Revision of the New World Lady Beetles of the Genus *Olla* and Description of a New Allied Genus (Coleoptera: Coccinellidae)

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ABSTRACT   The taxonomic and nomenclatural history of the genus *Olla* Casey is re-viewed. The polyphyletic nature of the Neotropical coccinelline fauna is discussed, and a diagnostic key to subgroups within the former Synonychini (sensu Blackwelder) is pro-vided. *Olla* is shown to be part of a monophyletic assemblage of primarily Neotropical Coccinellini, united by shared characteristics of the genitalia and larval armature. Four *Olla* species are recognized: *O. v-nigrum* (Mulsant), and three new species, *O. roatanen-sis, O. timberlakei,* and *O. hageni.* A new allied genus, *Cirocolla,* is proposed to accom-modate the species *Daulis conspicillata* Mulsant (paralectotype designated). *Neda cardi-nalis* (Erichson) is transferred to *Mononeda* Crotch. A hypothesis of the cladistic relations within *Olla* is presented using the sister genus *Cirocolla* as an outgroup. All taxa are described and keyed. Geographic distributions, synonymies, and illustrations of key char-acteristics are provided. Notes on biogeography, prey–host plant records, and the distri-bution and inheritance of elytral color patterns are included. The immature stages of *O. v-nigrum* and *O. hageni* are illustrated and compared.

KEY WORDS   Insecta, *Olla,* phylogeny, systematics

THIS WORK TREATS the evolution and classifica-tion of *Olla* Casey and a closely allied new genus. *Olla* is a small genus of coccinelline lady beetles which is widely distributed in temperate and tropical America. It also occurs on Guam, Hawaii, and Midway, where *Olla v-nigrum* (Mulsant) was introduced for biological control purposes (Timberlake 1943, E. Chapin 1965, Gordon 1985). The current revision recognizes four species of *Olla: O. v-nigrum* (Mulsant), plus three new species, *O. timberlakei, O. hageni,* and *O. roatanensis.* Members of the genus are primarily psyllid and aphid predators and prefer arboreal habitats or tall shrubs. In North Amer-ica, the endemic species *O. v-nigrum* is widely acknowledged as a key predator in commercial walnut and pecan groves (Bugg & Dutcher 1989).

The four species of *Olla* are extremely similar in habitus (Fig. 1–4) and have often been con-fused by previous authors who did not examine the genitalia. A revision of this important genus is therefore long overdue.

A new genus, *Cirocolla,* is proposed to accom-modate the single species *Daulis conspicillata* Mulsant, which is determined to be *Olla*'s clos-est relative among the described coccinellids of the New World. This species has been misclas-sified for over a century in *Cycloneda* Crotch (=*Daulis* Mulsant), a genus to which it is only very distantly allied. *Cirocolla* is recorded from only a few scattered localities in northern South America, and nothing is known about its habitat or prey preferences. Although this genus is cur-rently monotypic, it probably will not remain so for long as the Neotropical fauna becomes better known.

Systematic Placement of *Olla* and Allied Genera; Polyphyletic Nature of the Neotropical Coccinelline Fauna

Olla and *Cirocolla* form part of a monophyletic assemblage of primarily Neotropical Coccinel-lini, including *Spiloneda* Casey, *Paraneda* Timberlake, *Clynis* Mulsant, *Neda* Mulsant, *Mononeda* Crotch, *Neoharmonia* Crotch, *Proc-ula* Mulsant, and several as yet undescribed gen-era (Vandenberg 1987). Most of the species placed in *Cycloneda* also belong in this sub-group, although not *Cycloneda sanguinea* L. (the genotype) or any of its North American conge-ners.

Olla and its allies are distinguished by a suite of genitalic characters which are detailed in the following "Key to Major Groups. . . ." In addi-tion, all the known larvae share a fused biconical configuration of both the dorsal and dorsolateral abdominal processes (Fig. 5 a–f). This larval
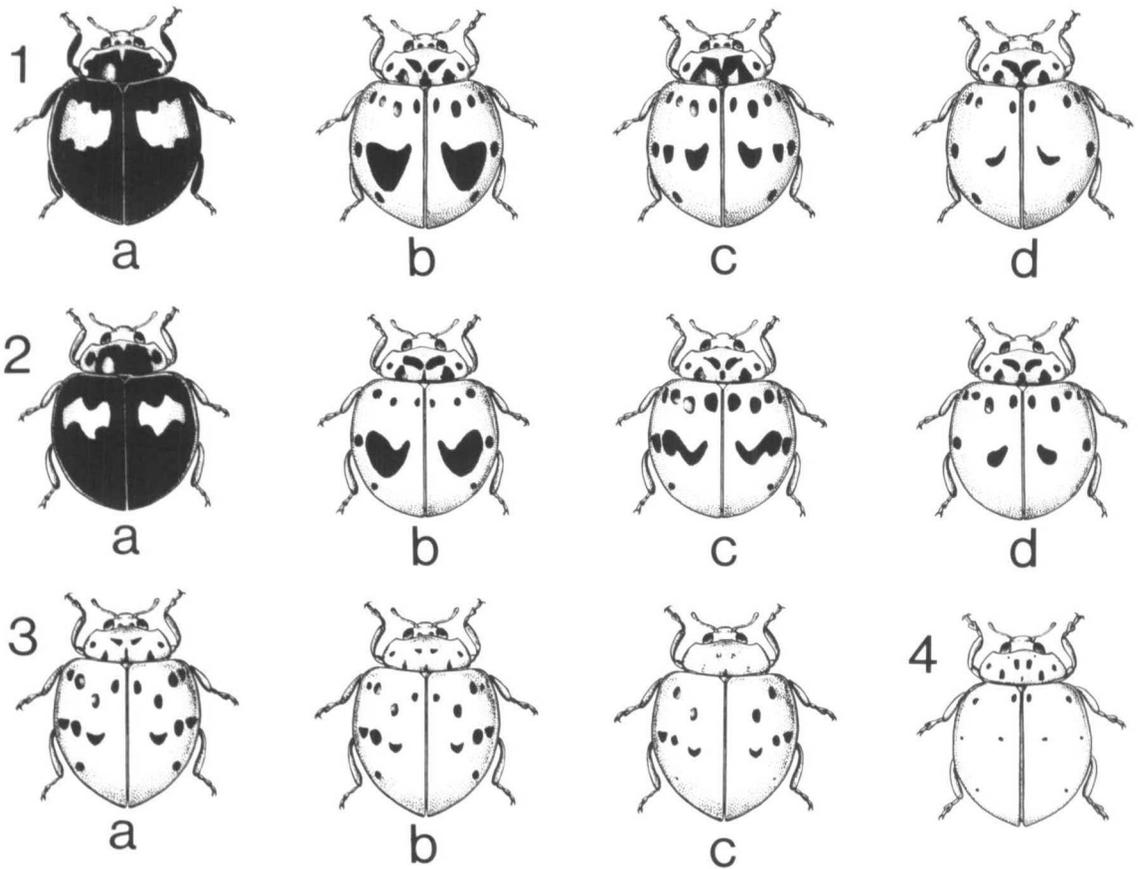
Fig. 1–4. Dorsal habitus views of *Olla* spp., males. (1) *O. v-nigrum:* (a) Melanic colorform. (b–d) Pale colorforms. (2) *O. timberlakei:* (a) Melanic colorform ("Coccinella No. 18" [Gorham 1982]). (b) Specimen from Temax, Yucatan, Mexico. (c) Holotype. (d) Specimen with reduced maculation from Villa de Cura, Venezuela. (3) *O. hageni:* (a) Fully maculate individual. (b) Holotype (c) Common aberration with reduced maculation. (4) *O. roatanensis,* holotype.

character is particularly useful for separating misclassified species (allied to *Olla*) from true *Cycloneda* (Fig. 6), but unfortunately, an analogous configuration occurs independently in the unallied genus *Eriopis* Mulsant. The ultimate diagnostic value of such larval characters must await a more complete investigation of the entire New World coccinelline larval fauna, particularly of the poorly studied Neotropical region.

Olla and allies form a very closely knit group as evidenced by the high degree of similarity found within the character systems discussed above; however, the adults present a diverse facies suggesting rapid radiation into a multitude of different niches. Indeed, the supremacy of this subgroup of predacious coccinellines is relatively unchallenged by its sister lineages in the Neotropics, except in the cooler upland habitats and the more temperate or drier parts of the far south.

Currently, there is no formal taxonomic designation for any of the major subgroups within the Coccinellini. Historically, many authors grouped

Olla along with various other tropical coccinellines in a separate tribe Synonychini, but in 1968 Sasaji introduced a new classification of the family Coccinellidae which synonomized Synonychini with Coccinellini. This action has been widely accepted by most modern authorities (Fursch 1990).

Although the New World genera previously placed in Synonychini coincide with many of those allied to *Olla*, it is clear this tribe was simply a random collection of rounded or shield-shaped species (Vandenberg 1987) with no particular affinity to the Old World *Synonycha* Mulsant (type genus of the tribe). By the opposite criterion, the genera *Clynis* and *Neoharmonia*, which are related to *Olla* (Iablokoff-Khnzorian 1984, Vandenberg 1987), were excluded from Synonychini because of their more elongate body forms.

Studies that attempted to unite the entire synonychine complex on the basis of genitalic characters (Dobzhansky 1926, Lall & Kanakavalli 1960) have provided diagnoses which clearly ap-
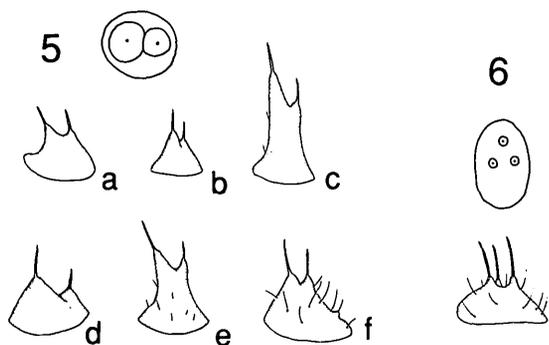
Fig. 5 and 6. Larval armature of fourth-instar Coccinellini (views of right dorsal setose process, abdominal segment 4). (5) *Olla* and allies. Above, generalized topographical view showing primary setae. Below, right lateral views. (a) *Olla hageni.* (b) *Paraneda gutticollis* (Mulsant). (c) *Cycloneda graphiptera* (Mulsant) (*Olla* lineage near *Neda;* currently misclassified). (d) *Mononeda cardinalis* (Erichson), n. comb. (e) *Cycloneda conjugata* (Mulsant) (*Olla* lineage near *Neda;* currently misclassified). (f) *Neoharmonia venusta venusta* (Melsheimer). (6) *Cycloneda* spp. (sens. str.). Above, generalized topographical view showing primary setae. Below, *Cycloneda sanguinea.*

plied to only a minority of the included fauna and thus inadvertently confirmed the polyphyletic nature of the group. Among the synonychine fauna listed in Blackwelder's checklist (1945), *Cycloneda* s. str. and those species currently placed in *Erythroneda* Timberlake are more closely related to the holoarctic *Coccinella* L. than to *Olla* (Wilson 1926, Vandenberg & Gordon 1988). Other species included in the Synonychini would be best transferred to *Egleis, Mulsantina,* or a new allied genus; this group of New World lady beetles has its greatest diversity in the Neotropical realm (sensu Wallace 1876) but is largely restricted to temperate or upland habitats, with a single genus penetrating into North America. The Australian *Archegleis* Iablokoff-Khnzorian appears to be related to the New World *Egleis* and its allies taken collectively.

Edward Chapin (1941) observed that, within the New World representatives of Synonychini, there are "three or more definite types of genitalia present . . . to one of which each species can be assigned." Unfortunately, he was swayed by the similarity of body types found among the "synonychine" coccinellids and failed to attach proper significance to the genitalic categories he observed. The key presented below uses genitalic characters and the presence–absence of tibial spurs to distinguish three major divisions within the Synonychini and associates members of this former tribe with some of their close allies in Coccinellini (in the restricted sense of Blackwelder [1945]). Gordon (1985) can be consulted

for helpful illustrations of species exhibiting the different genitalic types.

Key to Major Groups Formerly Classified in the New World Synonychini (sensu Blackwelder 1945)

1. Genitalia typical of *Coccinella:* male with sipho constricted before apex, terminating in a membranous pouch and spicules, ejaculatory duct never protruding beyond apex; basal lobe tapered distally, often ogival or lanceolate; basal piece with base and length subequal. Female with portion of sperm duct modified to form an infundibulum which is flared at either or both ends
. . . . . *Cycloneda, Erythroneda,* and allies
Genitalia of another type: male with sipho not as above, tubular or tapered at apex, often with preapical projections or lobes, ejaculatory duct often protruding beyond apex; basal lobe variable, often with lateral margins sinuous or apex divided; basal piece variable in dimensions, often highly elongate. Female with sperm duct unmodified, or with a portion forming a simple sclerotized tubular sheath 2
2. Middle and hind legs lacking tibial spurs. Genitalia typical of *Mulsantina:* male with siphonal capsule feebly S-shaped with inner and outer arms subequal, attached at right angles to end of siphonal tube or with slight inward tilt of its main axis; sipho emerging from ventral side of basal lobe near base and curving well away from it; trabes strongly widening distally, apex deeply cleft; basal lobe with apex tapered, truncate, or knobbed, never bifurcate; lateral margins often sinuate. Female genitalia with sperm duct attached to distal end of bursa
. . . . *Egleis, Mulsantina,* and allies
Middle and hind legs with a pair of tibial spurs except in *Neoharmonia,* where spurs are lacking. Genitalia not as above: male with siphonal capsule never S-shaped, inner and outer arms dissimilar in size or shape, or both, siphonal capsule attached with outer arm in line with end of siphonal tube or with a slight eccentric tilt; sipho emerging from ventral side of basal lobe near apex and remaining approximately in line with it; trabes compressed along entire length or rarely somewhat dilated distally, apex entire or feebly depressed at middle; basal lobe with apex bifurcate except in *Clynis* and *Neoharmonia,* which have tapered, undivided apices; lateral margins of basal lobe approximately parallel-sided at least in basal half. Female genitalia with sperm
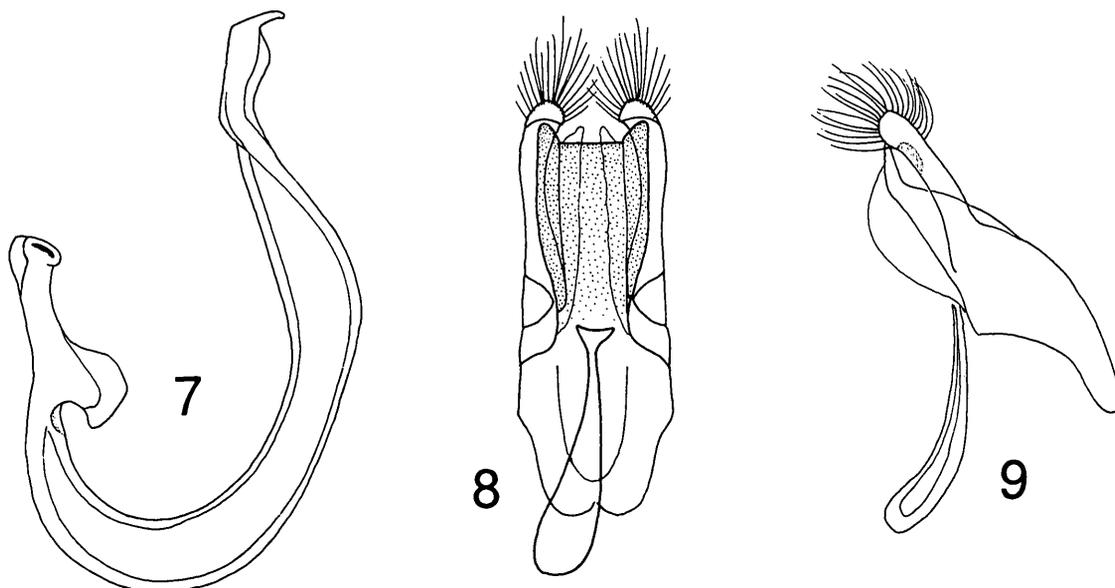
Fig. 7–9. Male genitalia of *Olla roatanensis*, holotype. (7) Lateral view of sipho. (8) Ventral view of phallobase. (9) Lateral view of phallobase.

duct attached to basal, distal, or me-
diodorsal part of bursa . . . . *Olla* and allies

Historical Review of *Olla* Casey

Olla was proposed by Casey in 1899. At the
time the genus was established, four species
names were included: *Olla abdominalis* (Say)
(originally described in *Coccinella*), *O. plagiata*
Casey, *O. sobrina* Casey, and *O. fenestralis*
Casey. *Coccinella abdominalis* Say was sub-
sequently designated as the type species by
Korchefsky (1932). The generic status of *Olla* has
been widely accepted among revisers with the
exception of Leng (1903), who initially placed it
as a subgenus of *Coccinella*. Although authors
have listed multiple species in *Olla*, of those
species previously described, only *O. v-nigrum*
(=*abdominalis*) is recognized as a valid name
within the genus. Other names have proven to be
synonyms of this species, misapplied names
originally referring to unrelated species (e.g.,
Coccinella oculata F. and *Coccinella binotata*
Say), or misclassified species.

Gorham (1892) described and illustrated what
he mistakenly believed to be a variety of the
species currently known as *O. v-nigrum* (=*ab-
dominalis*). This species was subsequently given
the name *Olla Gorhami* by Casey (1908) and is
listed in the catalogs of Korchefsky (1932) and
Blackwelder (1945). The same species was inde-
pendently described by both Mulsant (1850) and
Crotch (1874) as *Daulis conjugata* and *Cy-
cloneda antillensis*, respectively; it does not be-
long in *Olla* as currently recognized but falls
within the *Olla* lineage near *Neda*.

In his 1908 paper, Casey suggested that *Cy-
cloneda sallei* Mulsant should be assigned to
Olla and tentatively included *Coccinella macu-
losa* Gorham and *C. quichensis* Gorham as well.
None of these species fits the present concept of
Olla: *Cycloneda sallei* is another species whose
closest affinities lie with *Neda*, *Coccinella mac-
ulosa* is a synonym of a European species *Oeno-
pia conglobata* (L.) (Weise 1904), and *Coccinella
quichensis* belongs in the lineage containing *Eg-
leis* and *Mulsantina*.

Materials and Methods

Label data are quoted verbatim for all avail-
able type specimens except those already treated
by Gordon (1985) in his revision of the North
American Coccinellidae and in his catalog of the
Crotch collection of Coccinellidae (Gordon
1987). Only locality records, prey species, and
host plant associations are cited for nontype
specimens examined during the study; North
American distributions are briefly summarized
following Gordon (1985). Depositories of type
and other material examined are specified using
the abbreviations listed in the acknowledgment.

Genus *Olla* Casey
(Fig. 1–4, 7–33)

Olla Casey 1899: 93; Casey 1908: 405–6 (in
part); Leng 1920: 216; Korchefsky 1932: 288
(in part); Timberlake 1943: 24, 55; Black-
welder 1945: 453 (in part); Wingo 1952: 24; E.
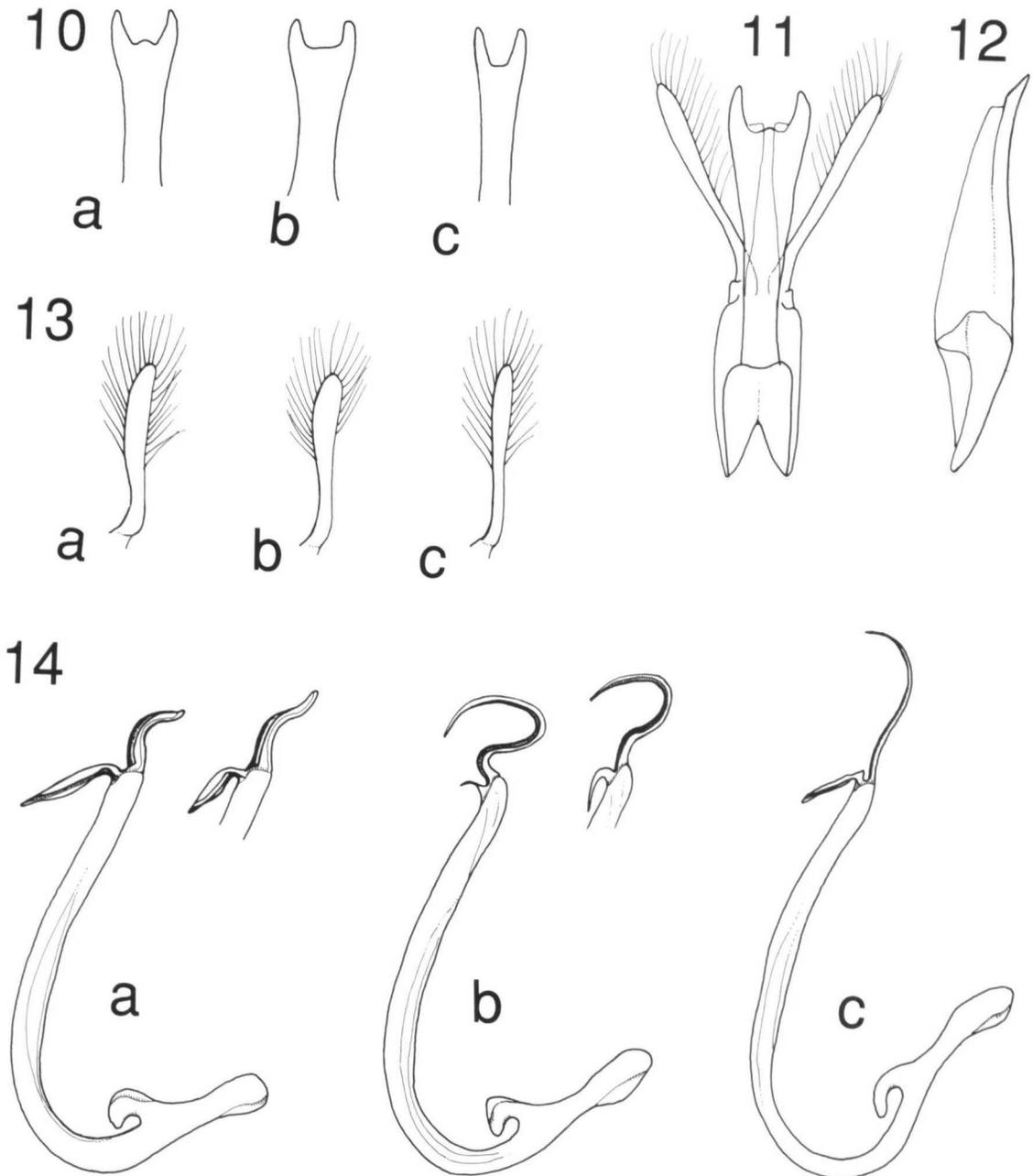Chapin 1965: 219; J. Chapin 1974: 64; Belicek
1976: 329; Gordon 1985: 826.

Fig. 10–14.   Male genitalia of *Olla* spp. (10) Basal lobes. (a) *O. v-nigrum.* (b) *O. timberlakei.* (c) *O. hageni.* (11) Ventral view of phallobase, *O. v-nigrum.* (12) Lateral view of phallobase, trabes and parameres removed, *O. v-nigrum.* (13) Paramere. (a) *O. v-nigrum.* (b) *O. timberlakei.* (c) *O. hageni.* (14) Sipho, lateral view. (a) *O. v-nigrum,* full structure, and apex only, showing range of variation. (b) *O. timberlakei:* left, holotype; right, apex only of specimen from Villa de Cura, Venezuela. (c) *O. hageni,* holotype.

Coccinella (Olla): Leng 1903: 197.

Type Species. *Coccinella abdominalis* Say, by subsequent designation of Korchefsky, 1932.

Description. Length, 3.2–6.2 mm. Form robust, circular to oval, moderately convex to hemispherical, slightly pointed posteriorly. Punctation on dorsal surface fine and even; punctures

slightly more pronounced on outer margin of elytron; surface between punctures distinctly shagreened on head and pronotum, nearly polished to shagreened on elytron. Species monomorphic or dimorphic in color pattern.

Pale color form (basic pattern) as follows (Fig. 1c): ground color of dorsal surface ivory, yellow,

Fig. 15–17. Female genitalia of *Olla* spp. Right lateral view with spermatheca at top of figure. (15) *O. v-nigrum*. (16) *O. timberlakei*. (17) *O. hageni*.

gray, or beige in life; often brown or parchment-colored in death. Outer margins of pronotum and lateral margin of elytron clear to light amber. Elytral suture reddish amber to blackish brown. Each elytral puncture accentuated with minute pinpoint of brown or black pigment; row of punc-

Fig. 18–22. Body parts of *Olla* spp. (18) Ventral view of abdomen, *O. roatanensis,* male holotype. (19) Same of *O. v-nigrum:* (a) Male. (b) Female. (20) Same of *O. timberlakei:* (a) Male. (b) Female. (21) Same of *O. hageni:* (a) Male. (b) Female. (22) Antenna of *Olla* spp.

tures bordering elytral suture and 2 rows adjacent to lateral margin more prominently marked. Dorsal spots brown or black, arranged in a characteristic pattern: head with 2 rounded median spots; pronotum with 7 spots, 1 at middle of each lateral third, 5 forming a disjunct or entire M in median third; each elytron with 8 spots, 4 in an uneven row near base (humerolateral, humeral, median, subsutural), 3 across middle (lateral, mediolateral, median), 1 near outer margin at apical ¼. Variations on dorsal maculation of pale color form derived from basic pattern through loss or fusion of spots (Fig. 1 b–d, 2 b–d, 3 a–c, 4). Ventral surface, including mouthparts and appendages, brown to yellowish brown, often marked with cream or yellow; hypomeron (=pronotal epipleuron), and elytral epipleuron same color as dorsal surface.

Melanic color form as follows (Fig. 1a and 2a): ground color of dorsal surface black or piceous; head diffusely darkened, entirely pale, or pale with 2 black spots; pronotum with an irregular white border on anterior and lateral margins, often with a white medial spur-shaped mark projecting posteriorly from anterior margin; each elytron with an irregular red to yellow mark on anterior half of disk. Ventral surface varying from uniformly yellowish brown to predominantly black with brown abdomen, tarsi, antennae, and
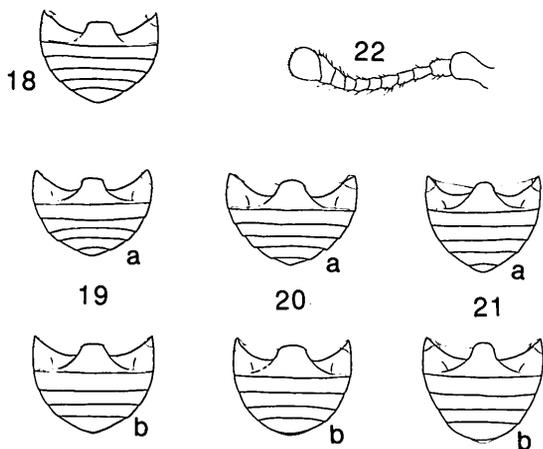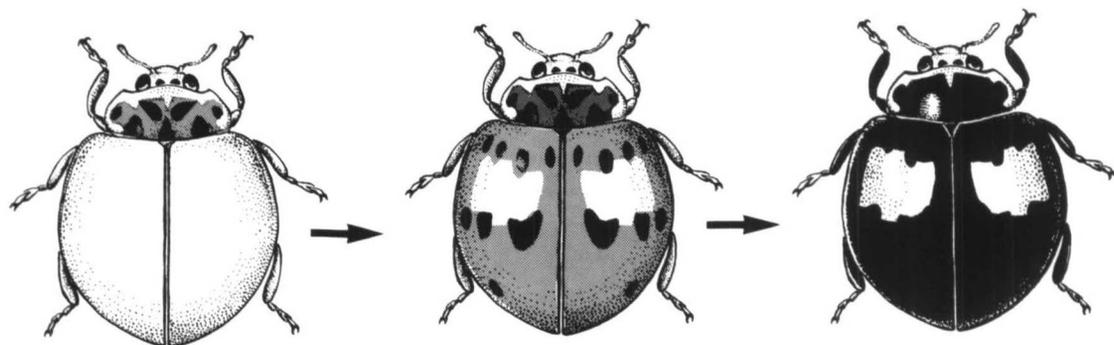
Fig. 23. Development of the dorsal color pattern in an individual of *O. v-nigrum* (heterozygote) from left to right: immediately after eclosion from pupa; several minutes after eclosion; fully melanized.

mouthparts, and variable cream-colored markings on metathorax.

Eyes finely faceted, separated by approximately twice the diameter of an eye; inner orbits parallel to weakly convergent or weakly divergent. Pronotum moderately convex; feebly explanate at extreme outer edge; lateral and basal margins rounded in outline. Elytron feebly explanate at outer margin with fine raised ridge moderately distinct. Antenna slightly longer than separation between eyes, composed of short, compact segments (Fig. 22); club not strongly expanded. Terminal segment of maxillary palp small and robust. Intercoxal process of prosternum with fine, raised ridge on outer margins, or pair of median carinae. Mesosternum shallowly emarginate at middle of anterior margin. Elytral epipleuron concave, descending externally, with or without faint foveae for reception of middle and hind femur, maximum width equal to from 1/5

to 1/7 width of body at base of abdomen. Apex of middle and hind tibia each with 2 spurs. Tarsal claw small with subquadrate basal tooth; claws of fore, middle, and hind tarsus of approximately equal length. Abdomen fairly short and broad (Fig. 18–21), subogival in outline, widest at or near suture between segments 1 and 2; form shorter and more tapered in male than in female. Abdominal segment 1 slightly longer to 1.5 times longer along midline than minimum distance between hind coxae; postcoxal line curved posteriad and laterad, closely parallelling posterior margin for most of length, fading before attaining lateral margin; oblique line present or absent. Abdominal segments 1–4 with hind margins linear to weakly curved; male with hind margin of abdominal segment 5 truncate or shallowly, roundly emarginate, exposing segment 6; female with hind margin of abdominal segment 5 ogival, covering all or most of segment 6. Male genitalia
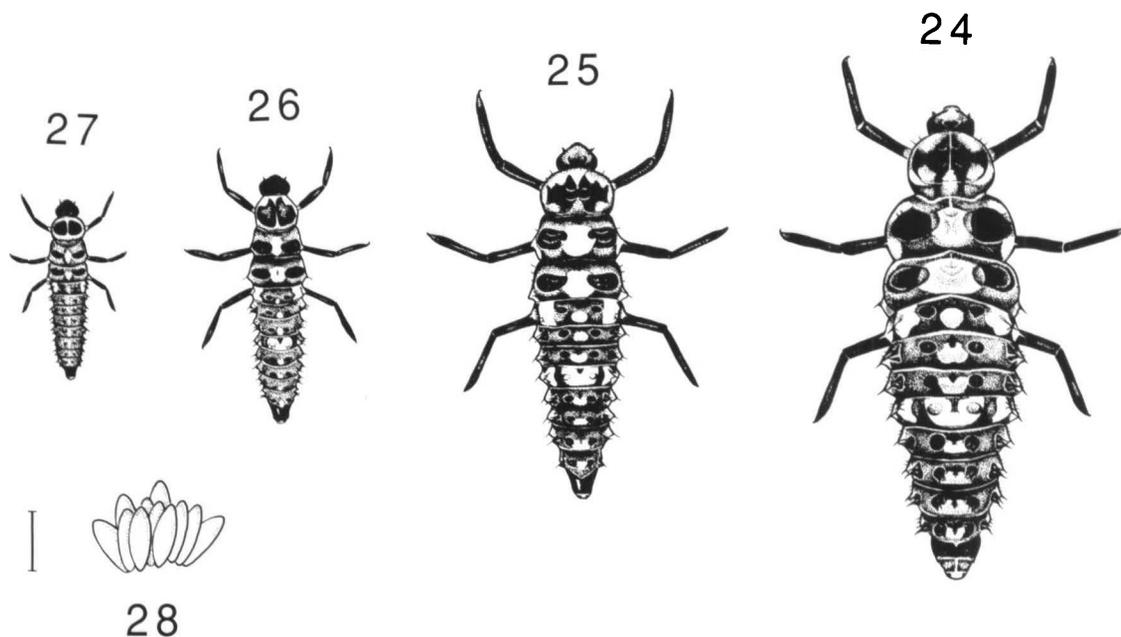

Fig. 24–28. Immature stages of *O. v-nigrum*. (24) Fourth instar. (25) Third instar. (26) Second instar. (27) First instar. (28) Egg mass. Scale line, 1.0 mm.
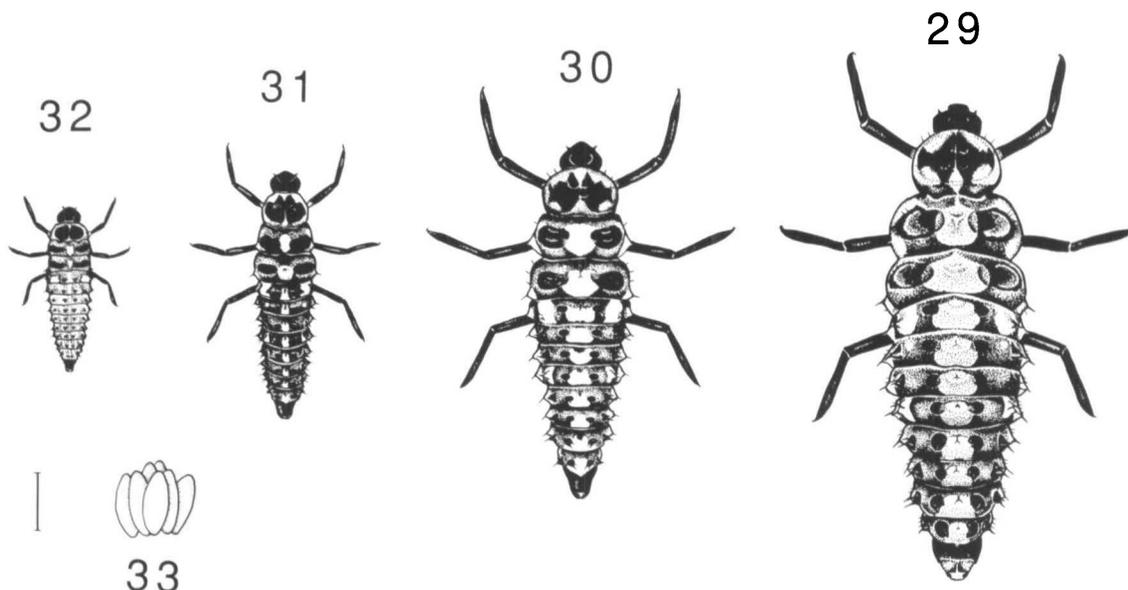
Fig. 29–33. Immature stages of *O. hageni.* (29) Fourth instar. (30) Third instar. (31) Second instar. (32) First instar. (33) Egg mass. Scale line, 1.0 mm.

with apex of basal lobe divided (Fig. 8 and 10); apical projections roughly triangular in outline, well separated and approximately parallel in orientation. Sipho with knifelike (Fig. 7) or whiplike (Fig. 14 a–c) apex terminating in median orifice; sclerotized subapical projection free or enwrapping apex. Siphonal capsule with outer arm narrow, elongate, crested on outer edge; inner arm short, curved. Female genitalia (Fig. 15–17) with curved cornu; distinct ramus with moderate-sized accessory gland; small, poorly differentiated nodulus set into concavity in lower part of spermatheca; sperm duct fine, fragile, easily collapsed, without sclerites, situated dorsal to bursa and attached dorsally where bursa narrows (configuration of female genitalia not known for *O. roatanensis*).

Remarks. *Olla* can be distinguished from most coccinellines by the general body form and dorsal color patterns. *Egleis, Mulsantina,* and allied genera may be confused with the pale color form of *Olla,* but they lack the tibial spurs and the genitalia have a radically different form (see "Key to Major Groups. . .").

Among its closer allies, *Olla* is most easily confused with some of the small spotted species in or near *Neda.* Even at this taxonomic level, the genitalia can provide an effective means of separation. *Neda* and its closest allies have the sperm duct of the female genitalia more robust and attached to the distal end of the bursa; the nodulus is often more highly developed in these species as well. In the male genitalia of *Neda* and close allies, the outer arm of the siphonal capsule is more strongly expanded distally, forming a funnel. Externally, the fauna allied to *Neda* will

often possess broader elytral epipleura than *Olla,* or the abdominal segmentation is conspicuously different in shape and proportion. The elytral maculae in non-*Olla* species may suggest (but will never duplicate) the characteristic arrangements found in *Olla.*

Melanic specimens of *Olla* are not usually mistaken for other coccinelline genera in the New World. They are sometimes confused by nonspecialists with the chilocorine coccinellids, from which they differ in numerous features (Sasaji 1971, Gordon 1985).

Olla is most closely allied to the monotypic genus *Cirocolla,* but the much larger size and unusual markings of *C. conspicillata* make it unlikely that these two genera will ever be confused. The male genitalia of *Olla* and *Cirocolla* have the same general form of the siphonal capsule and the siphonal apex. Females of *C. conspicillata, O. hageni,* and *O. v-nigrum* share the unusual form of the common oviduct, which is swollen basally and has thick, folded walls.

Key to species of *Olla* Casey

1. Postcoxal line with oblique line absent (Fig. 18). Male genitalia (Fig. 8) with basal lobe short and broad; parameres curving over sides of basal lobe at apex. Known only from Roatan Island of the Bay Island group off Honduras
   . . . .*roatanensis* Vandenberg, n. sp.
   Postcoxal line with oblique line present (Fig. 19–21). Male genitalia (Fig. 10) with basal lobe elongate, narrow; parameres not curving over sides of basal lobe at apex. Widely distributed 2

2. Intercoxal process of prosternum with fine raised ridge on outer margins; median carinae lacking. Ground color of elytron bright canary yellow. Abdomen somewhat elongate (Fig. 21). Known only from Galapagos Islands
. . . . *hageni* Vandenberg, n. sp.
Intercoxal process of prosternum with a pair of median carinae. Ground color of elytron black, gray, or beige. Abdomen short and broad (Fig. 19 and 20). Not known from Galapagos Islands 3

3. Siphonal apex of male genitalia terminating in a corkscrew-shaped projection distinctly longer than subapical projection (Fig. 14b). Female genitalia as in Fig. 16. Elytral markings variable but often with the inner two spots of middle row joined to form a tilde-shaped mark on each elytron (Fig. 4c). Form usually rounder and more convex than *O. v-nigrum.* Many specimens can be reliably placed based on collection locality (Fig. 41)
. . . . *timberlakei* Vandenberg, n.sp.
Siphonal apex of male genitalia terminating in a weakly sinuous projection subequal in length to subapical projection (Fig. 14a). Female genitalia as in Fig. 15. Elytral markings variable but very rarely with the inner two spots of middle row joined to form a tilde-shaped mark on each elytron. Form usually more elongate and less convex than *O. timberlakei.* Many specimens can be reliably placed by collection locality (Fig. 41)
. . . . *v-nigrum* (Mulsant)

Olla roatanensis Vandenberg, new species
(Fig. 4, 7–9, 18, 41)

Description of Male (Holotype). Length, 4.6 mm; width, 3.8 mm. Form oval, slightly pointed posteriorly, moderately convex. Surface between elytral punctures distinctly shagreened. Color pattern (Fig. 4) derived from basic pale color form found in all *Olla* species. Ground color of dorsal surface yellowish ivory with brownish-black spots. Head immaculate with clypeus and labrum brownish. Pronotum with 9 spots corresponding to standard 7; typical slash-shaped discal mark on each side of midline, broken to form short upright mark and small anterolateral dot; lateral spot and median basal spot less intense than other markings. Each elytron with 5 small, punctiform spots arranged 2:2:1 as shown (lacking humerolateral, median spots of basal row, and mediolateral spot of middle row found in basic pale color form). Elytral suture and scutellar margins brownish black. Ground color of ventral surface, including mouthparts and appendages, medium yellowish brown; meso- and metepimeron paler; median area of abdomen

darker; hypomeron and elytral epipleuron same color as dorsal surface. Eyes with inner orbits slightly divergent dorsally. Prosternal process with fine, raised ridge on outer margins. Elytral epipleuron weakly concave, strongly descending externally; maximum width approximately ⅕ width of body at base of abdomen. Shape and segmentation of abdomen as in Fig. 18; postcoxal line with oblique line absent. Male genitalia (Fig. 7–9) with basal lobe short and broad; apex consisting of 2 triangular teeth separated by a concave border. Parameres curved over sides of basal lobe. Sipho with short, flat, triangular apex and subapical projection twisted around one another; tube forming main body of sipho broad and flat with wide membranous area.

Type Material. HOLOTYPE (male), "BRITISH HONDURAS: Roatan Island, French Harbor, 0-50m., July 31, 1975 N.L.H. Krauss" (AMNH).

Remarks. The holotype is the only known specimen of this distinctive species. It can be easily distinguished from the other *Olla* species by the postcoxal line lacking an oblique line and by the distinctive male genitalia. The intercoxal process of the prosternum lacks the median carinae found in *O. v-nigrum* and *O. timberlakei;* instead, it has a fine raised ridge on the outer margins as in *O. hageni.* The pronotal and elytral markings of this individual are also quite distinct from the various aberrations of the other three species. It will be interesting to discover whether or not *O. roatanensis* has a melanic color form and whether some individuals of the pale form possess the full complement of eight spots per elytron. This species is named for the island on which it was collected.

Locality Records (Fig. 40). Known only from the type locality.

Olla v-nigrum (Mulsant)
(Fig. 1[a–d], 10a, 11, 12, 13a, 14a, 15, 19[a,b], 23, 41)

Harmonia V-nigrum Mulsant 1866: 64; Gorham 1892: 172 (as synonym of *Cycloneda abdominalis*).

Coccinella abdominalis Say 1824: 95 (not *Coccinella abdominalis* Thunberg, 1794).

Daulis abdominalis: Mulsant 1850: 316 (in part); 1866: 218 (in part).

Coccinella V-nigrum: Crotch 1874: 109.

Daulis binotata: Mulsant 1850: 322 (not *Coccinella binotata* Say 1826); 1866: 221; Crotch 1874: 166 (as synonym of *Cycloneda oculata* F.).

Daulis v-nigrum: Belicek 1976: 329 (incorrect citation of the original genus).

Cycloneda sayi Crotch 1871: 6 (new name for *abdominalis* Say).

Cycloneda oculata var. *abdominalis:* Crotch 1873: 372 (not *Coccinella oculata* Fabricius, 1792).

Cycloneda abdominalis: Crotch 1874: 163 (in part); Gorham 1892: 172 (in part).

Cycloneda abdominalis var. *chapalensis* Weise 1895: 125.

Cycloneda abdominalis var. *v-nigrum:* Weise 1895: 125.

Olla abdominalis: Casey 1899: 93; Blatchley 1910: 514; Palmer 1914: 232; Leng 1920: 216; Stehr 1930: 36; Korchefsky 1932: 288 (in part); Blackwelder 1945: 453 (in part); Wingo 1952: 46; E. Chapin 1965: 220; J. Chapin 1974: 64.

Olla plagiata Casey 1899: 94; J. Chapin 1974: 64; Belicek 1976: 329 (as synonym of *O. v-nigrum*); Posada & Garcia 1976: 7; Gordon 1985: 828 (as synonym of *O. v-nigrum*).

Olla sobrina Casey 1899: 94; J. Chapin 1974: 64; Belicek 1976: 329 (as synonym of *O. v-nigrum*); Gordon 1985: 828 (as synonym of *O. v-nigrum*).

Olla fenestralis Casey 1899: 95; Korchefsky 1932: 288 (as synonym of *O. abdominalis* ab. *plagiata*); Blackwelder 1945: 453 (as synonym of *O. abdominalis* ab. *plagiata*); Belicek 1976: 329 (as synonym of *O. v-nigrum*); Gordon 1985: 828 (as synonym of *O. v-nigrum*).

Olla Sayi: Korchefsky 1932: 289 (as synonym of *Olla abdominalis*).

Olla sayi: Blackwelder 1945: 453 (as synonym of *Olla abdominalis*).

Olla oculata: Mader 1958: 248.

Coccinella (Olla) oculata var. *plagiata:* Leng 1903: 204.

Coccinella (Olla) oculata var. *sobrina:* Leng 1903: 204.

Coccinella (Olla) oculata var. *fenestralis:* Leng 1903: 204.

Coccinella (Olla) abdominalis: Leng 1903: 205.

Olla minuta Casey 1908: 406; Casey 1924: 157; Belicek 1976: 329 (as synonym of *O. v-nigrum*); Gordon 1985: 828 (as synonym of *O. v-nigrum*).

Olla semilunaris: Leng 1920: 216 (as synonym of *O. abdominalis*); Korchefsky 1932: 289 (as synonym of *O. abdominalis*); Blackwelder 1945: 453 (as synonym of *O. abdominalis*); Gordon 1985: 828 (as synonym of *O. v-nigrum*).

Olla abdominalis arizonae Casey 1924: 158; Korchefsky 1932: 289; Mader 1958: 248; Belicek 1976: 329; Gordon 1985: 828.

Olla arizonae: J. Chapin 1974: 64.

Olla abdominalis var. *semilunaris* Johnson 1910: 66.

Olla abdominalis ab. *minuta:* Korchefsky 1932: 289; Blackwelder 1945: 453; Mader 1958: 248.

Olla abdominalis ab. *plagiata:* Korchefsky 1932: 289; Blackwelder 1945: 453; Mader 1958: 248.

Olla abdominalis ab. *sobrina:* Korchefsky 1932: 289.

Olla abdominalis ab. *chapalensis:* Korschefsky 1932: 290; Blackwelder 1945: 453; Mader 1958: 248.

Olla abdominalis ab. *v-nigrum:* Korschefsky 1932: 289; Mader 1958: 248.

Olla v-nigrum: Timberlake 1943: 24; Belicek 1976: 329; Gordon 1985: 828.

Olla v-nigrum var. *plagiata:* Timberlake 1943: 24.

Olla quinquenigrum Arioli & Link 1987: 204 (incorrect transliteration of *v-nigrum*).

Procula orientalis Zayas 1988: 80; Ivie 1991: 400 (as synonym of *O. v-nigrum*)

Description of Male (Specimen from Oaxaca, Mexico). Length 4.8 mm, width 4.2 mm. Form oval, slightly pointed posteriorly, strongly convex. Surface between elytral punctures shagreened. Color pattern conforming to basic pale color form found in all *Olla* species. Ground color of dorsal surface pale parchment yellow (typically ashy gray in life) with blackish spots. Head with pair of rounded spots near base; clypeus and labrum brownish. Pronotum with 7 marks arranged as in Fig. 1d. Each elytron with full complement of 8 spots arranged as in Fig. 1c; in basal row, median spot set slightly farther back than other 3 spots; in middle row, median spot crescentiform; remaining spots irregular oval. Elytral suture and scutellar margins reddish brown. Ground color of ventral surface, including mouthparts and appendages, medium yellowish brown; metepisternum, meso-, and metepimeron creamy white; hypomeron and elytral epipleuron same color as dorsal surface. Eyes with inner orbits parallel, separated by slightly less than twice the diameter of an eye. Prosternal process with median carinae converging anteriorly. Elytral epipleuron moderately concave, descending externally; maximum width approximately ⅙ width of body at base of abdomen. Shape and segmentation of abdomen as in Fig. 19a; postcoxal line with incised oblique line at middle of coxal plate, fading to an ill-defined

wrinkle as it continues posteriorly to join main arc.

Male genitalia (Fig. 10a, 11, 12, 13a, 14a) with basal lobe long and slender; apex in outline consisting of two triangular teeth separated by a convex border (Fig. 10a). Parameres not curved over sides of median lobe. Sipho (Fig. 14a) with sinuous apex set at right angle to subapical projection and approximately equal in length; tube forming main body of sipho slender, oval in cross-section, with membranous area as shown.

Female. Same as male except for sexual characters. Elytral epipleura slightly narrower than in male. Shape and segmentation of abdomen as in Fig. 19b. Genitalia as in Fig. 15; spermatheca roughly C-shaped; base of common oviduct swollen with thick folded walls.

Variation. Length 3.7–6.2 mm, width 3.0–4.6 mm. Shape varies from oval to nearly circular. Dorsal color pattern strongly dimorphic (Fig. 1 a–d). Dorsal surface of melanic form (Fig. 1a) as given in generic description; ventral surface including legs predominantly black except for cream-colored meso- and metepimeron, cream-colored apex of hypomeron, cream markings on mesepisternum (variable), and yellowish brown to piceous abdomen, tarsi, antennae, and mouthparts. Pale color form variable in dorsal pattern through loss or fusion of spots; common aberrations shown in Fig. 1 b–d; ventral surface with lateral margin of abdominal segment 1 and anterior coxa sometimes pale; metepisternum variable brown to cream-colored; metasternum occasionally dark brown with a pale inverted V on anterior intercoxal process. Sipho of male genitalia variable as to precise form of the siphonal apex (Fig. 14a and intermediate configurations). Spermatheca of female genitalia variable as to length of ramus and length and curvature of cornu.

Type Material. See Gordon (1985) for type localities, depositories, determination of type material, and lectotype designations of *v-nigrum*, *plagiata*, *sobrina*, *fenestralis*, *minuta*, *semilunaris*, and *arizonae*. The type locality of *Daulis abdominalis* is given as "arkansa"; type lost (Gordon 1985). The description of *Olla abdominalis* var. *chapalensis* agrees with a specimen from the ZMHB labeled "Mexico Degis [green paper]/var. chapalensis/Zool. Mus. Berlin". According to Article 1 of the Code (ICZN 1985), no lectotype designation is necessary because of the infrasubspecific status of this name.

Remarks. This species is most often confused with *O. timberlakei* and cannot be easily separated using external characteristics alone. Small specimens of *O. v-nigrum* tend to be oblong, whereas those of *O. timberlakei* approach circularity, but there is much individual variation. The larger individuals of both species converge toward the same oval form. Many otherwise dubious examples can be reliably determined by

collection locality (Fig. 41). The siphonal apex of the male genitalia in *O. v-nigrum* (Fig. 14a) is distinct from all the other known species of *Olla*. The female genitalia are also distinctive in this species, although the spermatheca is somewhat variable (see variation above) and the diagnostic membranous parts of the genital tract (Fig. 15) may be poorly preserved or difficult to dissect.

Olla v-nigrum has become well known under the name *Olla abdominalis* (Say). Timberlake (1943) first proposed the use of the synonym *Olla v-nigrum* (Mulsant) as a replacement name for *O. abdominalis* (Say) because *Coccinella abdominalis* Say is a junior primary homonym of *Coccinella abdominalis* Thunberg. Many popular identification guides for North American insects have overlooked this nomenclatural correction and continue to use the invalid species name.

The lectotype of *Harmonia v-nigrum* Mulsant, designated by Gordon (1985), is clearly part of the original type series. The specimen does not, however, agree completely with the detailed description of Mulsant (1866), which was based on a more lightly marked individual.

From the discussion by Gorham (1892), it is evident that there were once multiple "types" of *Harmonia v-nigrum* in Salle's collection. The lectotype is the only surviving example from that series in The Natural History Museum (formerly British Museum [Natural History]). Both *Olla v-nigrum* and *Olla timberlakei* can be found in Oaxaca, Mexico, which is the type locality for *Harmonia v-nigrum*, but only one species of *Olla* occurs in Arkansas, the type locality for *C. abdominalis* Say (type lost). I have examined the lectotype of *Harmonia v-nigrum* and agree with Gorham (1892), Timberlake (1943), Belicek (1976), and Gordon (1985) that it is conspecific with *C. abdominalis* Say.

Olla abdominalis arizonae Casey is a variation of the pale color form of *O. v-nigrum* in which the inner two elytral spots of the middle row are joined to form a large cordate mark on each elytron (Fig. 1b). This aberration cannot be considered a true subspecies because it occurs in only a small proportion of the individuals from several different localities. The name *O. abdominalis* var. *semilunaris* Johnson refers to the same aberration as the preceding. *Olla minuta* Casey is an abnormally small individual of the pale color form, with the middle row of spots contiguous; it is otherwise unremarkable. *Olla abdominalis* var. *chapalensis* Weise is a lightly marked individual of the pale color form with the posterior elytral spots absent or indistinct.

The Casey names *O. plagiata*, *O. sobrina*, and *O. fenestralis* refer to the melanic color form of *O. v-nigrum* and differ from one another only in minor characteristics of size, pronotal markings, and the color and size of the elytral spot. The use of the names *oculata* F. and *binotata* Say for a melanic form of *O. v-nigrum* must be rejected on

the grounds that the original descriptions of *Coccinella oculata* F. (1792) and *Coccinella binotata* Say (1826) clearly do not apply to any species in the genus *Olla*. *Coccinella oculata* F. is described as having a large rounded white spot at each side of the pronotum, whereas in melanic forms of *Olla* spp., the front and lateral margins have a narrow irregular white border. Casey (1899, 1908) states that *C. oculata* might belong to the genus *Neda* or possibly the exotic genus *Coelophora* Mulsant, provided the locality cited was in error. The description of *C. oculata* does not fit any species of *Neda* with which I am familiar but may agree with a species of *Coelophora* or *Oenopia* (also exotic), or even a coccinellid of another subfamily. *Coccinella binotata*, on the other hand, is described as having a "rufous, orbicular, central spot" on each elytron (Say 1826); in contrast, the elytral spot on melanic forms of *Olla* is irregularly shaped and located in the anterior half of the elytron. The dimension given for *C. binotata* of "less than 3/20 of an inch" is also rather small for *Olla*. Casey (1899) suggests that this species belongs in the genus *Hyperaspis*. Unfortunately, the type material of *C. oculata* and *C. binotata* is no longer in existence to verify or confute these different speculations.

Pupa. The pupa of *O. v-nigrum* was described and illustrated by Palmer (1914), Phuoc & Stehr (1974), and Machado (1982); it was photographed in color by Saini (1985). These references should be examined for a complete description. The main body of the pupa is cream-colored with black spots.

Fourth Instar (Fig. 24). Size and habitus as shown. Legs black. Head whitish with black vertex. Ground color of body medium gray. Pale areas on prothorax and lateral pale marks on all segments creamy white. Median pale marks on meso- and metathorax, dorsolateral pale marks on abdominal segments 1 and 4, and median pale marks on all abdominal segments yellow to orangy yellow.

Third Instar (Fig. 25). Size and habitus as shown. Color pattern same as fourth instar.

Second Instar (Fig. 26). Size and habitus as shown. Basic color pattern same as in third and fourth instars, except head entirely black, and pale area on prothorax light gray.

First Instar (Fig. 27). Size and habitus as shown. Head and legs black. Ground color of body light gray marked with black. Prothorax, median area of meso- and metathorax, and dorsolateral spot on first abdominal segment pale dusky yellow.

Eggs (Fig. 28). Size and shape as shown. Color orangy yellow with a glossy sheen. Deposited in batches of 3–46 (average, 19; *n* = 32).

Remarks about Immature Stages. The egg, (third?) instar, and pupa of *O. v-nigrum* were first described and illustrated by Palmer (1914).

Machado (1982) illustrated and compared all the immature stages of this species with *Cycloneda conjugata*. Saini (1985) photographed the fourth instar and pupa in color.

Olla hageni is the only other species of *Olla* for which the immature stages have been examined. *O. v-nigrum* can be distinguished by the narrower, more orange egg; the more slender larva (primarily the first two instars); and the distinct dorsal color pattern of the second through fourth instars. Particularly diagnostic is the yellow dorsal parascolus of the fourth abdominal segment in the second through fourth instars (black in *O. hageni*) and the cream coloration on the head of the third and fourth instars (black in *O. hageni*). The ground color of the pupa of *O. v-nigrum* is cream, whereas that of *O. hageni* is yellow.

Locality Records (Outside North America) (Fig. 41). ARGENTINA: *Buenos Aires:* San Isidro. BRAZIL: *Minas Gerais:* Lavras. *Parana:* Curitiba. *Rio de Janeiro:* Rio de Janeiro. *Rio Grande do Sul:* Porto Alegre. *Santa Catarina:* Joinville. *Sao Paulo:* Piracicaba. COLOMBIA: *Valle del Cauca:* Buga; Cali; Palmira. EL SALVADOR: *San Andres;* San Nicolas Lempa. GUATEMALA: "Finca, Los Cerritos"; *Sacatepequez:* Antigua. HONDURAS: *Yoro:* La Lima. JAMAICA: "Jamaica"; Kingston. MEXICO: "Jalapa"; "Lerdo"; "Victoria". *Aguascalientes:* Aguascalientes. *Baja California Norte:* Marte, 3 mi. N Punta Prieta; 7 mi. SW Mission San Borja; 21 mi. NW Rancho Chapala, 2,500'; Rancho Santa Marguerita, 28 mi. S El Arco; 9 mi. SE San Augustin; 65 mi. S San Felipe. *Baja California Sur:* La Paz; Loreto. *Chihuahua:* 12 mi. N Chihuahua; 9 mi. S Hidalgo de Parral; Samalayuca; Sierra Madre Mts., 35 mi. S Creel. *Colima:* Colima Vulcano. *Durango:* Rio Chico; 5 mi. E Vicente Guerrero. *Guerrero:* Iguala; Petaquillas; Piedefuesta. *Hidalgo:* Colonia. *Jalisco:* Hwy. 15, 25 mi. SE Jocotepec, 5,500'. *Morelos:* Cuernavaca; 9 mi. S Cuernavaca; Yautepec. *Nayarit:* Rosamorada. *Nuevo Leon:* Cerro Potosi, 10,300', Guajuco; Chipinque Mesa, 5,400', nr. Monterrey; Huasteca Canyon nr. Monterrey; Linares; 5 mi. S Monterrey; Nuevo Laredo. *Oaxaca:* Oaxaca. *Puebla:* Cacaloapan; Tehuacan. *Sinaloa:* 5.5 mi. NW Choix; 16 mi. S Guaumuchil; 25 mi. N of Los Mochis; Mazatlan. *Sonora:* La Chiripa; 40 mi. N Hermosillo; Minas Nuevas; 6 mi. S Presa Obregon; 11 mi. S of Ciudad Obregon; Saric. *Tamaulipas:* 42.3 km N. Ciudad Mante, Highway 85; 7 km SSE Gomez Farias; Xicotencatl. *Veracruz:* Cordoba; Ciudad Mendoza; Orizaba. Zacatecas: 32 mi. NW Fresnillo. NICARAGUA: Nagarote, Leon. PARAGUAY: *Central:* Asuncion; Univ. Nac. Agric., San Lorenzo. PUERTO RICO: Camuy. BAHAMAS: San Salvador Island. (AMNH) (BMNH) (CAS) (CCC) (CNC) (ESALQ) (ICA) (ICN) (IML) (LSUC) (MCZ) (MNHP) (TAMU) (UCB) (UCR) (USNM) (UFRGS) (UNP) (ZMHB).

North American Distribution. Southeastern Canada to Florida, west to southern British Columbia and southern California.

Prey Species and Host Plant Associations. Gordon (1985) identifies members of the genus *Olla* as aphid predators and lists seven prey species. His remarks presumably apply to *O. v-nigrum* because he was dealing only with the North American fauna. In the United States, this coccinellid is a common aphid predator in commercial walnut and pecan groves (Bugg & Dutcher 1989). I have collected it feeding on *Chromaphis juglandicola* (Kaltenbach) on walnut, *Myzus persicae* (Sulzer) on peach, and *Rhopalosiphum padi* (L.) on cherry. Nita Davidson (personal communication) reports larvae and adults of the coccinellid attacking *Dysaphis plantaginea* (Passerini) on apple trees. In the laboratory, *Therioaphis trifolii* (Monell) and *Acyrthosiphon pisum* (Harris) are accepted and are suitable prey, but *O. v-nigrum* is rarely collected on the low vegetation which harbors these species.

In the tropics, psyllids, as opposed to aphids, probably constitute the principle prey group. At several localities in Brazil, I collected *O. v-nigrum* feeding on psyllids infesting leguminaceous trees. Machado (1982) collected large numbers of this species in Piracicaba, Brazil, on sibipruna, *Caesalpinia pelthophoroides* Benth, attacking *Psylla* sp. She also observed *O. v-nigrum* feeding on aphids on *Brassica napus* Metzg. In California, the introduced psyllid *Psylla uncatoides* (Ferris & Klyver) is a favorite prey species found on *Albizia julibrissin* Durazz (silk trees) and *Acacia* spp. Nymphs of the introduced pear psyllid *Psylla pyricola* Förster, which enclose themselves in a droplet of honey dew, were not readily accepted when offered under laboratory conditions; however, Westigard et al. (1968) recorded large numbers of *O. v-nigrum* in pear trees infested with these psyllids in southern Oregon. In Sonora, Mexico, two specimens were collected feeding on *Aleyrodes* sp. (Homoptera: Aleyrodidae) (Timberlake 1943).

Heredity of Color Pattern. Much work has been devoted to the heredity of color patterns in polymorphic species of coccinellids (see Komai [1956] and Hodek [1973] for references). Most of these studies explain the observed color forms based on a series of multiple alleles of a single gene, or of a group of closely linked genes which behave as a single gene ("para-allelic" genes). Minor variations on a basic color form, such as occur in species of *Hippodamia* (Komai 1956), are apparently the result of polygenes (modifiers).

I made a series of observations on the inheritance of the melanic and pale color forms of *O. v-nigrum* in my laboratory colonies. Virgin females of the basic pale color form, mated with males of the same color form, produced progeny

identical to the parents. Virgin females of the melanic color form, when mated with melanic males, usually produced progeny of both color forms but with a higher proportion of melanic individuals. In one instance, a pair of melanic parents yielded only melanic progeny, and these continued to breed true through the six generations during which the colony was maintained.

Clausen (1916) observed that in California, the melanic form of *O. v-nigrum*, to which he referred under the name *Olla oculata*, would sometimes "show faintly the markings of *O. abdominalis*" during the teneral stage following eclosion from the pupa. It now appears that the individuals that Clausen observed were heterozygous, and that the pale color form, which seems to be recessive in the fully mature adult, is expressed temporarily in such individuals.

In my own cultures, individuals from the true-breeding melanic colony never exhibited elytral spots in the teneral stage, whereas the melanic progeny resulting from a cross between a true-breeding melanic and an individual of the pale color form always did show them (Fig. 23). The simplest interpretation of these observations is that the melanic and pale forms are governed by two different alleles of a single gene; the heterozygote expresses the phenotypes of both alleles, but the contribution of the pale allele is masked in the fully melanized, mature specimen (Fig. 23, right). If the heterozygote is killed while still teneral, the process of melanization is halted, and the specimen becomes fixed at the intermediate state (Fig. 23, middle). It was probably teneral specimens of this sort which caused Belicek (1976) to remark on the "existence of intermediates between seemingly distinct color morphs."

Distribution of Color Forms. The relative proportions of the melanic and pale color forms of *O. v-nigrum* vary with geographic location. The melanic form predominates in the eastern parts of the United States and in South America. The pale color forms constitute a majority in Mexico and most of California, Arizona, New Mexico, and Texas. In the southern half of Mexico, the pale color form occurs exclusively. The aberration of the pale color form, in which the elytron has a large cordate discal mark (Fig. 1b), is known from northern Mexico, southern California, Arizona, New Mexico, and Texas, but it is still fairly uncommon in these areas.

The observed variation in the proportion of melanic and pale color forms of *O. v-nigrum* is roughly in accordance with Allen's or Gloger's rules, which state that arid regions are generally inhabited by light-colored varieties or races, whereas in humid regions, dark ones predominate (Komai 1956). Adherence to these rules has been observed in a number of coccinellid species, but a selective advantage of dark or light forms in relation to humidity has not been demonstrated experimentally. Temperature has been

shown to affect the degree of melanization expressed by the adult coccinellid, but only the temperature experienced by the individual during a critical period in the pupal or prepupal stage is of any consequence (Hodek 1973). A correlation between temperature and distribution of color forms is not suggested by the data from *Olla* (above), and has been demonstrated only in a few other species. Some of the most extensive work on the distribution of color forms in coccinellids was conducted by Dobzhansky (1933). Komai (1956) and Hodek (1973) give a list of references on this topic.

Olla timberlakei Vandenberg, new species
(Fig. 2[a–d], 10b, 13b, 14b, 20[a,b], 41)

Daulis abdominalis var. D: Mulsant 1850: 316 (in part).

Daulis abdominalis: Mulsant 1866: 218 (in part).

Cycloneda abdominalis: Crotch 1874: 163 (in part).

Cycloneda abdominalis: Gorham 1892: 172 (in part).

"Coccinella No. 18": Gorham 1892: 161.

Description of Male (Holotype). Length, 4.7 mm; width, 4.3 mm. Form nearly circular, hemispherical, slightly pointed posteriorly. Surface between elytral punctures faintly shagreened but mostly polished. Color pattern (Fig. 2c) derived from basic pale color form found in all *Olla* species. Ground color of dorsal surface pale beige with dark brown spots; head darker beige, immaculate except for pair of basal spots mostly covered by pronotum. Pronotum with 7 marks arranged as in Fig. 2c; pronotal base bordered in brown. Each elytron with full complement of 8 spots; in basal row, median spot slightly more posterior than other 3 spots; in middle row, mediolateral and median spots joined to form a tilde-shaped mark; in same row, lateral mark irregular, approaching lateral margin; subsutural spot of basal row semicircular; remaining elytral spots subcircular. Elytral suture and scutellar margins reddish brown. Ground color of ventral surface, including mouthparts and appendages, golden brown; anterior coxa, meso- and metepisternum, meso- and metepimeron creamy white; hypomeron and elytral epipleuron same color as dorsal surface. Eyes with inner orbits parallel, separated by approximately twice the diameter of an eye. Prosternal process with median carinae converging anteriorly. Elytral epipleuron moderately concave, descending externally; maximum width equal to ≈⅙ width of body at base of abdomen. Shape and segmentation of abdomen as in Fig. 20a; postcoxal line with incised oblique line at middle of coxal plate, fading to an ill-defined wrinkle as it continues posteri-

orly to join main arc. Male genitalia (Fig. 10b, 13b, 14b) with basal lobe long and slender; apex in outline consisting of 2 triangular teeth separated by a straight border (Fig. 10b). Parameres not curved over sides of basal lobe. Sipho with corkscrew-shaped apex several times longer than small down-turned subapical projection (Fig. 14b); tube forming main body of sipho slender, oval in cross-section, with membranous area as shown.

Description of Female (Allotype). Length 5.1 mm, width 4.4 mm. Similar to holotype except form more elongate; dorsal maculae slightly heavier; ground color of dorsal and ventral surfaces darker, more unicolorous. Shape and segmentation of abdomen as in Fig. 20b.

Female Genitalia (Fig. 16). Spermatheca bent, with tapered cornu; base of common oviduct not particularly swollen or thickened.

Variation. Length, 3.5–6.2 mm; width, 3.5–5.5 mm. Form varying from perfectly circular to oval; males generally shorter than females from same locality; larger specimens more elongate than small ones. Pale form: dorsal maculation varying in intensity, number, and confluence of markings but never exceeding number of marks in basic pattern of the generic description (typical range of variation shown in Fig. 2b–d); ventral coloration with sides of abdomen, pro- and mesosternum, meso- and metepisternum, and anterior coxa variable cream or brown. Melanic form known from a single specimen (Fig. 2a): ground color of dorsal surface piceous; head and irregular pronotal border whitish cream; clypeus and labrum brown; elytral spots yellowish orange; venter including mouthparts and appendages light reddish brown.

Genitalia somewhat variable; siphonal apex of male genitalia shorter in example from Venezuela (Fig. 14b, apex only shown) than in those from Middle America; subapical projection of sipho varying somewhat in length.

Type Material. HOLOTYPE, ♂; "MEX: Yucatan: Izamal. Coll. Cliff Gold VI.24.81." (CAS). ALLOTYPE, ♀: "MEX: Yucatan: Piste nr. Chichen Itza. Coll. Cliff Gold, VI.25.81" (USNM). PARATYPES (total 32): 2 with same data as holotype (MHNP); 6, "Temax, N. Yucatan Gaumer./B.C.A. col., VII" (BMNH); 2, same first label as preceding/"Donated by F. Du C. Godman 1907./Am. Mus. Nat. Hist. Dept. Invert. Zool. No. 18354" (AMNH); 1, "57 71/*abdominalis* Say var. Mexiq. Amer./Named by Mulsant" (BMNH); 4, "Guatemala City. Champion./B.C.A. col., VII. Cycloneda abdominalis Say" (BMNH); 1, "Guatemala City. Champion./B.C.A. col., VII. Coccinella Sp.? no. 18/Coccinella sp.?" (BMNH); 5, "Tixkokob, Yuc., Mex. VII-5-1952 J. & D Pallister/C. R. Vose Fund Explorers Club A.M.N.H. Exped." (AMNH); 5, "Cordeleria Mayapan, Yuc., Mex. June 30, 1952 J. & D. Pallister/C. R. Vose Fund Explorers Club A.M.N.H.

Exped." (AMNH); 1, "Mex: Yucatan 2 km. E. Chichen Itza V-26-1981 C. L. Bellamy" (CAS); 4, "MEXICO, Yuc. Merida VII-29-30-1964 Paul J. Spangler" (USNM); 1, "Acapulco Mex 7-16-75 Joe Eger" (LSUC).

Remarks. This species is most closely allied to *Olla v-nigrum*, with which it has frequently been confused. The male genitalia should be examined for a definitive determination, but many individuals can be correctly assigned based on collection locality or minor differences in facies. See "Remarks" section of *O. v-nigrum* for further comparisons.

It is interesting that, although many species names have been proposed in the genus *Olla*, none of them has referred to this commonly collected new species. Mulsant, Crotch, and Gorham had encountered specimens of *Olla timberlakei* and evidently based their concepts of *"abdominalis"* on a mixed series containing both *Olla v-nigrum* and *O. timberlakei*. Mulsant (1850, 1866) clearly refers to the species *O. timberlakei* when he remarks that some specimens of *Daulis abdominalis* have the fifth and sixth spots of the eltyra united to form a transverse tilde. In the Crotch collection at Cambridge, there is a single specimen of *O. timberlakei* from Yucatan which Crotch was evidently considering when he described *Cycloneda abdominalis* as "very variable, the central band of spots often forms a fascia. . ." (Crotch 1874). Gorham (1892) illustrated a specimen of *Olla timberlakei* and described it as "a pretty variety [of *C. abdominalis*] (Fig. 23) which occurred rather commonly at Temax in Yucatan. . . ." In the same publication, Gorham identified specimens of the typical pale form of *Olla timberlakei* (collected by Champion in Guatemala City) as *Cycloneda abdominalis*, and he described the melanic color form of *Olla timberlakei* (also collected by Champion in Guatemala City) under the heading "Coccinella No. 18." Weise (1904) concluded that "Coccinella No. 18" was actually a melanic variation of the European species *Oenopia conglobata* (then placed in *Coccinella*), but his conjecture was based entirely on Gorham's rather meager description of the specimen.

Olla timberlakei is named in honor of P. H. Timberlake, who has contributed important information on the systematics of the Coccinellidae.

Locality Records (Fig. 41). COSTA RICA: *Guanacaste:* Filadelfia; 2 km E Hacienda Palo Verde; La Pacifica, 4 km NW Canas. EL SALVADOR: Sta Cruz Porrilla; 5 mi. E La Libertad. GUATEMALA: Guatemala City. HONDURAS: *Choluteca:* La Lujosa. MEXICO: *Campeche:* 10 mi. N Hopelchen Camp. *Chiapas:* Tuxtla Gutierrez, 1800 ft. *Guerrero:* Acapulco. *Oaxaca:* La Ventosa; 23 mi. S Matias Romero; Salina Cruz; Tehuantepec. *Quintana Roo:* 20 km, N Felipe Carrillo Puerto; San Miguel, Cozumel [island].

Vera Cruz: 30 mi. S Acayucan. *Yucatan:* 2 km E Chichen Itza; Colonia; Cordeleria Mayapan; Dolores Otero; Izamal; Merida; Motul; 49 mi S Muna; Temax; Tixkokob; Uxmal; Vicente Solis. VENEZUELA: *Aragua:* Villa de Cura. (AMNH) (BMNH) (CAS) (CCC) (LSUC) (MNHP) (UCB) (USNM) (ZMHB).

Prey Species. Two specimens from Villa de Cura in Venezuela were recorded feeding on nymphs and larvae of Psyllidae.

Olla hageni Vandenberg, new species
(Fig. 3[a–c], 5a, 10c, 13c, 14c, 21[a,b], 29–33, 41)

Olla abdominalis: Mutchler 1938: 17 (not *Olla abdominalis* [Say]); Van Dyke 1953: 65; Linsley & Usinger 1966: 147.

Adalia galapagoensis Van Dyke 1953: 65 (in part; mixed type series).

Description of Male (Holotype). Length, 5.2 mm; width, 4.4 mm. Form subogival, strongly convex. Surface between elytral punctures faintly shagreened but mostly polished. Color pattern (Fig. 3b) conforming to basic pale color form found in all *Olla* species. Ground color of dorsal surface canary yellow with medium brown spots. Head with pair of rounded spots near base; clypeus and labrum yellowish brown. Pronotum with 7 marks arranged as shown. Each elytron with full complement of 8 spots; in basal row, median spot set well back from other 3 spots, subsutural spot indistinct; in middle row, median spot weakly crescentiform; in basal and middle row, lateral spot obtriangular; remaining elytral spots circular to oval. Elytral suture and scutellar margins reddish amber. Ground color of ventral surface, including mouthparts and appendages, yellowish brown; pro- and mesosternum, meso- and metepisternum, meso- and metepimeron creamy yellow; sides of abdomen paler than middle; hypomeron and elytral epipleuron same color as dorsal surface. Eyes with inner orbits parallel, separated by approximately twice the diameter of an eye. Prosternal process with fine, raised ridge on outer margins. Elytral epipleuron moderately concave, descending externally; maximum width equal to ≈⅐ width of body at base of abdomen. Shape and segmentation of abdomen as in Fig. 21a; postcoxal line with incised oblique line at middle of coxal plate, fading to an ill-defined wrinkle as it continues posteriorly to join main arc. Male genitalia (Fig. 10c, 13c, 14c) with basal lobe long and slender; apex in outline consisting of 2 triangular teeth separated by a straight border (Fig. 10c). Parameres not curved over sides of basal lobe. Sipho with long, sinuous, whiplike apex 3.5 times longer than down-turned subapical projection (Fig. 14c); tube forming main body of sipho

slender, oval in cross-section, with membranous area as shown.

Description of Female (Allotype). Same as holotype except length 5.6 mm, width 4.2 mm. Pronotal markings indistinct. Median spot in middle row of elytron transverse oval. Elytral epipleuron weakly concave. Shape and segmentation of abdomen as in Fig. 21b.

Female Genitalia (Fig. 17). Spermatheca curved, with tapered cornu; base of common oviduct swollen, with thick folded walls.

Variation. Length, 5.0–5.8 mm; width, 4.0–4.5 mm. Pronotal markings often indistinct. Some elytral spots often missing or indistinct. Typical variations shown in Fig. 3 a–c. Raised ridge on intercoxal process of prosternum sometimes indistinct.

Type Material. HOLOTYPE, ♂: "Galapagos Islands. Santa Cruz Island. Near Academy Bay. col. Natalia Vdb VIII-6-1976" (CAS). ALLOTYPE, ♀: same data as holotype (USNM). PARATYPES (total 18): 2, same data as holotype, distributed 1 (UCB), 1 (ZMHB); 6, "Indefatigable I. Nov. 5 1935/Ecological zone C [written on back of first label]/Galapagos Is. W. von Hagen" (AMNH); 1, same labels as preceding/"Nunenmacher Collection" (CAS); 2, "Galapagos Arch. Isla Santa Cruz Horneman Farm. 220 m V-7 1964/D. Q. Cavagnaro Collector" (CAS); 1, same labels as preceding except 5-IV-1964 (CAS); 2, "Galapagos Is. Santa Cruz I. XII.1968. R. D. Sievers B. M. 1969-76" (BMNH); 1, same labels as above plus additional label "Santa Cruz, Dec 68 coll: R. D. Sievers Ch. Darwin Station" (BMNH); 3, "GALAPAGOS: I. SANTA CRUZ; Academy Bay, C. Darwin Res. Sta. 2 Jul '70. Alt.+/− 5 m. R. Silberlied./at U.V. blacklight" (MCZ).

Remarks. *Olla hageni* is most closely allied to *O. v-nigrum*, but it can be easily distinguished by the fact that it is the only *Olla* species found on the Galapagos Islands. Key characteristics of *O. hageni* include the bright yellow elytra, the more elongate body form, and the intercoxal process of the prosternum which lacks median carinae. Eight examples of this new species, collected by Dr. Wolfgang von Hagen on Santa Cruz Island, were described by Mutchler (1938) as belonging to "the typical form of *abdominalis*, but ... [with] ... a variation in the number and density of the spots on either or both the pronotum and elytra." Van Dyke (1953) followed the misidentification of Mutchler and compounded his error by including a single female specimen of *Olla hageni* in the series of 22 paratypes of *Adalia galapagoensis* Van Dyke. The misidentified paratype is the only known specimen of *O. hageni* from the island of Isabela. It differs from examples collected on the adjacent island of Santa Cruz in having the elytra slightly narrower than average and the marks on the elytra much less distinct than those on the pronotum. The

paper by Linsley & Usinger (1966), which lists *Olla abdominalis* from Santa Cruz Island, is a compilation of previous work and no doubt refers to the same specimens described by Mutchler (1938) and Van Dyke (1953).

The specific name *hageni* is a joint dedication to K. S. Hagen of the University of California, Berkeley, who has written numerous papers on coccinellid bionomics, and W. von Hagen, who made the first recorded collection of this species in 1935.

Pupa. Same as *O. v-nigrum* except ground color medium yellow.

Fourth Instar (Fig. 29). Size and habitus as shown. Head and legs black. Ground color of body medium gray marked with black and canary yellow (all pale areas shown).

Third Instar (Fig. 30). Size and habitus as shown. Same basic color pattern as 4th instar.

Second Instar (Fig. 31). Size and habitus as shown. Same basic color pattern as 3rd and 4th instars.

First Instar (Fig. 32). Size and habitus as shown. Head and legs black. Ground color of body light gray marked with black as shown, and with pale dusky yellow on prothorax, median area of meso- and metathorax, and dorsolateral spot on abdominal segment 1.

Eggs (Fig. 33). Size and shape as shown. Color pale yellow with a satiny sheen. Deposited in batches of 3–12 (average, 8; $n = 22$).

Remarks on Immature Stages. A comparison between the morphology of the immature stages of this species and those of *O. v-nigrum* can be found under the same heading for the latter species. *Olla hageni* lays fewer and larger eggs than does the related *O. v-nigrum*. When reared together in the laboratory, the first instars of *O. hageni* remained for a long time on top of the egg mass after hatching, whereas first instars of *O. v-nigrum* dispersed rapidly. Some larvae of *O. hageni* could molt to the second instar without feeding except on the egg shell remnants. I have not observed this ability in the >50 other coccinellid species reared in the laboratory; apparently *O. hageni* has evolved the strategy of producing unusually few offspring while making a large initial investment in each one.

Locality Records (Fig. 41). ECUADOR: *Galapagos Islands:* Santa Cruz Is. [Indefatigible Is.]: near Academy Bay; Academy Bay, C. Darwin Res. Stn.: "Ecological zone C"; Horneman Farm, 220 m., Isabela Island [Albemarle Island], 500 ft. (AMNH) (BMNH) (CAS) (MCZ) (UCB) (USNM) (ZMHB).

Prey Species and Host Plant Associations. I observed adults and larvae of *O. hageni* devouring aphids on tall bushes at the type locality.

Hybridization Experiments. I obtained a colony of *O. hageni* from Santa Cruz Island and a colony of *O. v-nigrum* from Berkeley, Calif., for laboratory studies. Reciprocal crosses between
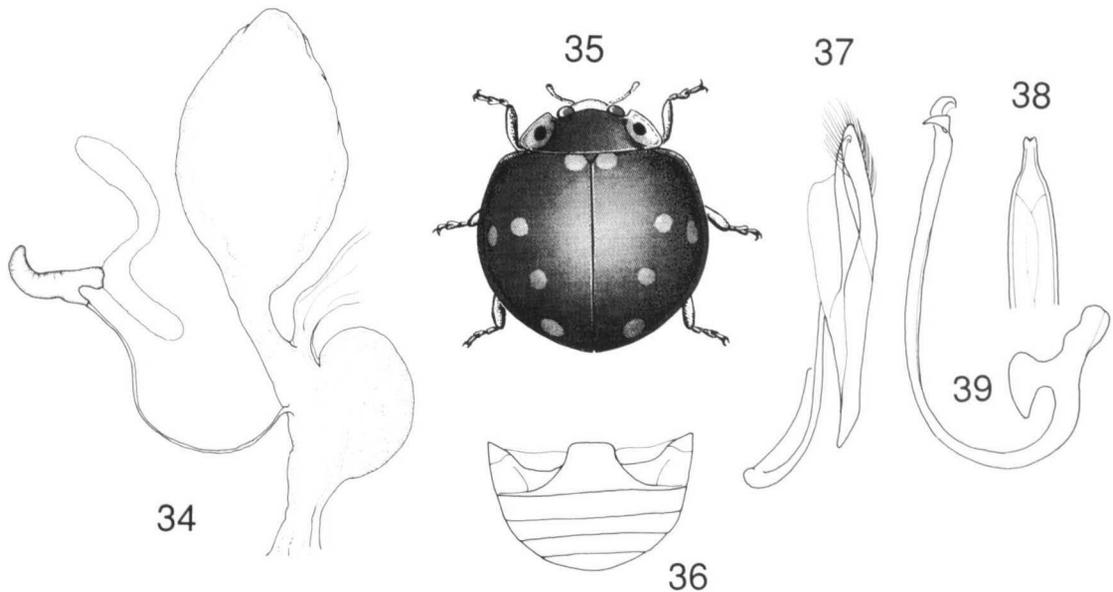
Fig. 34–39. *Cirocolla conspicillata.* (34) Right lateral view of female genitalia. (35) Habitus view of adult. (36) Ventral view of female abdomen. (37) Lateral view of phallobase. (38) Ventral view of basal lobe. (39) Lateral view of sipho.

F_1 individuals of the two species were attempted to assess species compatibility. Copulation occurred readily between members of the two species. Females of hybrid pairs laid their eggs in batches and in numbers characteristic of their species. Advanced hybrid embryos were produced in 12 of 320 eggs laid by females of *O. v-nigrum* mated with males of *O. hageni.* All hybrid embryos died in the shell. Reciprocal hybrid crosses failed to show any advanced embryonic development. Eggs produced from conspecific pairings of both species showed >99% viability when maintained under the same conditions as the hybrid eggs.

Cirocolla Vandenberg, new genus
(Fig. 34–39)

Type Species. *Daulis conspicillata* Mulsant.

Description. Length, 5.5–6.2 mm. Form nearly circular, subhemispherical. Eyes with moderate-sized facets. Pronotum moderately convex; feebly explanate at extreme outer edge; lateral and basal margins strongly rounded in outline. Elytron with translucent outer margin weakly explanate from base to apical ⅙; extreme outer edge with pronounced raised ridge along entire length; elytral base broad relative to pronotal base. Elytral epipleuron broad, concave, descending externally. Apex of middle and hind tibia each with 2 spurs. Tarsal claw with subquadrate basal tooth; claws of fore, middle, and hind tarsi of approximately equal length. Abdomen (Fig. 36) short and broad, widest near base; intercoxal process approximately equal in length

to minimum distance between hind coxae, apex strongly truncate; postcoxal line curved posteriad and laterad; oblique line present. Male genitalia (Fig. 37–39) with notch at apex of basal lobe (Fig. 38); siphonal capsule with inner and outer arms well developed; siphonal apex terminating in short sickle-shaped projection (bearing median orifice); triangular subapical projection wrapped around apex (Fig. 39). Female genitalia (Fig. 34) with small spermatheca as shown; accessory gland of spermatheca large, sinuous; sperm duct fine, fragile, easily collapsed, without sclerites, situated dorsal to bursa and attached dorsally where bursa narrows; base of common oviduct swollen and ridged.

Remarks. The single species in this genus can be easily recognized by the large size, circular form, the very broad and rounded abdomen, strongly truncate intercoxal process of the abdomen, and the broad elytral epipleuron. Only a few of the coccinellines allied to *Olla* possess members of equivalent body size; these include species in or near *Neda*, which can be distinguished by the much broader explanate elytral margin or the strongly arched hind margin of the fourth abdominal segment, and from some of the *Paraneda* species, which can be distinguished by the coarsely faceted, more closely placed eyes. *Cirocolla* was somewhat difficult to define objectively because it is currently monotypic. The large, sinuous spermathecal accessory gland of the female genitalia is quite distinctive and may prove to be a stable generic character should additional *Cirocolla* spp. be discovered.

In most respects, the male and female genitalia of *Cirocolla* are very similar to those found in the genus *Olla*. Some characteristics, such as the form of the siphonal apex in the male genitalia and the swollen common oviduct in the female genitalia (secondarily lost in *O. timberlakei*), probably represent unique characteristics which occurred for the first time within the *Olla–Cirocolla* line. Other shared characteristics, such as the configuration of the bursa and sperm duct of the female genitalia, may be either primitive or derived because either of the alternative configurations found in the genera most closely allied to *Olla* also occur in more distantly allied genera.

The generic name has the meaning "Olla of the winds," derived from "ciroc" (an alternative spelling of siroc or sirocco, a warm cyclonic wind) + Olla.

Cirocolla conspicillata (Mulsant), new combination
(Fig. 34–39, 41)

Daulis conspicillata Mulsant 1850: 333; Mulsant 1866: 227.

Cycloneda conspicillata: Crotch 1871: 6; Crotch 1874: 165; Mader 1958: 246.

Description of Female (Paralectotype). Length, 6.0 mm; width, 6.0 mm. Form circular, subhemispherical, rounded posteriorly. Punctation on dorsal surface fine and even; punctures slightly more pronounced on outer margin of elytron; surface between punctures distinctly shagreened on head and pronotum, nearly polished but still discernibly shagreened on elytron.

Dorsal color pattern as in Fig. 35, but with subapical elytral spot less distinct than shown: Head yellowish brown; pale lateral areas of pronotum, and 5 pale marks on elytron light yellow; median area of pronotum, scutellum, and ground color of elytron warm reddish brown; rounded mark in each lateral third and curved line between median and lateral thirds of pronotum darker reddish brown. Venter, including mouth parts, appendages, pronotal hypomeron, and elytral epipleuron same as ground color of elytron; mes- and metepimeron paler.

Eyes separated by ≈2 times the diameter of an eye; inner orbits parallel. Antenna slightly longer than separation between eyes; club well developed. Terminal segment of maxillary palp moderate sized, robust. Prosternal process with carinae reaching half way to anterior border. Mesosternum very broadly, feebly emarginate. Elytral epipleuron very faintly foveate for reception of hind femur, maximum width equal to ⅕ width of body at base of abdomen. Abdomen (Fig. 36) ≈1.6 times as wide as long; form broadly rounded. Length of first abdominal segment (along midline) approximately equal to

minimum distance between hind coxae; postcoxal line closely paralleling posterior margin of segment for most of length, nearly attaining lateral margin; oblique line curved, joined to main curve of postcoxal line. Abdominal segments 1 through 4 with hind margins approximately linear; segment 5 rounded, covering segment 6.

Female Genitalia. As in Fig. 34; cornu weakly curved; ramus moderately well developed, with elongate accessory gland as shown; nodulus short and tapered.

Male. Same as female except for sexual characters. Hind margin of abdominal segment 5 truncate, exposing segment 6; hind margin of segment 6 with small, rounded median notch. Genitalia as in Fig. 37–39.

Variation. Length, 5.5–6.2 mm; width, 5.5–6.2 mm. Ground color of dorsal surface darker or lighter than in paralectotype; pronotum with or without a dark reddish brown border between median and lateral thirds, median third sometimes showing faintly the same spotting pattern found in *Olla* spp. (Fig. 1–4); lateral margins of elytron sometimes paler than disk; elytral spots more or less distinct than in paralectotype.

Type Material. LECTOTYPE: gender unknown, designated Gordon (1987) (CCC). PARALECTOTYPE: ♀, by present designation, "type [white disk with red border]/57 71 [blue disk]/ *conspicillata* Reiche Muls Cayenne [green label]/Named by Mulsant" (BMNH).

Remarks. This species can be distinguished from all other Neotropical Coccinellinae by the unique dorsal color pattern combined with the large size and highly rounded body form. The male genitalia should be examined to confirm species identification.

Mulsant (1850) indicated that his description of *Daulis conspicillata* was based on material from the collections of Reiche and Buquet having the collection locality of "Cayenne." Gordon (1987) designated a Reiche specimen from the Crotch collection at Cambridge as the lectotype; this work should be consulted for exact label data. A second specimen belonging to this series was located at the Natural History Museum, London, and is here designated as paralectotype (label data given above). The species redescription is based on this specimen because of its superior preservation and more vivid maculation. The lectotype bears similar but fainter elytral maculae, and the pronotum shows faint additional dark maculae in the median third, which are lacking in the paralectotype.

Locality Records. (Fig. 41). "la vallee de l'Amazone" BRASIL: *Amazonas:* Ega. FRENCH GUIANA: *Guyane:* Cayenne. PERU: "Peru (Deyrolle)" (cited by Crotch [1874]). VENEZUELA: "Venezuela S. amer." (BMNH) (CAS) (CCC) (USNM) (MNHP).
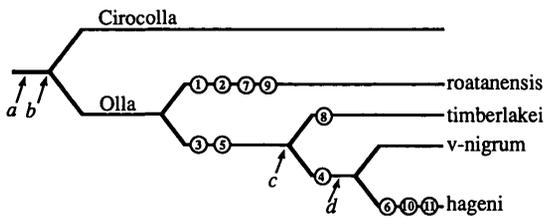
Fig. 40. Proposed phylogeny of *Olla* using the sister genus *Cirocolla* as the outgroup. Numbered items on the cladogram represent the derived states of characters described in the text. Lettered items represent geological and other events of potential importance in delineating the chronological framework for the evolution of *Olla* (see text for additional details and references): *a*, island "stepping stones" allow for a filtered exchange of flora and fauna between South America and Central America–Mexico, Tertiary; *b*, earliest fossil records of extant coccinelline genera, upper Oligocene; *c*, climatic oscillations result in biotic elevational shifts and fragmentation of ancestral species, Pleistocene; *d*, genesis of the Galapagos Islands, 3–4 m.y.a.

Phylogeny and Zoogeography

The cladistic relationships within the genus *Olla* were determined using traditional Hennigian methods. Assignment of primitive versus derived character states within *Olla* was via outgroup comparison (Watrous & Wheeler 1981) with the genus *Cirocolla*. *Cirocolla* is believed to be *Olla*'s sister group; that is to say, the two genera share a more recent common ancestor than either does with any other coccinellid genus. The assumption of monophyly for the *Cirocolla–Olla* line is based on the shared characteristics of the male and female genitalia discussed in the remarks section following the generic description of *Olla*. These characteristics are regarded as derived because they are not found within the other Neotropical genera allied to *Olla*. A compelling overall similarity in the facies of *Olla* and *Cirocolla* also supports the assumption that these genera are closely allied. The branching sequence in the phylogenetic diagram (Fig. 40) was deduced using the distribution of shared derived character states. The description of the characters and assessment of their primitive and derived states follow (p, primitive state; d, derived state):

1. Basal lobe: long, slender (p); short, broad (d). The primitive state is found in the sister genus and in most species of the allied genera.
2. Parameres: not hooked over sides of basal lobe (p); hooked over sides of basal lobe (d). Within the New World Coccinellini, the derived state is known only in a single *Olla* species.

3. Subapical projection of sipho: wrapped around siphonal apex (p); not wrapped around siphonal apex (d). Conditions analogous to the derived state occur occasionally in allied genera, resulting in a diversity of subapical lobes, flaps, and prongs; however, these structures are probably not strictly homologous to the angularly tapered projection found in *Olla* and its sister genus.
4. Subapical projection of sipho: poorly developed (p); well developed (d). In two *Olla* species, the subapical projection is folded back over the dorsal surface of the basal lobe, effectively preventing the sipho from being easily withdrawn beyond that point.
5. Siphonal apex: short (p); long (d). The primitive state occurs in the sister genus and among those genera that appear to be most closely related to *Olla*. The derived state occurs in two of the *Olla* species and, independently, in more distantly related allied genera.
6. Siphonal apex: flattened, relatively broad (p); narrow, approximately cylindrical (d). The primitive state is shared with the sister genus and those genera most closely related to *Olla*. The derived state occurs only in one of the *Olla* species.
7. Main body of sipho: cylindrical, narrow (p); flat, wide (d). The primitive state is retained by the sister genus and all but a single species of *Olla*. This character is quite variable within the rest of the allied genera.
8. Base of common oviduct: swollen, ridged (p); not swollen or ridged (d). The derived state, which is found in a single *Olla* species, is actually a reversion to the even more primitive state which occurs widely outside of *Olla* and its sister genus. Data are lacking for *Olla roatenensis*.
9. Postcoxal line of abdomen: with oblique line (p); without oblique line (d). The presence or absence of the oblique line is often used to characterize different coccinelline genera in the North American fauna. Most of the fauna allied to *Olla* show the primitive state, whereas the derived state occurs in only one species of *Olla* and independently in single species or small species groups within some of the allied genera.
10. Shape of abdomen: short, broad (p); somewhat elongate (d). The primitive state is characteristic of all but one of the *Olla* species and the three most closely allied genera.
11. Ground color of elytron (pale color form): ivory, gray, or beige (p); bright yellow (d). This character is considered only within *Olla*. The derived state occurs in a single species.

Remarks. Although it is impossible to say when the split between *Olla* and *Cirocolla* oc-

curred, we do know from the scant fossil record that a number of extant coccinelline genera were established by the Upper Oligocene (Watson 1956). According to most models, the geographical configuration of Central America would have been quite different during this time (Coney [1982], Buskirk [1985], Smith [1985], and Liebherr [1988] summarize many of the later models), and the isthmus which connects Central and South America would not yet have been established. There is considerable evidence for the existence of an island chain (the proto-Antilles) which could have allowed some interchange of coccinellid fauna through island-hopping during the Tertiary (Fig. 40, *a*). These opportunities would vary according to changes in interisland distances, climatic fluctuations, and the island surface area available for colonization (governed by changes in sea level and regional tilting) (Buskirk 1985).

At some point in time, the common ancestor of *Olla* and *Cirocolla* may have spread, via the island chain, from South America (source area for this group [Vandenberg 1987]) to upper Central America and southern Mexico. The split between these two genera might then have occurred when the populations (due to some of the factors mentioned above) became isolated: the *Cirocolla* line in South America and the *Olla* line in Central America. Using the time framework provided by the fossil records of other coccinellid genera, we would expect that the two genera diverged some time in the Tertiary and probably before the Upper Oligocene (Fig. 40*b*).

At the second node (Fig. 40), *O. roatanensis* diverged from the remaining *Olla* species. If we assume that *O. roatanensis* is endemic to Roatan Island and did not simply disperse there from the mainland, then the maximal amount of time for the diversification of all the known species of *Olla* could be established by determining the age of the island after it last rose above sea level. Although dispersal is actually a rather likely scenario for members of this highly vagile genus, the analysis is carried out here as an intellectual exercise.

Williams (1969) suggested that with low islands such as Roatan, the final emergence did not occur until sometime in the Pleistocene. It is not clear, however, whether Williams considered only the present height of Roatan in conjunction with past changes in sea level, or whether he considered that the complex regional uplift and tilting that have occurred in recent times (McBirney & Bass 1967) may have altered the absolute height of the island from what it once was. Determining the chronological framework for the evolution of the *Olla* species must await a more complete resolution of the geological history of the island, but it could represent a span of less than 1.6 million yr if the analysis of Williams and the biological–evolutionary assumptions of the
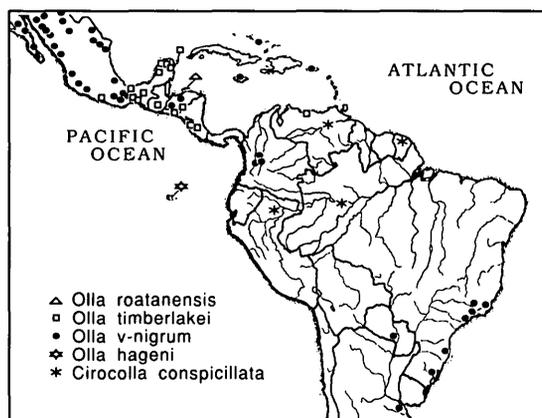

Fig. 41. Plot of locality data for *Olla* and *Cirocolla* spp. excluding North American range of *O. v-nigrum*. Westernmost two localities for *Cirocolla conspicillata* represent country-only data for Peru and Venezuela.

current model are correct. The pronounced differences between the male genitalia of *O. roatanensis* and its congeners suggest that cladogenesis occurred much earlier than this, perhaps in the Miocene or Pliocene.

The second node separates *O. timberlakei* from *O. v-nigrum* plus *O. hageni*. The locality records for *O. timberlakei* and *O. v-nigrum* suggest there may be some areas of sympatry between them, whereas regions of higher elevation separate these two species over much of their range. This observation suggests that either the distribution of their ancestral species was divided by the uplift of the mountain ranges, or the ancestral species dispersed over a preexisting mountain barrier and could not maintain genetic continuity across it. Pleistocene climatic oscillations, acting in combination with preexisting geographical features, could have resulted in disjunction of the ancestral species via biotic elevational shifts (Fig. 40, *c*) (Brown & Gibson 1983, Kohlmann & Halffter 1988). A third possibility is that the mountains were not directly involved in the speciation event but simply mark a boundary between different ecological habitats which tend to favor one or the other of the two species.

Assuming a Central American origin, a southward dispersal of *Olla* is evidenced by the present-day distribution of its member species (Fig. 41). However, it is not possible to place this event chronologically or even in relation to dichotomies in the cladogram. The establishment of a Panamanian land bridge in the late Pliocene–early Pleistocene would certainly have facilitated southward expansion during periods of favorable climate. Nevertheless, earlier dispersal across the sea barrier by the antecedent of *O. timberlakei* and its sister taxon cannot be ruled out. In this latter scenario, the origin of the *O. v-nigrum–hageni* stock could be due to isolation in South America, and the presence of *O.*

v-nigrum in Central America the result of a more recent reentry.

The terminal cluster in the phylogenetic diagram contains the species *O. v-nigrum* and *O. hageni*. Although this cluster is supported by a single character only, a very recent divergence between these species is strongly suggested by the formation of hybrid embryos in laboratory crosses (see hybridization experiments for *O. hageni*). It is reasonable to speculate that the endemic Galapagos species, *O. hageni*, was derived directly from *O. v-nigrum* because the latter is widespread and a successful colonizer of islands (see Fig. 41). If founding individuals of *O. v-nigrum* resulted in an established colony on the Galapagos Islands, that colony might be expected to evolve rapidly because of genetic drift and the unique selection pressures found in the new island habitat. It is notable that the only other coccinelline species known from the Galapagos are *Cycloneda sanguinea* (L.) (a good island colonizer and almost as ubiquitous as *O. v-nigrum*) and *Adalia galapagoensis* which, despite its current generic placement, is clearly a sister species of *C. sanguinea*.

A maximal age for *Olla hageni* can be determined from an estimate of the age of the Galapagos Islands. Recent work by Hickman & Lipps (1985) suggests that these islands are younger than previously believed and that all adaptive radiation in the terrestrial biota has occurred since 3–4 m.y.a. For a group such as *Olla,* the maximal time span must actually be considerably less because these predators would first require the breakdown of volcanic rock into soil, the establishment of flora, and the introduction of a suitable phytophagous insect fauna before they could colonize the islands successfully (Fig. 40, *d*).

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