoa & Lane (124)] or feathers [Howden & Ritcher (76)]. Some genera such as *Deltochilium* utilize all three kinds.

Aphodiine larvae are predominately dung feeders but some kinds feed on organic matter in the soil and a few species prefer the roots of living plants. Downes (32) and Ritcher & Morrison (148) have described injury to turf by larvae of *Aphodius pardalis* LeConte, in North America. In Minnesota, Hoffman (69) observed larvae of *Ataenius* injuring grass roots. In Australia and Tasmania *Aphodius howetti* Hope and *Aphodius pseudotasmaniae* Given cause extensive damage in pastures [Erlich (42); Martyn (102)].

Nothing is known about larvae of the Ochodaeinae. According to Gardner (52) larvae of Hybosorinae are found in soil or in dung.
Larvae of most species of Geotrupinae feed on such materials as dung, humus, duff, or litter, all provisioned for them by the adults [Howden (75)]. Larvae of the European *Lethrus aipturus* Laxman feed on leaves, buds and shoots of grapes and other plants, which have been cut by the adults and packed into underground cells [Schreiner (152)]. Some species, such as *Geotrupes blackburni* Fabricius, use either dung or leaf duff for the larval food [Howden (75)]. Larvae of *Geotrupes ulkei* Blanchard feed on decomposing leaves [Loding (96)].

The interesting subfamily Pleocominae is found only in western North America, being especially common in Oregon and California. Larvae of several species of *Pleocoma* feed on tree roots [Ritcher & Olney (149); Ellertson (38)], but I have found larvae of one species in California, feeding on grass roots (142).

Published accounts of the feeding habits of glaphyrine larvae have been few. According to Franklin (49) working in Massachusetts, larvae of *Lichnanthe vulpina* (Hentz) were found damaging the roots of cranberries as early as 1911 and had become a considerable pest by 1917. My observations in Oregon show that larvae of *Lichnanthe rathvoni* LeConte feed on decaying leaves and other organic matter in sandy areas along streams. Although locally abundant, none have ever been found injuring crops.

Information about acanthocerine larvae is also scanty. Lugger (97) mentions rearing *Cloeotus* and mentions that the larval food is decaying material beneath the bark of dead trees. Hesse (68), in discussing African Acanthocerinae, states that according to Ohaus the food of the larvae is rotten wood.

Larvae of Troginae are usually found feeding in soil beneath carcasses of dead animals. A few species, as will be mentioned later, feed on grasshopper eggs [van Emden (40)].

The lamellicorn leaf chafers include many species whose larvae are of economic importance because they prefer to feed on the roots of living plants. These belong principally to the Melolonthinae and in part to the Rutelinae and Dynastinae. At the same time, there are also many species whose larvae feed on humus, duff, decaying organic matter, or decaying wood. This is the case with most larvae of the Cetoniinae, with many dynastine larvae and with some ruteline larvae.

De Fluitier (47), working in Java, divided white grubs into 3 categories, according to their feeding habits: (a) grubs feeding only on dead organic matter (Cetoniinae); (b) grubs which normally feed on dead organic matter but will attack living roots in its absence (certain Rutelinae and Dynastinae); (c) grubs feeding by preference on living roots of crop plants (Melolonthinae). In other parts of the world, numerous members of the Rutelinae, such as the Japanese beetle (*Popillia japonica* Newman) and the Chinese rose beetle (*Adoretus sinicus* Burmeister), also belong in the third group.

In many parts of the world, larvae of Melolonthinae cause extensive damage to the roots of grasses, legumes, small fruit plants, shrubs and trees. Larvae of greatest economic importance belong mainly to the tribes Melo-
lonthini or Sericini. First-stage larvae feed, in part, on organic matter in the soil; second and third instars feed largely on roots or underground stems.

Throughout Europe larvae of the genus *Melolontha* are of major importance, attacking grasses, vegetable crops, and the roots of young trees (14, 18, 77, 130). *Amphimallon* larvae are destructive to the roots of field and forage crops, lawns and nursery stock both in Europe and in the northeastern United States [Gyrisco et al. (60)]. In North America, from Mexico to Canada, larvae of many species of *Phyllophaga* cause widespread damage to roots of pasture grasses, corn, Irish potatoes, and tree seedlings (9, 19, 135). In Chile, larvae of *Phytolaema*, *Sericoides* and *Shizochelus* cause extensive damage to cereal and forage crops [Duran (35)].

The most injurious species of melolonthine larvae in New Zealand belong to the genus *Costelytra* (*Odontria*) [Given & Hoy (55)], but *Calonota* larvae are also important [Cumber & Cowie (27)]. In India, *Leucopholis* larvae injure the roots of coconut palms and also attack cassava, sweet potatoes, yams and *Colocasia* [Nirula, Antony & Menon (111)]. In Java, larvae of *Lepidiota*, *Holotrichia* and *Psilopholis* feed on the roots of rubber trees [de Fluiter (47)]. In Africa, in Sudan, larvae of *Schizonycha* feed on peanuts and the roots of sorghum [Pollard (128)].

In Tanganyika, Jepson (78) reports that larvae of *Cochliotes melolonthoides* (Gerstaecker) cause extensive damage to the roots of sugar cane. Other melolonthine larvae of economic importance are species of *Cnemarachis* in the West Indies [Wolcott (172)] and the genus *Clemora* (*Phytalus*) in Mauritius and Barbados [Box (12)].

Of the Rutelinae, larvae of species belonging to the Anomalini usually feed on roots of living plants. A few species of the Rutelini feed on living roots, but many others belonging to such genera as *Pelidnota* and *Parastasia* feed on decaying wood (139). In the Philippines, a few species feed on decaying vegetable matter [Viado (163)].

Larvae of various species of *Popillia*, *Anomala* (including *Phyllopertha*), all belonging to the Anomalini, are of economic importance. Larvae of *Phyllopertha horticola* (Linnaeus) injure grass roots in England (104, 105, 129). Larvae of *Anomala vetula* Wiedemann injure roots of turf in South Africa [Bradford (13)]; in Japan larvae of *Anomala albopilosa* Hope injure roots of pine wind breaks [Nitto & Tachibana (113)]. In Virginia, larvae of *Strigoderma arboricola* (Fabricius) damage peanuts [Grayson (57)]. Mitchell (106) reports that in Rhodesia, grubs of *Anomala* and *Adoretus* feed primarily on rotting vegetation in the soil but occasionally damage tobacco transplants.

In the United States, larvae of the introduced Japanese beetle, *Popillia japonica* Newman, cause extensive damage to turf grasses [Pepper & Gesell (120); Schread (151)]. Smith & Hadley (156) made a careful analysis of the contents of the fore-gut of larvae collected in grass sod and found that 64.3 percent of the material consumed was from roots of living plants. The balance consisted of decayed plant tissue (19.6 per cent) and mineral matter (16.1 per cent).
Of all the subfamilies, larvae of the Dynastinae exhibit the most diverse food habits. Preferred foods for larvae of the various species include dung, humus, decaying vegetable matter, litter, duff, decaying wood, and the roots of living plants. There is even provisioning for the larvae by adults of certain species (Strategus).

According to de Fluiter (47) dynastine larvae occurring in Java rubber plantations normally feed on dead organic matter but will also attack living roots. Jepson (78) found in Tanganyika that larvae of *Heteronychus tenuistratius* Fairmaire usually feed on decaying roots and detritus but, when numerous, damage live roots of sugar cane. Larvae of *Heteronychus licus* Klug, in Mozambique, feed on organic matter in the soil, in wet low-lying areas beside rivers [del Valley y March (162)]. Larvae of *H. consimilis* Kolbe, however, in Kenya, damage the roots of wheat (119). In the United States, larvae of the rice beetle, *Dyscinetus trachypygus* (Burmeister) feed in compost or in soil near pig pens [Phillips & Fox (125)].

In the United States, larvae of *Cyclocephala immaculata* Olivier feed both on decaying organic matter and on roots of grasses and grain (138). Martelli (101) states that larvae of *Pentodon punctatus* Villers feed on grape-vine cuttings. According to Plaut (127) *Pentodon* larvae damage roots of young apple trees and seedlings in Israel.

Food habits of *Oryctes* larvae in various parts of the world also vary greatly (25). In India, larvae of *O. rhinoceros* feed in cattle dung [Nirula, Antony & Menon (112)], but Gressitt (58) found that larvae of this same species feed on dead wood, compost, or dung in the Palau Islands. In Germany, Korschefsky (84) reports that older larvae of *Oryctes nasicornis* Linnaeus are found in compost heaps, manure, tanning beds, old piles of street sweepings, and sawdust piles.

Larvae of Cetoniinae almost never feed on the roots of living plants. Instead, they feed commonly on decaying vegetable matter in the soil, on dung, or in dead wood. Larvae of such genera as *Trichiotinus* and *Osmoderma* feed largely on wood [Hoffman (72); Ritcher (140)]. *Valgus* larvae feed on the walls of termite burrows in logs or standing dead trees (140).

Some cetonine larvae cause plant injury but this results from disturbance of the soil and roots rather than from feeding. In this way, larvae of the green June beetle, *Cotinis nitida* Linnaeus, have recently caused extensive injury to ladino clover pastures and lawns in the southeastern United States [Davich *et al*. (29)].

**NIDIFICATION**

Nest building or the provision made by adults for their progeny has been studied in some detail by a number of European workers [Fabre (45); Schreiner (151); Lengerken (90)], but has been paid little attention in this country. Strangely enough, while looking after the future needs of the larva is usually the rule among beetles of the subfamilies Coprinae and Geotrupi-
nae, both subfamilies of so-called lamellicorn scavengers, this habit also occurs among certain species of *Strategus* belonging to the subfamily Dynastinae, a subfamily of the lamellicorn leaf chafer. Although the Coprinae are popularly known as tumble bugs, actually only a few genera, such as *Canthon* and *Deltochilum*, roll balls (141). *Copris* and *Phanaeus* form balls, but this is done in an underground chamber [Lindquist (92, 93)]. Most other genera pack tubular burrows with food materials for their larvae.

The ball of *Canthon* and *Copris* is usually composed of dung; that of *Phanaeus* has a center of dung and an outer covering of soil. The ball of *Deltochilum*, which the adult rolls, has a core of fur or feathers. This is later coated with mud and the whole is wrapped in pieces of dead leaves (76). Unlike *Canthon*, *Deltochilum* does not bury its ball but places it within a shallow cup-like depression in the soil, beneath fallen leaves. This is quite similar to the habits of *Nesosisyphus* in the island of Mauritius described by Vinson (164).

Adults of *Geotrupes blackburni* (Fabricius) provision a shallow burrow with an elongate, more or less horizontal wad of dung or duff in which they lay a single egg [Howden (75)]. According to the same writer, adults of *Bolboceras* (*Odontaeus*) and related genera provision their burrows with humus obtained from the top-most layer of soil.

Species of *Strategus* differ in the provision they make for their larvae. Larvae of *Strategus quadrifoveatus* (Beauvois), found in Puerto Rico, feed in wood and the adults make no provision for their larvae other than laying their eggs in small cells having walls composed of minute pieces of wood mixed with soil [Plank (126)]. Adults of *Strategus mormon* Burmeister, however, provision burrows with horse dung and therein deposit their eggs [Knaus (83)].

In North Carolina *Strategus antaeus* (Fabricius) has been found to provision its burrow with surface litter such as pine needles. The entrance to the burrow is marked by a pushup of sand and the burrow often has the shape of an inverted Y. Adults are active in August; small larvae may be found feeding in the mass of litter in September.

**Number of Molts**

It has generally been believed that all scarabaeids, without exception, have three larval instars. Thus, van Emden (39) states "the larvae of the Lamellicornia moult thrice, the third ecdysis releasing the pupa." Floyd Ellertson and the writer, in studying the biology of several species of *Pleocoma* in Oregon, have found that larvae of this peculiar genus may molt from 7 to 11 times with one molt occurring each year.

**Pupation Habits**

The mature scarabaeid larva constructs a cell in which to pupate. A pre-pupal stage precedes actual pupation. Some dung feeding larvae such as cer-
tain species of *Aphodius* pupate in cells within the old dung mass, but most dung feeding species pupate in the soil. Larvae of *Geotrupes blackburni* make a cell in the soil within the old dung or duff mass stored there by the female (75). Wood feeding forms such as *Osmoderma* prepare a pupal case made of wood fragments or of humus-like material accumulated in tree cavities [Hoffman (72)]. Soil inhabiting forms such as *Phyllophaga* make an elongate cell in the earth (136).

In most subfamilies the last larval skin is pushed to the rear of the pupal cell, but in the subfamily Rutelinae the pupa is cradled in the inflated larva skin which first splits longitudinally along the middorsal line (13, 15, 51). Most dynastids have similar habits, however, in a few genera such as *Oryctes* [Gressitt (58)] and *Strategus*, the pupa pushes the larval skin to the rear.

The time of year when pupation occurs varies within most subfamilies and often varies within a single genus (Table II). For example, I have found that in the genus *Anomala*, *Anomala nigropicta* Casey and *Anomala binotata* Gyllenhal pupate in the fall, overwinter as adults, and appear in flight early the next spring. In the same locality *Anomala innuba* (Fabricius) overwinters as a full grown larva, pupates in the spring and does not appear in flight until early June (137). Similarly, most species of *Serica* common to the eastern United States pupate in the fall, overwinter in the soil as adults, and fly in the early spring. In California, in contrast, I have found that most species of *Serica* overwinter as full grown larvae and pupate in the late winter and early spring (144).

A summary of information on pupation gleaned mostly from the literature or based on personal observations is given in Table II. It will be noted that the average length of the pupal stage, under field conditions, is a minimum of 14 days and may be much longer. Exact information on this point is difficult to obtain and is lacking for several species. In laboratory studies Vogel & Ilic (165) have shown that the length of the pupal period for *Melolontha melolontha* Linnaeus varies with the temperature, being 3 to 4 months at 12° C. and 4 to 5 weeks at 20 to 25°C.

*Pupation habits of Phyllophaga.*—A detailed study of the pupation habits of several species of *Phyllophaga*, made several years ago by the writer, serves to emphasize the fact that species, even though closely related taxonomically, are distinct entities biologically (136). This basic fact is often ignored by those engaged in economic work.

Like species of *Serica* and *Anomala* some species of *Phyllophaga* pupate in the summer while others pupate in the spring (Table II). Those pupating in the summer (July or August) remain within their pupal cells for part or all of the winter, depending again upon the species, and then emerge in the spring to feed on foliage. Species such as *Phyllophaga ephi Iida* (Say) overwinter as full grown larvae, pupate in June and appear in flight, as adults, in July.

The depth of pupation is also characteristic for each species, seemingly...
regardless of latitude (136). Phyllophaga hirticula (Knoch) was found to pupate at an average depth of 12.3 to 15.6 in. in Kentucky, while Phyllophaga inversa (Horn), another summer-pupating form, averaged from 4.5 to 6.9 inches in depth in the same localities. Phyllophaga ephilida (Say), a spring-pupating form, averaged only 3.3 in. in pupation depth.

LENGTH OF LIFE CYCLE

Scarabaeids' life cycles vary with the climate, being longest in more temperate regions. The shortest life cycles are to be found in tropical areas with no climatic seasons [Gressitt (58)]. Life cycles may be comparatively long in some regions having a dry, hot season since larvae may aestivate for several months until the rainy season begins [Moutia (107)].

The life cycles of many scarabaeids have been worked out in detail but those of such subfamilies as Aphodiinae, Troginae, and Acanthocerinae are little known. According to Madle (99), large species of Aphodius have one generation a year, while smaller species have two. In general, in temperate regions, the Coprinae [Cooper (24); Lindquist (93)] and most Geotrupinae [Howden (73, 75)] have life cycles of one year. In Oregon we have evidence that the life cycle of Pleocoma spp. (Pleocoma) is very long, perhaps requiring eight or more years. In the Melolonthinae, Rutelinae, Dynastinae and Cetoniinae the life cycles may be one, two, or three years or in the case of the Melolonthinae, even four or five years in northern latitudes.

In the Melolonthinae, most species of the tribe Melolonthini have rather long life cycles, especially in temperate regions. In the United States the many species of Phyllophaga have a two- or three-year life cycle [Hayes (65, 66); Reinhard (133, 134, 135); Ritcher (136)]. Some species having a three-year cycle in the northern states may have only a two-year cycle in states south of the Ohio River (136), while some species having a two-year cycle in the northern states have only a one-year cycle in Texas [Reinhard (131, 132)].

In Europe, Melolontha hippocastani Linnaeus requires from three to five years to complete its life cycle according to Korschefsky (84) and Schwerdtfeger (154) while Melolontha melolontha Linnaeus requires from three to four years depending upon latitude [Regnier (130)]. Work by Thiem (159) with Melolontha spp. indicates that differences in the length of life cycle of a given species depend on the rate of development of the first and second instars. In Germany, the life cycle of Polyphylla fulla Linnaeus takes three or four years [Korschefsky (84)].

Species belonging to the Melolonthine tribes Sericini and Macroductylini usually have a one-year life cycle, but some species in more temperate climates have a two-year cycle. In the United States it appears that Macroductylus and various species of Serica require one year for the complete life cycle. Schread (151) states that Autosera castanea Arrow also has a one-year life cycle. According to Murayama (109), Serica orientalis Motschulsky
### Table II

**Pupation Habits of Soil Inhabiting Scarabaeidae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Subfamily</th>
<th>Time of Year</th>
<th>Av. Length of Stage</th>
<th>Depth Range</th>
<th>Depth Av.</th>
<th>Country</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geotrupes blackburnii</td>
<td>Geotrupinae</td>
<td>Sept.</td>
<td>17.5 days</td>
<td>3-6.5&quot;</td>
<td>4&quot;</td>
<td>United States</td>
<td>(75)</td>
</tr>
<tr>
<td>Bolboceras darlingtoni</td>
<td>Geotrupinae</td>
<td>June</td>
<td>24 days</td>
<td>8-12&quot;</td>
<td>10&quot;</td>
<td>United States</td>
<td>(75)</td>
</tr>
<tr>
<td>Pleocoma dubitalis</td>
<td>Pleocominae</td>
<td>July-Aug.</td>
<td>—</td>
<td>5-9.5&quot;</td>
<td>7&quot;</td>
<td>United States</td>
<td>(146)</td>
</tr>
<tr>
<td>Pleocoma crinita</td>
<td>Pleocominae</td>
<td>Aug.-Sept.</td>
<td>—</td>
<td>9-21&quot;</td>
<td>12.5&quot;</td>
<td>United States</td>
<td></td>
</tr>
<tr>
<td>Lichnanthe rathvoni</td>
<td>Glaphyrinae</td>
<td>May-July</td>
<td>—</td>
<td>3-10&quot;</td>
<td>6.4&quot;</td>
<td>United States</td>
<td></td>
</tr>
<tr>
<td>Phyllophaga ephilita</td>
<td>Melolonthina</td>
<td>June</td>
<td>19.5 days</td>
<td>2-6&quot;</td>
<td>3.3&quot;</td>
<td>United States</td>
<td>(136)</td>
</tr>
<tr>
<td>Phyllophaga hirticula</td>
<td>Melolonthina</td>
<td>July</td>
<td>27.2 days</td>
<td>7.5-23&quot;</td>
<td>14.6&quot;</td>
<td>United States</td>
<td>(136)</td>
</tr>
<tr>
<td>Polyphyla decemlineata</td>
<td>Melolonthina</td>
<td>June</td>
<td>—</td>
<td>5-7.5&quot;</td>
<td>6.5&quot;</td>
<td>United States</td>
<td></td>
</tr>
<tr>
<td>Melolontha hippocastani</td>
<td>Melolonthina</td>
<td>August</td>
<td>38-40 days</td>
<td>—</td>
<td>—</td>
<td>Switzerland</td>
<td></td>
</tr>
<tr>
<td><em>M. hippocastani &amp; M. melolontha</em></td>
<td>Melolonthina</td>
<td>—</td>
<td>—</td>
<td>14-16&quot;</td>
<td>—</td>
<td>Prussia</td>
<td>(153)</td>
</tr>
<tr>
<td>M. melolontha</td>
<td>Melolonthina</td>
<td>Mar.-Aug.</td>
<td>5-6 wk.</td>
<td>—</td>
<td>12-14&quot;</td>
<td>England</td>
<td>(45)</td>
</tr>
<tr>
<td>Amphimallon majalis</td>
<td>Melolonthina</td>
<td>May-June</td>
<td>15 days</td>
<td>2-10&quot;</td>
<td>—</td>
<td>United States</td>
<td>(60)</td>
</tr>
<tr>
<td>Costelytra zealandica</td>
<td>Melolonthina</td>
<td>Oct.</td>
<td>6 wk.</td>
<td>—</td>
<td>12&quot;</td>
<td>New Zealand</td>
<td>(33)</td>
</tr>
<tr>
<td>Cochliotis melolonthoides</td>
<td>Melolonthina</td>
<td>Feb.-Sept.</td>
<td>14 wk.</td>
<td>12&quot;-3&quot;</td>
<td>—</td>
<td>Tanganyika</td>
<td>(78)</td>
</tr>
<tr>
<td>Anomala vetula</td>
<td>Rutelinae</td>
<td>Nov.-Jan.</td>
<td>30 days</td>
<td>9-12&quot;</td>
<td>—</td>
<td>South Africa</td>
<td>(13)</td>
</tr>
<tr>
<td>Anomala orientalis</td>
<td>Rutelinae</td>
<td>June-July</td>
<td>14 days</td>
<td>3-12&quot;</td>
<td>—</td>
<td>United States</td>
<td>(51)</td>
</tr>
<tr>
<td>Phyllopertha horticola</td>
<td>Rutelinae</td>
<td>April-May</td>
<td>4 wk.</td>
<td>.8-3.8&quot;</td>
<td>2&quot;</td>
<td>England</td>
<td>(105)</td>
</tr>
<tr>
<td>Popillia japonica</td>
<td>Rutelinae</td>
<td>May-June</td>
<td>14 days</td>
<td>—</td>
<td>—</td>
<td>United States</td>
<td>(155)</td>
</tr>
<tr>
<td>Cyclocephala immaculata</td>
<td>Dynastinae</td>
<td>May-June</td>
<td>16 days</td>
<td>3-6.5&quot;</td>
<td>3.6&quot;</td>
<td>United States</td>
<td>(136)</td>
</tr>
<tr>
<td>Euetheola rugiceps</td>
<td>Dynastinae</td>
<td>Aug.-Sept.</td>
<td>14 days</td>
<td>—</td>
<td>—</td>
<td>United States</td>
<td>(125)</td>
</tr>
<tr>
<td>Cotinis texana</td>
<td>Cetoniinae</td>
<td>May-June</td>
<td>—</td>
<td>2-5&quot;</td>
<td>—</td>
<td>United States</td>
<td>(110)</td>
</tr>
<tr>
<td>Cotinis nitida</td>
<td>Cetoniinae</td>
<td>May-June</td>
<td>16-18 days</td>
<td>3-8&quot;</td>
<td>—</td>
<td>United States</td>
<td>(31)</td>
</tr>
</tbody>
</table>
has a one-year life cycle in Manchuria and Korea. In New Zealand, *Costelytra (Odontria) zealandica* (White) also has a one-year life cycle [Dumbleton (33)].

In the Rutelinae, few detailed studies have been made of the length of cycle for species belonging to the Rutelini. Hoffman (71), working in Kansas, U.S.A., reports a two-year life cycle for *Pelidnota punctata* (Linnaeus). My work in Kentucky indicated that this species and *Parastasia brevipes* (LeConte) each have a two-year life cycle (139). Hayes (65) reared 21 individuals of *Cotalpa lanigera* (Linnaeus) and found that this species has either a two- or three-year life cycle.

Because of the great economic importance of the Anomalini, many workers have made detailed studies of their life cycles (13, 15, 51, 57, 64, 104, 105). *Popillia japonica* Newman, *Anomala orientalis* Waterhouse, *Anomala kansana* Hayes and McColloch, *Anomola innuba* (Fabricius), *Anomala nigropicta* Casey and *Strigoderma arboricola* (Fabricius) all have one-year life cycles in the United States. *Phyllopertha horticola* (Linnaeus) has a one-year life cycle in Sweden [Brammanis (14)] and England [Raw (129); Milne (105)]. Friend (51) states that a few larvae of *Anomala orientalis* Waterhouse have a two-year life cycle in Connecticut. The same is true for *Anomala albopilosa* Hope in Japan [Nitto & Tachibana (113)].

Species of Anomalini having a two-year life cycle include *Anisoplia segetum* Herbst in Germany [Korschefsky (84)] and *Anomala vetula* Wiedemann in South Africa [Bradford (13)].

Little information is available about the life cycles of species belonging to other tribes of the Rutelinae. *Hylamorpha elegans* (Burmeister), belonging to the tribe Anoplognathini, is said to have a one-year life cycle in southern Chile [Duran (35)]. Mitchell (106) states that in Rhodesia *Adoretus* sp. (belonging to the Adoretini) also has a one-year life cycle.

In the United States, a number of species belonging to the Dynastinae such as *Cyclocephala immaculata* Olivier, *Euetheola rugiceps* (LeConte), *Ligyrus gibbosus* DeGeer and *Xyloryctes satyrus* (Fabricius) have one-year life cycles (63, 65, 125, 136, 138). My work indicates that *Dynastes tityus* (Linnaeus) has a two-year life cycle. Gressitt (58) studied *Oryctes rhinoceros* (Linnaeus) in the Palau Islands where there are no discernible climatic seasons. He found that, given favorable conditions, more than three generations may develop in one year.

Detailed rearing work by Plank (126) in Puerto Rico shows that the average length of the complete life cycle of *Strategus quadrifoveatus* (Palisot de Beauvois), from egg to first oviposition is 595 days. My studies in North Carolina, indicate that *Strategus antaeus* (Fabricius) has a two-year life cycle.

In northern Venezuela, *Podischnus agenor* (Olivier) apparently has a one-year life cycle, according to Guagliumi (59). In France, *Pentodon punctatus* Villers has a one- or two-year life cycle [Martelli (101)]. *Pentodon idiota* Herbst is said to have a three-year life cycle [Tchouvakhine (158)].

Such genera of the subfamily Cetoniinae as *Colinis, Euphoria, Trichio-
tins and Valgus, all of which occur in the United States, have one-year life cycles (31, 65, 70, 110, 140). Osmoderma erimicola has a two- or three-year life cycle depending on latitude [Hoffman (72)]. Gnorimus octopunctatus Fabricius, which occurs in Germany, has either a two- or three-year life cycle according to Korschensky (84).

**Mating Habits**

Mating between males and females of the same species is the usual thing among scarabaeids and, in fact, the sclerotized, accessory genital processes of both male and female are so constructed that cross-mating between most species is physically impossible. However, in the case of closely related species some evidence has been found that cross-mating does occur and that hybrids may be produced.

Some years ago, in examining many thousands Phyllophaga adults at the Madison, Wisconsin, Federal White Grub Laboratory, we ran across a few individuals, perhaps one in 5000, which appeared to represent a cross between Phyllophaga hirticula (Knoch) and Phyllophaga rugosa (Melsheimer). When one considers that the male Phyllophaga must find his mate at night, from among thousands of individuals often including some six or more other species, all feeding on the same tree, the wonder is that more such hybrids are not produced.

Failure to find morphological differences between larvae of Cyclocephala immaculata Olivier and Cyclocephala borealis Arrow, two closely related, common dynastine species, once led me to investigate the possibilities of interbreeding. In the laboratory, males of C. borealis mated freely with females of C. immaculata. Eggs were laid and appeared to develop normally but the fully formed larvae were never able to emerge. In comparable matings between beetles of the same species, development proceeded normally.

Mating sites.—Choice of mating sites varies with the subfamily and from genus to genus within some subfamilies. Beetles of the genus Geotrupes (Geotrupinae) and of Plecocoma (Pleocominae) mate in burrows in the soil [Howden (75); Smith & Potts (157)]. Geotrupes splendidus (Fabricius) mates in the fall, but eggs are not laid until the following spring (75). Similar habits for Plecocoma have been found in California and Oregon [Ritcher & Beer (146)].

Among the Melolonthinae, many species of Serica, Diplotaxis, and Phyllophaga mate at night while the female continues feeding on foliage. Other melolonthine beetles such as Hoplia and Macroductylus mate on flowers in the daytime. Among the Dynastinae, mating of some genera such as Ligyrus occurs in the soil. Cumpston (28) found that adults of Heteronychus sanctae-helenae Blanchard and Metenastes vulgivagus Olliff copulate beneath the surface of the ground. Other genera such as Cyclocephala mate on the surface of the soil with many males fighting for possession of a single female.

Of the Cetoniinae, genera such as Trichiotinus and Trigonopeltastes mate on flowers. In Valgus, mating occurs within termite galleries in stumps or fallen trees.
INTERRELATIONSHIPS WITH OTHER INSECTS

Scarabaeids exhibit a number of interesting relationships with other insects, in addition to those with insect parasites and predators which will be discussed in a later section. Some scarabaeids are actually predaceous on other insects while many species of the Cetoniinae are myrmecophilous or termitophilous.

Of the Coprinae, Canthon deplanatus var. fastuosus Harris is predaceous in Brazil upon the queen ants of Atta spp. using the dead body of the female as a component of the ball in which its larva later develops (from correspondence with E. Navajas). Canthon conformis Harris and Canthidium sp. seem to be occasional predators of the same ants. According to Pereira (122) Haroldius philippensis Pereira was found associated with ants of the genus Diacamma by P. J. Darlington of Harvard, on Luzon Island. Haroldius heimi Wassman has been found in nests of Pheidole latinoda.

Aphodius porcus Horn is a predator in the egg cavity of Geotrupes stercorearius Linnaeus [Chapman (20)]. After destroying the egg of the Geotrupes, this aphodian lays its eggs in the dung mass which the geotrupid had provided for its own larva. What appears to be a similar case, involving Aphodius lividus (Olivier) as a “parasite” of Onthophagus medorensis Brown, is reported by Howden (74).

Among the Troginae, larvae of two species of Trox, Trox procerus Harold and Trox suberosus Fabricius, are known to prey on grasshopper eggs and are of considerable economic importance [van Emden (40)].

Beetles of several genera of the subfamily Acanthocerinae are termitophilous [Hesse (68)]. Philharmostes is associated with termites in Madagascar and Costa Rica and two species of Acanthocerus are associated with termites in Brazil. Both larvae and adults appear to feed on rotten wood [Ohaus (114)].

Numerous genera of the Cetoniinae are known to be associated with ants or termites throughout the world [Wheeler (169)]. Myrmicophilous genera include Cremastocheilus in the United States (169); Plagiochilus and Myrmecochoilus in South Africa [Wasmann (168)]; Placodius, Tricholoplius, Scaptobius and Lissogenius in South Africa [Peringuey (123)]; and Potosia cuprea Fabricius in Germany [Korschefsky (84)]. Termitophilous genera are Coenochilus in South Africa [Wheeler (169)], and Valgus in many parts of the world.

Wheeler concludes that beetles of the genus Cremastocheilus are degenerate symphyles which may have once been of use to the ants but are now persecuted intruders (synethrans). The larvae of Cremastocheilus and of certain Euphoria apparently feed within the vegetable debris of the ant colony. Both genera are usually associated with ants of the genus Formica.

Lee Townsend of the University of Kentucky and the writer have made numerous observations on the biology of Valgus canaliculatus (Fabricius) and Valgus seticollis (Beauvois), both common in the nests of the termite Reticulitermes flavipes (Kollar). A third species, Valgus californicus Horn, is
found in California associated with termites of the genus *Zootermopsis nevadensis* (Hagen) [Linsley & Michener (94)].

All stages of *Valgus* may be found in decaying wood associated with termite colonies. The larvae apparently feed on the walls of the old termite galleries. Pupation of *Valgus canaliculatus* occurs in July and early August within small oval cells constructed of wood fragments or soil (140). Colonies of *V. canaliculatus* contain males and females in almost equal numbers; colonies of *V. seticollis* usually contain a great majority of females.

**Natural Enemies**

Pleurostict scarabaeids are attacked by many parasites and predators. Among the parasites are mites, Diptera, Hymenoptera, bacteria, fungi, protozoa, and nematodes. Common predators are various mammals, fish, birds, amphibians and certain Coleoptera, Hymenoptera, and Diptera. Of the four life stages, larvae and adults have the greatest number and variety of natural enemies.

*Insect parasites.*—Insect parasites attacking melolonthine, ruteline, and dynastine larvae include many species of Tiphiidae and Scoliidae, and numerous species of Tachinidae [Clausen (20)]. Less common insect parasites of these scarabaeid larvae are one species belonging to the Pelecinidae [Forbes (48)], one ichneumonid [Davis (30)], and several species of bombyliids (20). Parasites of adult scarabaeids belong mainly to the family Tachinidae but include several species of pyrgotids and a few species of sarcophagids.

No insects are known to be parasitic on scarabaeid eggs but several dipterous parasites of pupae have been recorded. Handlirsch (61) describes a nemestrinid parasite on pupae of *Amphimallon solstitialis* Linnaeus in Europe. Asilid and bombyliid larvae have been found parasitizing *Phyllophaga* pupae in the United States (30, 136, 147).

Tiphiid and scoliid wasps are fossorial, seeking out grubs both in the soil and in decaying wood [D’Emmerez de Charmoy (41); Clausen (21)]. Eggs are deposited singly and the parasite larvae feed externally on the paralyzed scarabaeid grubs. Host identity can often be determined, at least to genus, by examination of the head capsule, usually found attached to the parasite cocoon.

Some of the factors governing host selection are host size, host habitat, and synchronization with the host’s biology [Dumbleton (33) and Given (54)]. These principles have been utilized in attempted biological control of such important pests as the Japanese beetle *Popillia japonica* (Newman), *Clemora smithi* (Arrow), *Costelytra zealandica* (White), and *Oryctes* spp. (22, 41, 54, 108). Members of the genus *Tipha* tend to be limited to a host genus, or to closely related genera [Gardner & Parker (53); Clausen, King & Tera-nishi (22)]. In Australia, Burrell (17) found several genera of Thynninae exhibiting similar preferences for grubs of a certain genus.

Some Tiphiiids and scoliids are remarkably specific as to host [Lloyd (95)].
and Guagliumi (59). Several species of thynnid parasites occurring in Chile are each restricted to a single host species [Lloyd (95)]. According to King & Holloway (82), in the Orient, strains of *Tiphia popilliavora* Rohwer which are indistinguishable morphologically differ in their distribution and seasonal appearance and select different host species of *Popilia*.

**Bacteria, fungi and rickettsiae.**—Larvae of soil-inhabiting scarabaeids are often attacked by bacterial disease, and most workers with this group of insects have observed epizootics at one time or another. Davis in his review of the natural enemies of *Phyllophaga* states that up to 1919 only one bacterial disease (that caused by *Micrococcus nigrofaciens* Northrup) of white grubs was known to occur in the United States although at least two diseases of related species were known in Europe (30).

Dutky, in 1940, described two new sporeforming bacteria, *Bacillus popilliae* Dutky (Type A) and *Bacillus lentimorbis* Dutky (Type B), causing milky diseases in the Japanese beetle (36). These have since been used widely in the United States in the biological control of the beetle [Beard (6)]. According to Dumbleton a native bacillus, distinct from *B. popilliae*, causes a milky disease in larvae of *Odontria sealandica* White, in New Zealand (34). Recently, Beard has described two milky-disease bacteria from Australian scarabaeids, *Bacillus lentimorbis* var. *Australis* Beard affecting *Sericesthis pruinosa* (Dalman) and *Bacillus euloomarahae* Beard affecting the introduced *Heteromychus sanctae-helenae* Blanch (7).

The fungus *Metarrhizium anisopliae* (Metchnikoff) is an important factor in white-grub control in several continents. In one area of Algeria, Moutia found 90 per cent of the *Geotrogus* larvae attacked (107). In the United States, Nichol (110) reports this fungus parasitic on larvae of *Cotinis texana* Casey, and Philips and Fox (125) mention all stages of the dynastid *Euetheola rugiceps* (LeConte) as susceptible to infection. The same fungus is known to infect the rhinoceros beetle (*Oryctes*). In Germany, Schaerffenberg found that * Beauveria densa* (Link) could cause up to 90 per cent mortality of *Melolontha* larvae (150). The spectacular *Cordyceps* fungus, mentioned by Davis, has long been known as a sporadic parasite of scarabaeid larvae (30). Apparently several species of *Cordyceps* are involved.

*Coxiella popilliae* Dutky & Gooden, the cause of a rickettsial disease of *Popillia japonica* and *Phyllophaga* larvae, was described in 1952 (37). According to Krieg (85) "lorsch" disease of *Melolontha* larvae in Europe is caused by the same or a closely related rickettsia, which he has described as *Rickettsia melolontha* Krieg.

**Insect predators.**—Major insect predators of scarabaeids are certain Asilidae, Tabanidae, Carabidae, Elateridae, Histeridae, and Formicidae. Less common insect predators belong to the Ithonidae (Neuroptera), Coenomyiidae, Mydidae and Passalidae. Larvae of scarabaeids are most subject to attack.

Asilid larvae are important predators of soil-inhabiting scarabaeids (21).
Davis lists 13 species as probable predators of *Phyllophaga* larvae (30). In Australia, Miller records larvae of two native asilids as predators of *Odontria* larvae (103). Lupo mentions *Asilis* sp. as predaceous on *Anomala* larvae (98).

Several species of tabanid larvae appear to be predaceous on *Phyllophaga* and *Cyclocephala* larvae (30). In two instances I have observed *Coenomyia* (Coenomyiidae) larvae attacking scarabaeid larvae, once in North Carolina attacking a *Trox* larva and once in Oregon attacking a *Dichelonyx* larva.

Balduf (5) reviews the literature on Carabidae, Elateridae and Histeridae all important predators of scarabaeids. Carabid adults prey on both adults and larvae, and sometimes on eggs. Gyrisco *et al.* (60) found carabid predators of *Amphimallon majalis* Razoumowsky extremely abundant. Grubs in an experimental plot were largely destroyed by *Harpalus pennsylvanicus* DeGeer and *Harpalus erraticus* Say was an important egg predator. According to Gressitt (58) carabids prey on both adults and larvae of the coconut rhinoceros beetle, *Oryctes rhinoceros* (Linnaeus), in the Palau Islands.

Elaterid larvae of a number of genera prey on scarabaeid larvae in soil, decaying wood and in dung. *Alaus* and *Ctenicera* are predaceous on *Oryctes* larvae [Freiderichs (50)], as are also *Pyrophorus* larvae [O’Connor (115)]. Xambeau (173) mentions *Corymbites cupreus* Fabricius consuming larvae and pupae of *Aphodius*. Wolcott (171) mentions larvae of *Pyrophorus luminator* Illiger as important predators of May beetle grubs in Puerto Rico.

Importance of histerids as predators of *Oryctes* larvae in and their use in biological control of *Oryctes* is discussed by Gressitt (58) and O’Connor (113). Both adults and larvae of some species feed on first instar *Oryctes*. Lupo records larvae of *Hister major* Linnaeus attacking larvae of *Anomola ansonia* var. *neopolitana* Reitter (98). Balduf (5) reviews records of histerids predaceous on larvae of *Aphodius*, *Teuchestes*, *Oxythhyrea* and *Cetonia* in Europe.

Several writers mention the importance of ants as predators of eggs and young larvae of scarabaeids (98). In 1926 Tillyard worked out the life history of a neuropteron, *Ithon fusca* Newman, which is a predator of melolonthine larvae in Australia (160, 161). Jepson (78) mentions finding larvae of a passalid, *Didimus sansibaricus* Harris which were feeding on *Cochliotis* larvae, in Tanganyika.

**Vertebrate predators.**—In some insular areas amphibians are important predators of scarabaeids. The Surinam toad, *Bufo marinus* Linnaeus, introduced into Puerto Rico about 1920 by Box (12) soon became so numerous that white grubs entirely disappeared from cane fields [Wolcott (171)]. A ground lizard, *Ameiva exsul* Cope, destroys eggs and larvae of May beetles in the same island. In Illinois, frogs, toads, and salamanders are mentioned as predators of *Phyllophaga* (30).

Many writers record instances in which birds are predaceous on both larvae and adults of soil-inhabiting scarabaeids. Moutia (107) states that in
France thousands of insectivorous crows, *Trypanocorax frugileus* Linnaeus, were observed feeding on larvae of *Melolontha melolontha* Linnaeus. In Morocco, he reports that the cattle egret, white stork, and blackbirds feed on *Amphimallon, Rhisotrogus* and *Anoxia* larvae. Other birds mentioned as predaceous on scarabaeid larvae include domestic fowl, meadow larks, owls, starlings, robins, song sparrows, grackles, pheasants, cat birds, woodpeckers, gulls and thrushes (30, 31, 51, 60, 125).

Among important mammalian predators are moles, hogs, shrews, coyotes, ground-squirrels, badgers, field mice, racoons, foxes, and skunks (30). In the United States the skunk is probably the most important predator. In the eastern half of the United States it feeds voraciously on *Phyllophaga* and *Amphimallon* larvae (30, 60). In Oregon, the skunk *Mephitis occidentalis* Baird is the main predator of adult *Pleocoma*. I have seen orchards in the Hood River Valley where as many as 25 adults have been dug from their burrows, beneath a single apple tree.
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