

THE NEW WORLD GENUS *CYCLONEDA* CROTCH
(COLEOPTERA: COCCINELLIDAE: COCCINELLINI): HISTORICAL
REVIEW, NEW DIAGNOSIS, NEW GENERIC AND SPECIFIC SYNONYMS,
AND AN IMPROVED KEY TO NORTH AMERICAN SPECIES

NATALIA J. VANDENBERG

Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, % National Museum of Natural History, Smithsonian Institution, Washington, DC, 20560-0168, U.S.A. (e-mail: nvandenb@sel.barc.usda.gov)

Abstract.—Taxonomic, nomenclatorial, and comparative morphological studies of *Cycloneda* Crotch are reviewed. The genus is diagnosed and compared to both related and superficially similar taxa. *Pseudadonia* Timberlake is recognized as a junior synonym (**n. syn.**). The species composition of the fauna is delineated, but the need to re-examine species limits and nomenclatorial priorities is stressed. New synonyms are proposed for two species of *Cycloneda* occurring in North America: *Coccinella krikkeni* Iablokoff-Khnzorian, reported from India, and *Cycloneda atra* Casey (of unknown origin) are **new junior synonyms** of *Cycloneda munda* (Say); *Cycloneda hondurasica* Casey (Honduras) and *Coccinella reflexa* Germain (Chile) are **new junior synonyms** of *Cycloneda sanguinea* (Linnaeus). *Adalia galapagoensis* Van Dyke is transferred to the genus *Cycloneda* (*Cycloneda galapagoensis*, **n. comb.**) and identified as a close relative of *Cycloneda sanguinea*. *Cycloneda sanguinea caymana* Chapin is elevated to full species status (*Cycloneda caymana*, **n. status**). A new key to species of North American *Cycloneda* is provided.

Key Words: *Cycloneda*, *Coccinellina*, *Pseudadonia*, Synonychini, Coccinellini, lady beetle, systematics, synonymy, Nearctic, Neotropical

Cycloneda Crotch is a New World genus of lady beetles in the tribe Coccinellini. In Central and South America (Blackwelder 1945), the genus is a composite one, comprising an assemblage of two dozen or more species which generally share a rounded convex body form, highly polished cuticle, and little else. In contrast, the three North America indigenes—*Cycloneda sanguinea* (L.) (type species), *C. munda* (Say), and *C. polita* Casey—appear to form a close-knit, monophyletic group, whose members often have been confused in the literature (Gordon and Vandenberg 1993). These species are characterized by red to yellowish elytra

without black spots, and a black pronotum with a white border design and pair of discal spots (Fig. 9). The basic components of the white design are often coalesced to form a complete or broken ring in each lateral third (Figs. 2, 5), and a median spur shaped mark is often present at anterior border (Figs. 2, 5, 8).

The North American *Cycloneda* were keyed and diagnosed most recently by Gordon (1985), who followed Leng (1903) in the use of pronotal color patterns and elytral ground color in the separation of species (treated as varieties by Leng 1903). Unfortunately, these selected attributes are less

than completely reliable, particularly in the identification of specimens from the western United States. In addition, both of the above authors excluded the species *Cycloneda atra* Casey (1899) from their revisions on the assumption that the unique all-black type specimen from an unrecorded locality was unlikely to be a member of the North American fauna.

Here, I resolve the identity of *Cycloneda atra* and that of a second equally mysterious specimen from Southern India described by Iablokoff-Khnzorian (1982) as *Coccinella krikkeni* Iablokoff-Khnzorian. The identities of *Coccinella reflexa* Germain (1854) from Chile and *Cycloneda hondurasica* Casey from Central America also are investigated. As a result, four new synonyms are proposed, two each for *Cycloneda munda* and *Cycloneda sanguinea*. The taxonomic history of the genus *Cycloneda* is reviewed, the composition of the Neotropical *Cycloneda* fauna discussed, and a new key to North American *Cycloneda* is proposed to make the identification of species more reliable.

HISTORICAL RESUMÉ

The name *Cycloneda* was first applied by Crotch (1871) as a replacement name for *Daulis* Mulsant (1850) (preoccupied by *Daulis*, Erichson 1842). Although Crotch had restricted use of the name to the New World fauna (about 40 species), he still referred to *Cycloneda* as "an unsatisfactory assemblage of species having but little in common" and lamented the lack of characters to separate it into meaningful groups (Crotch 1874). The subsequent designation of *Coccinella sanguinea* Linnaeus as the type species of *Cycloneda* (Crotch 1874) only added to existing taxonomic confusion. While *C. sanguinea* clearly exemplified the rounded convex body form (Figs. 8, 10) of most of its nominal congeners, it was not particularly closely related to the majority of them. Conversely, many of its true affiliates (Figs. 12, 13) were relegated to other genera because of their flatter, more

elongated forms. Subsequent authors provided keys and diagnoses for *Cycloneda* (Casey 1899, Leng 1920), but clearly concerned themselves only with an easily definable subgroup consisting of the three North American species (*C. sanguinea*, *C. munda*, *C. polita*) and synonyms thereof. Casey split off two new genera—*Olla* (1899) and *Spiloneda* (1908)—but this did little to improve the overall classification. With the transfer of additional species to *Olla* (Casey 1908), that genus soon proved as heterogeneous and ill-defined as *Cycloneda* (Vandenberg 1992). *Spiloneda*, on the other hand, has remained monotypic because it was stipulated for "such forms as Gilardini, Muls., from Colombia and Central America . . ." (Casey 1908) without detailing additional species names or distinguishing traits.

The examination of internal genital structures was an important advancement for lady beetle taxonomy, although it conferred no immediate benefit to the classification of *Cycloneda* species. Weise introduced the use of male genitalia (shape of basal lobe) for distinguishing lady beetles of similar habitus (e.g., Weise 1904b), but did not use these structures for defining genera or determining broader relationships. He contributed a heterogeneous assortment of new species to *Cycloneda* between 1898 and 1922 (Weise 1898, 1902, 1904a, 1906, 1922).

Wilson (1926) conducted a morphological study on the male and female genitalia of selected representatives of the family Coccinellidae. He found characteristics which suggested a close relationship between *Cycloneda* and *Coccinella*, and indicated that the male genitalia of *Olla* were so extraordinary as to set it well apart from the other genera studied. Wilson's observations appear to have been overlooked by a subsequent generation of lady beetle taxonomists who continued to stipulate minor differences in external morphology, while ignoring the abundant generic characters provided by genital structures.

Chapin (1941) was one of the first specialists to question the value of external characteristics used to separate *Cycloneda* from the Neotropical genera *Neda* Mulsant, *Procula* Mulsant, and *Olla*, all of which had been grouped together in the tribe Synonychini. He found that ranking a random selection of 17 species by epipleural width or depth of mesosternal emargination (at the time considered key differentiating characteristics), failed to segregate species according to their presumed generic placement or to produce significant breaks between groups of species in the series. In contrast, he observed that three or more definite types of genitalia could be found within the series, yet he made no attempt to revise generic assignments based on that observation.

Timberlake (1943) refined the definition of *Cycloneda* by restricting the name to “*sanguinea* and allies with immaculate elytra.” He described three new genera for some of the former *Cycloneda* species based on material in the famous Koebele Collection—*Paraneda*, *Erythroneda*, and *Chloroneda*. Unfortunately, he did not study types or material from South America which might have allowed him to resolve some of the erroneous species synonymies proposed by Crotch (1874) and perpetuated by other authors. He was uncertain, therefore, of the number of valid species which should have been included in each of these new genera.

Timberlake (1943) also described the genus *Coccinellina* (type species *Coccinella emarginata* Mulsant) (Fig. 13) for Neotropical species formerly classified in *Coccinella*, and the genus *Pseudadonia* (type species *Pseudadonia chiliana* Timberlake) (Fig. 12) based on a single male specimen from Chile with dilated front and middle basitarsi (compare Figs. 15 and 16). Timberlake’s generic key characterized the epipleura of *Coccinellina* and *Pseudadonia* species as “horizontal and never much expanded” and those of *Cycloneda* species as “more or less

inclined and descending externally or very broad.”

Despite an often noted resemblance between *Cycloneda* species (sensu Timberlake 1943) and *C. emarginata* (Mulsant 1850, Crotch 1874, Koebele in Timberlake 1943), Timberlake did not make a rigorous comparison between *Cycloneda* and his new genus *Coccinellina*, undoubtedly influenced by the fact that members of these genera conventionally were placed in two distinct tribes (Synonychini and Coccinellini, respectively) (Korchevsky 1932). Actually, both nominal genera exhibit a wide range of epipleural architecture with considerable cross-generic overlap. Although *Cycloneda sanguinea* (type) may be said to have broad epipleura which are steeply inclined externally (Fig. 7), its congeners, *C. polita* (Fig. 4) and *C. munda*, (Fig. 1) have narrower epipleura which are nearly horizontal, as in *Coccinellina emarginata*. The epipleura of *C. pulchella* (placed in *Coccinellina* by Timberlake) (Fig. 14) are broader than in either *Cycloneda polita* or *C. munda*. There is also significant sexual dimorphism: in all of the aforementioned species, the male epipleura tend to be broader and more steeply inclined than the female epipleura.

Mader (1958) provided a key to *Cycloneda* species and former *Cycloneda* species useful for identification purposes, but based almost entirely on color patterns. He made no attempt to validate or refute the genera proposed by Casey and Timberlake, and did not discuss male genital characters.

Chapin (1969) synonymized *Pseudadonia chiliana* with *Coccinella fulvipennis* (placed in *Coccinellina* by Timberlake). Chapin continued to recognize *Pseudadonia* as a valid genus even though the distinctive characteristic of the inflated basitarsi of the type specimen was confirmed as gender specific, and no derived characteristic was identified for *Coccinellina* which would exclude *C. fulvipennis* from membership.

Several important regional works covering the genus *Cycloneda* were published in the next two decades. Gordon (1985) re-

vised the North American *Cycloneda* species, but did not attempt to review non-North American species names and types for possible synonymies. Gordon compared the external morphologies of *Cycloneda* and *Olla* and contrasted the male and female genitalia, but recognized the need to study the Neotropical species in order to assess the significance of observed differences and determine generic boundaries. Iablokoff-Khnzorian (1982) included some remarks on New World Coccinellidae in his revision of the Old World species. He concluded that *Cycloneda* is most closely related to *Harmonia* and *Xanthadalia*, but he classified a newly discovered species (*C. krikkeni* Iablokoff-Khnzorian) with a remarkable resemblance to *Cycloneda munda* in the genus *Coccinella*.

Arioli (1985) contributed an analysis (similarity phenogram) of the Coccinellini of Rio Grande do Sul, Brasil. She utilized some characters with good potential as indicators of phylogenetic relationships (e.g., male genitalia, postmetacoxal line, pronotal maculation), but the addition of too many trivial (labile) characters (e.g., coloration of certain structures) had the effect of obscuring some of the relationships otherwise nicely revealed in her analysis, and in one case yielded the lowest similarity coefficient for a male and female of the same species.

The idea of synonymizing *Coccinellina* with *Cycloneda* was first suggested publicly by Iablokoff-Khnzorian in an informal correspondence to *Coccinella* newsletter (1990), although it was proposed earlier in a format not intended as a permanent scientific record (Vandenberg 1987). Vandenberg published a series of papers between 1988 and 1996 which refined and clarified the relationships between *Cycloneda* and other taxa, but which focused primarily on the revision (*Erythroneda*, *Olla*) or new description (*Cirocolla* Vandenberg, *Spilindolla* Vandenberg) of genera whose species had been improperly classified in *Cycloneda*. The close relationship between *Cyclo-*

neda and three other genera—*Coccinella*, *Erythroneda*, and *Neocalvia*—was briefly discussed in a revision of the genus *Erythroneda* (Vandenberg and Gordon 1988). Vandenberg (1992) revised the genus *Olla*, provided a key to major genitalic archetypes occurring in the former Synonychini and indicated the proper genus group affiliation for each genitalic configuration. These different archetypes undoubtedly correspond to the several categories referred to by Chapin (1941) in his studies of the male genitalia of *Cycloneda* sensu lato. Although Chapin's work did not list the species examined, his handwritten records and slide collection at the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), show that he dissected examples of each of the disparate lineages classified in *Cycloneda* at that time. Vandenberg's treatment of the new genus *Spilindolla* (Vandenberg and Gordon 1996) provided additional information and genitalic illustrations for separating Neotropical lady beetle genera and generic groups. Using these improved criteria to determine relationships, the male and female genitalia of most "*Cycloneda*" species segregate with *Neda*, *Olla*, *Spiloneda*, *Paraneda*, and allied genera, or with *Egleis* Mulsant and allies, while those of the type species and a minority of others reveal a much closer relationship to *Coccinella*. Vandenberg (1992) also indicated differences between the larval dorsal armature of *Cycloneda* and superficially similar species allied to *Olla*, and, in a later work (Gordon and Vandenberg 1993), identified distinctive features of the larval head capsule and microsculpturing for separating species of *Olla*, *Cycloneda*, and *Coccinella*.

Thus, *Cycloneda* has been a composite genus since its conception in 1871. A few species have been removed through the creation of new genera, but taxonomic progress has been hindered severely by 1) the nearly exclusive use of superficial and poorly defined external characters to determine generic assignments, 2) failure either

to examine the male and female genitalia or to attach proper evolutionary significance to their observed patterns of similarity, 3) a tendency for researchers to focus on taxa from only one region, one tribe or a single collection, and 4) the description of new species based on unknown (*Cycloneda atra*) or dubious (*Coccinella krikkeni*) type localities, which were then omitted from later regional studies.

The genus *Cycloneda* (as recognized here) is in need of a complete species level revision. Many species exhibit both clinal variation (Vandenberg 1997) and discrete polymorphism; others appear poorly differentiated from their congeners, making the delimitation of the different species particularly challenging. I hope that the present preliminary contribution will be of use to those who wish to pursue this interesting area of investigation.

Genus *Cycloneda* Crotch

Cycloneda Crotch 1871: 6 (list of species) (Type species: *Coccinella sanguinea* L., by subsequent designation of Crotch 1874); 1873a: 371 (U.S. revision); 1873b: 50 (N. Amer. checklist) 1874: 162 (world revision); Gorham 1892: 169 (C. Amer., distribution); Casey 1899: 84 (U.S., generic key); 1908: 404 (generic limits); Leng 1920: 216 (N. Amer. catalog); Wilson 1926: 63 (genital morphology, generic comparisons, higher classification); Korschefsky 1932: 282 (world catalog); Chapin 1941: 165 (generic comparisons); Timberlake 1943: 23 (generic limits); Wingo 1952: 24 (Mex., C. and S. Amer., W. Indies checklist); Mader 1958: 238 (Amer. key to species); Hatch 1961: 181 (N. Amer. generic key); J. Chapin 1974: 62 (Louisiana revision); Belicek 1976: 330 (W. Can., Alaskan revision); Gordon 1985: 819 (N. Amer. revision, prey, distributions, genitalia); Vandenberg and Gordon 1988: 33 (generic comparison); Iablokoff-Khnzorian 1990: 460 (diagnosis, generic comparison); Vandenberg 1992: 372 (higher classification);

Gordon and Vandenberg 1993: 302 (larval descriptions, N. Amer. larval key, larval generic comparisons); Vandenberg and Gordon 1996: 547 (generic comparisons); Vandenberg 1997 (example of clinal variation in *C. ancoralis*).

Neda (*Cycloneda*): Chapuis 1876: 201.

Daulis Mulsant 1850: 296 (Type species: not designated) (not *Daulis* Erichson 1842); Crotch 1874: 162 (as synonym of *Cycloneda*) (world revision); Berg 1874: 290; Chapuis 1876: 201 (as synonym of *Neda* (*Cycloneda*) (diagnosis).

Coccinella (*Cycloneda*) Leng 1903: 202 (N. Amer. key).

Coccinellina Timberlake 1943: 15 (Type species: *Coccinella emarginata* Mulsant); Iablokoff-Khnzorian 1990: 59 (as synonym of *Cycloneda*).

Pseudadonia Timberlake 1943: 53 (Type species: *Pseudadonia chiliana* Timberlake) (preoccupied name, not *Pseudadonia* Handlirsch 1906); Chapin 1969: 468.

New synonym.

Diagnosis.—Distinguished from most other genera by the characteristic repertoire of pronotal color patterns which vary as shown (Figs. 2, 5, 8, 9, 10, 11, 12, 13, 14), or derive from Figs. 8 and 9 through loss of discal spots, or from Figs. 2 and 5 through extension of pale areas to form complete ring or solid white oval in each lateral third; head with gender specific color patterns as shown (Figs. 8, 9), ranging to all or mostly white in males and all or mostly black in females; elytra deep red to flavous or rarely ashen, with or without additional black and or white marks; venter black to dark brown marked with lighter patches. Postmetacoxal line incomplete, closely paralleling hind margin of first abdominal sternite in outer third; oblique line obsolete or represented by faint to moderately distinct integumental wrinkle (as opposed to a sharply incised line). Middle and hind tibiae with pair of spurs at apex. Infundibulum of female genitalia (Fig. 25) well developed, flared at distal end and of-

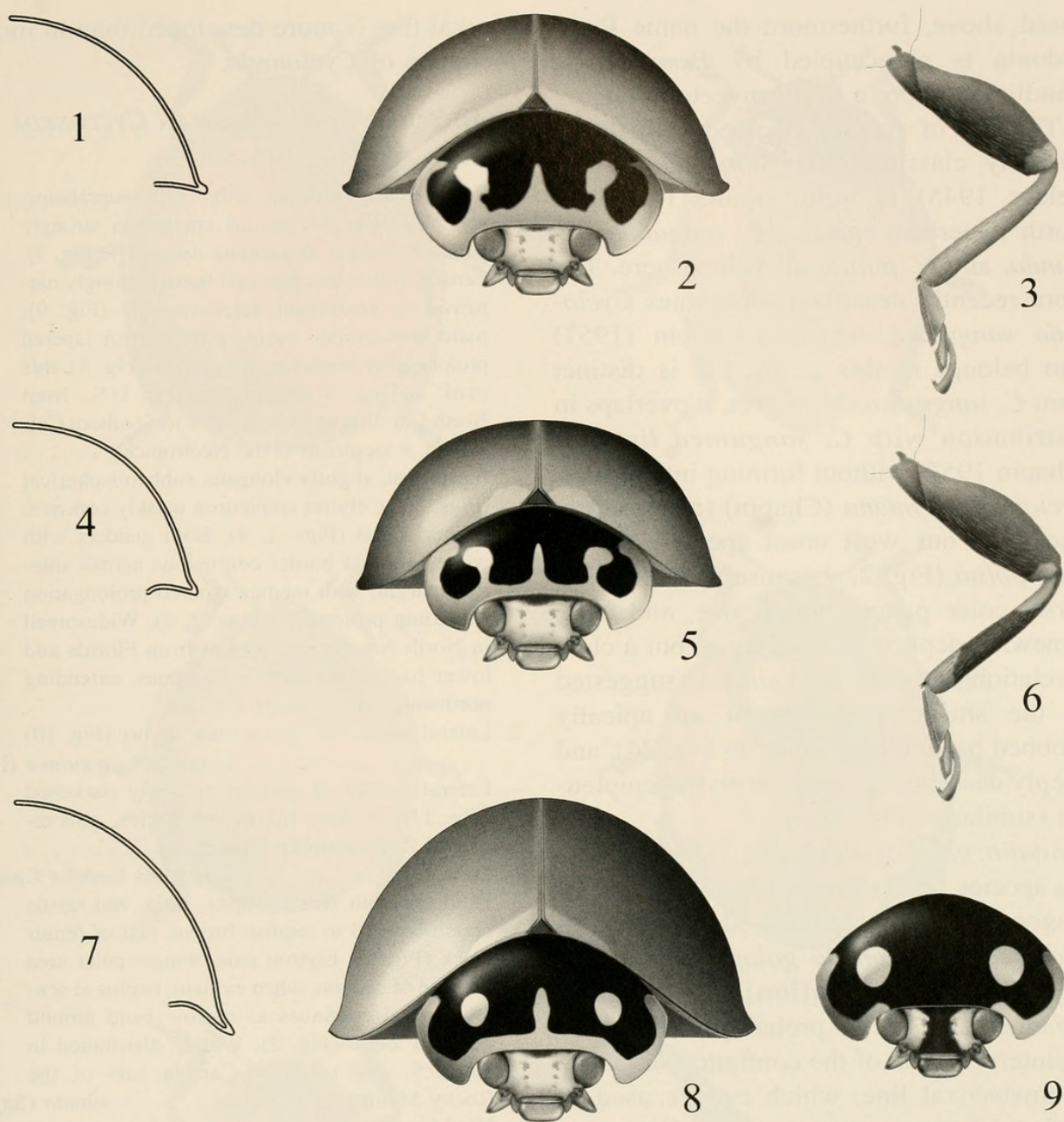
ten bearing a bulblike enlargement (sometimes obscure due to transparency) at proximal (bursal) end; siphon of male genitalia (Fig. 23) constricted before apex, terminating in a membranous area with imbedded spicules (reduced in some species); siphonal capsule well developed, often pigmented, with inner arm arcuate to angulate, outer arm often crested externally; basal lobe (Fig. 24) undivided; basal piece never highly elongated, more or less quadrate; parameres well separated at base.

Remarks.—Lady beetles with similar pronotal color patterns occur occasionally in other coccinelline genera. Species of *Adalia* with a very similar appearance can be distinguished by the form of the postmetacoxal line which recurves toward the abdominal base. *Olla* and allied genera, which make up the bulk of the Neotropical coccinelline fauna (*Olla*, *Ciocola*, *Spilindolla*, *Spiloneda*, *Neda*, *Mononeda* Crotch, *Neoharmonia* Crotch, *Procula*, *Paraneda*, *Clynis* Mulsant, *Chloroneda*), depart radically from *Cycloneda* in the form of the genitalia of both sexes: female with infundibulum absent or rarely present as a simple tubular and weakly sclerotized sheath; siphon of male genitalia not constricted before apex, terminating in a simple rounded opening, preapical projections or lobes often present; basal lobe often divided (Figs. 20–22); basal piece generally longer than wide, often highly elongate. Species related to *Mulsantina* Weise and *Egleis* can be separated by the absence of tibial spurs as well as by the form of the male (Fig. 19) and female genitalia (see Vandenberg 1992, Vandenberg and Gordon 1996 for further details).

Genera related to *Cycloneda* share the same major genitalic features outlined in the diagnosis above. Most of these can be separated easily by more obvious external characters. *Cycloneda* differs from the related genera *Erythroneda* and *Neocalvia* by the presence of black to very dark brown pigmentation on the head, pronotum and venter; the latter two genera also have ex-

ceptionally long antennae, coarsely faceted, often closely placed eyes (separated by less than two diameters) and the reddish areas of the pronotum and elytra entirely transparent (see Vandenberg and Gordon 1988 for a more detailed comparison). The Holarctic genus *Coccinella* (Figs. 17, 18) also is allied closely to *Cycloneda*. *Coccinella* can be distinguished by the very different repertoire of pronotal color patterns which feature a large, subtrapezoidal or triangular white mark in each anterior pronotal angle, sometimes narrowly joined along the anterior border. *Coccinella* species also have a more robust body and appendages, and the postmetacoxal line with a sharply incised oblique line. While *Cycloneda* is restricted to the New World and has its highest concentration in the Neotropics, *Coccinella* occurs in both the Eastern and Western Hemispheres, but does not extend south of Mexico.

Species composition.—As defined here, *Cycloneda* includes species formerly assigned to *Coccinellina* and *Pseudadonia*. Timberlake (1943) provisionally transferred the following species names from *Coccinella* when he proposed the genus *Coccinellina*: *C. ancoralis* Germar, *C. areata* Mulsant, *C. emarginata* Mulsant, *C. eryngii* Mulsant, *C. fulvipennis* Mulsant, *C. lucasii* Mulsant, *C. petiti* Mulsant, *C. pulchella* Klug. He also added two new species: *Coccinellina ecuadorica* Timberlake and *Coccinellina shannoni* Timberlake. Most of the older names have accumulated a number of synonyms as reported in the most recent checklists and catalogs (Korchevsky 1932, Blackwelder 1945), but Timberlake did not investigate the priority of existing names, nor examine the type material to determine which synonyms are justified. Gordon (1987) transferred additional species names to *Coccinellina* (*C. germainii* Crotch, *C. arcuata* Erichson, *C. ocelligera* Crotch), but cited Timberlake's work as the source of the change. Although Timberlake did not stipulate these additional names, he had made a general comment under his description of



Figs. 1–9. 1–3, *Cycloneda munda*. 1, Median cross-section, left elytron. 2, Head, pronotum and elytra, frontal view, male. 3, Left hind leg, ventral view. 4–6, *C. polita*. 4, Median cross-section, left elytron. 5, Head, pronotum and elytra, frontal view, male. 6, Left hind leg, ventral view. 7–9, *C. sanguinea*. 7, Median cross-section, left elytron. 8, Head, pronotum and elytra, frontal view, male. 9, Head, and pronotum, frontal view, female.

Coccinellina that “The neotropical species (except *C. transversoguttata* Fald.) which have been referred to *Coccinella* are rather different from the familiar holarctic species, . . .” (Timberlake 1943). Therefore, Gordon transferred all the remaining Neotropical species represented in the Crotch collection which had not already been removed through some other more recent revision. This was appropriate in all but the last case:

C. ocelligera does not belong here, but should be placed in or near *Neda*.

Pseudadonia Timberlake was always a monotypic genus. Following the synonymy proposed by Chapin (1969) it contributes only *Pseudadonia fulvipennis* (Mulsant) (= *Pseudadonia chiliana* Timberlake), a species which Timberlake also had placed in *Coccinellina*. This species fits well within the generic concept of *Cycloneda* as diag-

nosed above, furthermore the name *Pseudadonia* is preoccupied by *Pseudadonia* Handlirsch 1906, a fossil mycetophilid.

The list of species retained from those formerly classified in *Cycloneda* (Blackwelder 1945) is quite small. The three North American species, *C. sanguinea*, *C. munda*, and *C. polita*, all belong here. The more recently described subspecies *Cycloneda sanguinea caymana* Chapin (1957) also belongs in this genus, but is distinct from *C. sanguinea*. Moreover, it overlaps in distribution with *C. sanguinea limbifer* (Chapin 1957) without forming intergrades. *Cycloneda caymana* (Chapin) (**new status**) resembles our west coast species, *Cycloneda polita* (Fig. 2), because of the similar dorsal color pattern, small size, and oval, somewhat depressed body form, but a closer relationship to *C. sanguinea* is suggested by the shared attributes of an apically knobbed basal lobe (similar to Fig. 24), and steeply descending, concave elytral epipleuron (similar to Fig. 7).

Adalia galapagoensis Van Dyke (1953) is a species from Charles Island of the Galapagos Archipelago which also belongs to *Cycloneda* (*Cycloneda galapagoensis* Van Dyke (**new combination**)). Its original placement in *Adalia* probably is due to a misinterpretation of the configuration of the postmetacoxal line, which can be used to distinguish the two genera (see discussion under the diagnosis for *Cycloneda* and the ensuing remarks above). *Cycloneda galapagoensis* is a close relative of *Cycloneda sanguinea* (widespread on the island chain). The two species share a rounded convex body form and similar structure to the basal lobe of the male genitalia.

Cycloneda fryi Crotch and *Cycloneda bioculata* Korschefsky are two other species which belong in or near *Cycloneda*. *Coccinella* no. 18 in the *Biologia Centrali-Americana* (Gorham 1892) is an undescribed species which is better placed here than elsewhere. The elytra of this species are an unusual ashen color, and the oblique po-

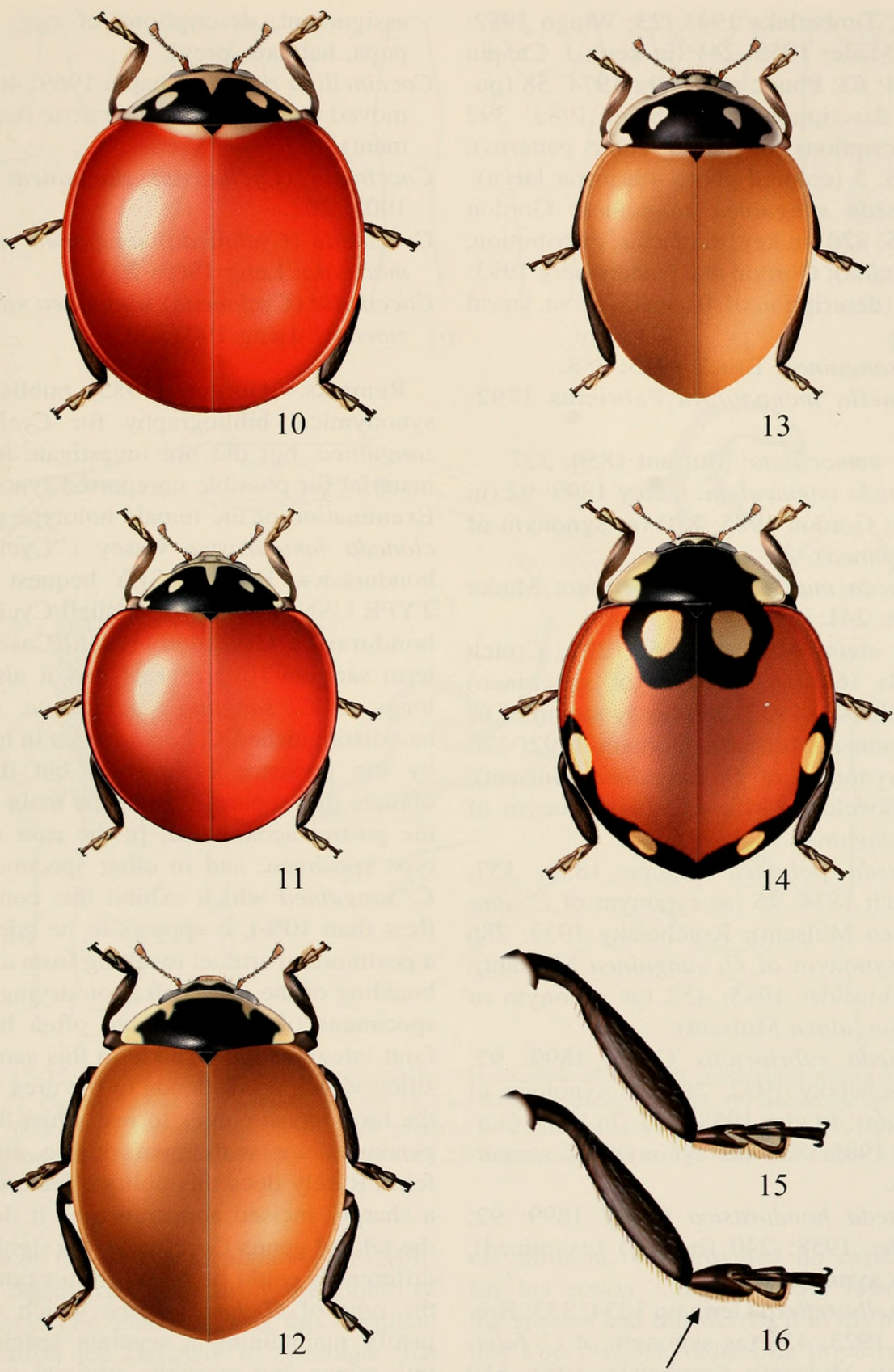
stcoxal line is more developed than in most members of *Cycloneda*.

KEY TO NORTH AMERICAN *CYCLONEDA* SPECIES

1. Form nearly circular (Fig. 10); suprahemispherical (Fig. 8); elytral epipleuron strongly concave, steeply descending externally (Fig. 7). Female with white pronotal border strongly narrowed or interrupted anteromedially (Fig. 9); male with border entire, with median tapered prolongation extending posteriorly (Fig. 8), this mark lacking in female. Southern U.S., from North Carolina to Florida, west to Southern California, widespread in the Neotropics 2
- Form oval, slightly elongate; subhemispherical (Figs. 2, 5); elytral epipleuron weakly concave, subhorizontal (Figs. 1, 4). Both genders with white pronotal border continuous across anterior margin, with median tapered prolongation extending posteriorly (Figs. 2, 5). Widespread in North America but absent from Florida and lower part of southern most states, extending northward into southern Canada 3
2. Lateral border of elytron clear amber (Fig. 10) *sanguinea sanguinea* (L.)
- Lateral border of elytron narrowly darkened (Fig. 11). A West Indian subspecies, also recorded from southern Florida *sanguinea limbifer* Casey
3. Hind leg with femoral apex, tibia, and tarsus cream colored to reddish brown, rest of femur black (Fig. 3). Elytron pale orange; paler area on base of elytron, when evident, begins at scutellum and continues as narrow band around humeral angle (Fig. 2). Widely distributed in the U.S. and southern Canada east of the Rocky Mountains *munda* (Say)
- Hind leg with femoral apex, small area at base and apex of tibia, and tarsus cream colored to reddish brown, rest of femur and tibia black (Fig. 6). Elytron pale orange to dark red; paler area on base of elytron, when evident, restricted to semicircular spot adjacent to scutellum, not attaining humeral angle (Fig. 5). Widely distributed in the western U.S. and southern Canada from the Pacific coast through the Rocky Mountains *polita* Casey

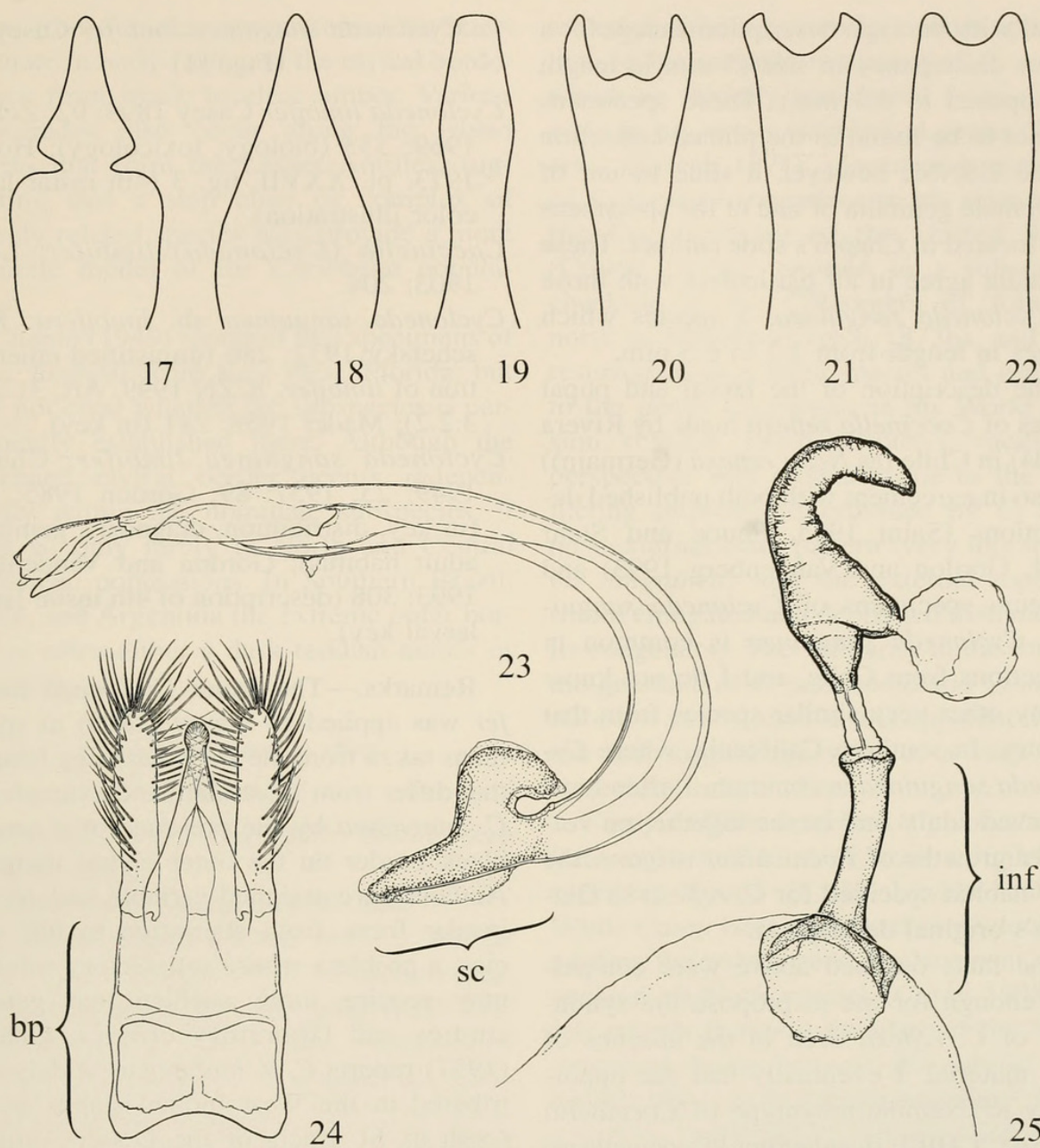
Cycloneda sanguinea sanguinea (L.) (Figs. 10, 23–25)

Coccinella sanguinea Linnaeus 1763: 10.
Daulis sanguinea: Mulsant 1850: 326.
Cycloneda sanguinea: Crotch 1871: 6;
 Crotch 1873a: 372; Crotch 1874: 164;
 Blatchley 1910: 515; Korschefsky 1932:



Figs. 10–16. 10–14, Habiti of *Cycloneda* species (male). 10, *C. sanguinea sanguinea*. 11, *C. sanguinea limbifer*. 12, *C. fulvipennis* (= *Pseudadonia chiliana*, type species of *Pseudadonia*). 13, *C. emarginata* (type species of *Coccinellina*). 14, *C. pulchella*. 15–16, Middle legs of *Cycloneda* species. 15, Middle leg of *C. emarginata* (male) showing unmodified basitarsus typical of most *Cycloneda* species. 16, Middle leg of *C. fulvipennis* (male) showing swollen basitarsus (arrow).

- 286; Timberlake 1943: 23; Wingo 1952: 46; Mader 1958: 241 (in key); J. Chapin 1974: 62; Phuoc and Stehr 1974: 58 (pupal description, key); Saini 1983: 392 (descriptions of larval color patterns); 1985: 5 (colored photo 4th instar larva).
- Cycloneda sanguinea sanguinea*: Gordon 1985: 820 (in key, diagnosis, distribution, genitalia); Gordon and Vandenberg 1993: 307 (description of 4th instar larva, larval key).
- Neda sanguinea*: Bruch 1915: 388.
- Coccinella immaculata* Fabricius 1792: 267.
- Daulis immaculata*: Mulsant 1850: 327.
- Cycloneda immaculata*: Casey 1899: 92 (in key); Gordon 1985: 820 (as synonym of *sanguinea*).
- Cycloneda munda* ab. *immaculata*: Mader 1958: 241.
- Daulis steini* Mulsant 1866: 222; Crotch 1874: 164 (as synonym of *sanguinea*) Korchefsky 1932: 286 (as synonym of *C. sanguinea* Mulsant); Gorham 1892: 170 (as synonym of *C. sanguinea* Mulsant); Blackwelder 1945: 452 (as synonym of *C. sanguinea* Mulsant).
- Cycloneda polonica* Hampe 1850: 357; Crotch 1874: 45 (as synonym of *C. sanguinea* Mulsant); Korchefsky 1932: 286 (as synonym of *C. sanguinea* Mulsant); Blackwelder 1945: 452 (as synonym of *C. sanguinea* Mulsant).
- Cycloneda rubripennis* Casey 1899: 92; Korschefsky 1932: 285 (as synonym of *munda*); Mader 1958: 241 (in key); Gordon 1985: 820 (as synonym of *sanguinea*).
- Cycloneda hondurasica* Casey 1899: 92; Mader 1958: 240 (in key) (examined).
- New synonym.**
- Coccinella reflexa* Germain 1854: 333; Brèthes 1923: 454 (as synonym of *C. fulvipennis* Mulsant); Korchefsky 1932: 510 (as synonym of *C. fulvipennis* Mulsant); Blackwelder 1945: 454 (as synonym of *C. fulvipennis* Mulsant) (examined). **New synonym.**
- Neda reflexa*: Rivera 1904: 16 (generic re-assignment, descriptions of egg, larva, pupa, habitats, prey).
- Coccinellina reflexa*: Chapin 1969: 467 (removed from synonymy, generic reassignment).
- Coccinella (Cycloneda) sanguinea*: Leng 1903: 202.
- Coccinella (Cycloneda) sanguinea* var. *immaculata*: Leng 1903: 203.
- Coccinella (Cycloneda) sanguinea* var. *rubripennis*: Leng 1903: 203.
- Remarks.—Gordon (1985) published a synonymical bibliography for *Cycloneda sanguinea*, but did not investigate foreign material for possible unreported synonyms. Examination of the female holotype of *Cycloneda hondurasica* Casey ("Cycloneda hondurasica: Hond/CASEY bequest 1925/TYPE USNM 35524 [red label]/Cycloneda hondurasica Csy[handwritten]/Casey determ sanguin-10") reveals that it also belongs to *C. sanguinea sanguinea*. Casey had distinguished *C. hondurasica* in his key by the presence of a short but distinct oblique line separated from the main arc of the postmetacoxal line. In the case of the type specimen, and in other specimens of *C. sanguinea* which exhibit this condition (less than 10%), it appears to be primarily a postmortem artifact resulting from a slight buckling of the abdomen upon drying. Live specimens of *C. sanguinea* often have a faint integumental wrinkle in this same position which corresponds to the area where the hind tarsus comes to rest when the appendages are withdrawn during a death feint. Rarely does this oblique feature have a sharply incised appearance as it does in the related genus *Coccinella*. No significant differences could be found from examining the type of *C. hondurasica* which would justify maintaining a separate species for this minor and possibly artificial variant. Casey, himself, designated the specimen as "sanguin-10" and placed it together with other *C. sanguinea* in a single unit tray.
- Germain (1854) reported the common occurrence of adult and larval *Coccinella*



Figs. 17-25. 17-22, Basal lobes of male genitalia, characteristic of different coccinelline genera (diagrammatic). 17, *Coccinella transversoguttata* Mulsant. 18, *Coccinella monticola* Mulsant. 19, *Mulsantina* sp. 20, *Olla* sp. 21, *Neda* sp. 22, *Paraneda* sp. 23-24, Male genitalia of *Cycloneda sanguinea sanguinea*. 23, Siphon (sc = siphonal capsule). 24, Phallobase (bp = basal piece). 25, Female genitalia of *Cycloneda sanguinea sanguinea* (inf = infundibulum).

reflexa on fennel (*Foeniculum vulgare* Miller) in Santiago, Chile during the month of February. The consistency of this hostplant association led Germain to speculate that the species is phytophagous; however, his description clearly indicates a glabrous habitus, and therefore not a member of the only phytophagous subfamily in the Neotropics: Epilachninae. Brèthes (1923) placed *C. reflexa* as a synonym of *Coccinella fulvipen-*

nis Mulsant, but provided no explanation for his action. Chapin (1969) resurrected the species and transferred it to his new genus *Coccinellina*, indicating important differences in the size and dorsal color patterns for the two nominate species. Although Chapin never examined the type material, he based his concept of *C. reflexa* on specimens taken in Arica, Chile in 1966 by Alfonso Aguilera P., which compared in

detail with the type description except for a minor discrepancy in size (5 mm in length as opposed to 6.3 mm). These specimens are not to be found in the pinned collection at the USNM; however, a slide mount of the female genitalia of one of the specimens was located in Chapin's slide cabinet. These genitalia agree in all particulars with those of *Cycloneda sanguinea*, a species which ranges in length from 3.2 to 6.5 mm.

The description of the larval and pupal stages of *Coccinella reflexa* made by Rivera (1904) in Chile (as *Neda reflexa* (Germain)) is also in agreement with both published descriptions (Saini 1985, Phuoc and Stehr 1974, Gordon and Vandenberg 1993) and museum specimens of *Cycloneda sanguinea*. *Cycloneda sanguinea* is common in collections from Chile, and I do not know of any other very similar species from that country. In southern California, where *Cycloneda sanguinea* is common, I often have observed adults and larvae together on volunteer growths of *Foeniculum vulgare*, the very habitat specified for *C. reflexa* in Germain's original description.

The facts outlined above were compelling enough for me to propose the synonymy of *C. reflexa* even in the absence of type material. I eventually had the opportunity to examine a syntype of *Coccinella reflexa* ("CHILE [handwritten]/Coccinella reflexa Germ.[handwritten]/SINTIPO/CHILE M.N.H.N. Tipo No 2158") from the Museo Nacional de Historia Natural, Santiago, and confirm my suspicions. It is a representative female of *Cycloneda sanguinea*, with head and pronotal markings much as in the example illustrated (Fig. 9). The specimen is card mounted, and the elytra are slightly parted at the sutural apex, giving an initial impression of less convexity, which is dispelled upon closer examination. The specimen is at the upper range of body size for the species (6.3 mm), but a number of examples from Chile and Argentina boast similar dimensions.

Cycloneda sanguinea limbifer Casey
(Fig. 11)

Cycloneda limbifer Casey 1899: 92; Zelený 1969: 333 (biology, toxicology); Hodek 1973: pl. XXVII, fig. 3 (4th instar larva color illustration).

Coccinella (*Cycloneda*) *limbifer*: Leng 1903: 204.

Cycloneda sanguinea ab. *limbifera*: Korschefsky 1932: 286 (unjustified emendation of *limbifer*, ICZN 1999, Art. 31.2.1–3.2.2); Mader 1958: 241 (in key).

Cycloneda sanguinea limbifer: Chapin 1949: 23; 1957: 89; Gordon 1985: 823 (in key, distribution, diagnosis, genitalia, adult habitus); Gordon and Vandenberg 1993: 308 (description of 4th instar larva, larval key).

Remarks.—The name *Cycloneda limbifer* was applied by Casey (1899) to specimens taken from the Bahamas (Egg Island), that differ from most mainland examples of *C. sanguinea* by the presence of a narrow black border on the outer elytral margins. Authors have assigned variable rank to this insular form, from aberration to full species, a problem whose satisfactory solution may require more sophisticated genetic studies and laboratory crosses. Chapin (1957) reports *C. s. limbifer* as widely distributed in the West Indian islands as far south as St. Lucia of the Lesser Antilles. However, not all of the island forms are strictly comparable. In specimens from Cuba, Haiti, Dominican Republic, and Puerto Rico, the elytral border is always darkened, and the beetles are further distinguished from their mainland relations by possessing a shorter body form, a broader elytral base (relative to pronotal width) and a tendency towards dwarfism, particularly in males (Fig. 11). If specimens from only these islands were compared to the mainland (Fig. 10), one might conclude that *limbifer* is deserving of full species status. On the other hand, specimens from the Bahamas are much like those from the mainland except for the darkened border, and speci-

mens from Jamaica appear somewhat intermediate in body form and the elytral border varies from black to clear amber. Various intergrades also occur along the island chains that form the Lesser Antilles, suggesting that a step cline or complex of closely related species may provide a more accurate model of the Caribbean populations.

Chapin (1949) reported two specimens of *C. s. limbifer* from Key West, Florida, but it is not clear whether the subspecies is permanently established there. Although the darkened elytral border occurs independently within the nominate subspecies, it does so only rarely in North and Central American populations. In Southern Brazil, Chile, and Argentina the extreme outer border is often either a dark reddish amber or blackish.

Cycloneda munda (Say)

(Figs. 1–3)

Coccinella munda Say 1835: 202; Crotch 1874: 107.

Daulis munda: Mulsant 1850: 324.

Cycloneda munda: Crotch 1871: 6; 1873a: 372 (as synonym of *C. sanguinea* Linnaeus); Casey 1899: 93; Leng 1920: 216; Korschefsky 1932: 284; Timberlake 1943: 23; Wingo 1952: 46; Mader 1958: 241 (in key); J. Chapin 1974: 63; Phuoc and Stehr 1974: 58 (pupal description, key); Gordon 1985: 820 (in key, distribution, diagnosis, genitalia, adult habitus); Gordon and Vandenberg 1993: 308 (description of 4th instar larva, larval key).

Coccinella (*Cycloneda*) *sanguinea* var. *munda*: Leng 1903: 203.

Cycloneda ater Casey 1899: 93; Gordon 1985: 820 (examined). **New synonym.**

Cycloneda atra Casey 1908: 405; Leng 1920: 216.

Coccinella krikkeni Iablokoff-Khnzorian 1982: 395 (examined). **New synonym.**

Remarks.—Crotch's confusion over the taxonomic boundaries of *Cycloneda* and its

included species is nowhere more apparent than in his variable treatment of *C. munda* which he initially transferred from *Coccinella* to his newly established genus *Cycloneda* (Crotch 1871), placed as a synonym of *Cycloneda sanguinea* in his revision of the Coccinellidae of the United States (Crotch 1873a), omitted in a subsequent checklist of the Coleoptera of America, north of Mexico (Crotch 1873b), and then resurrected as a valid species and returned to the genus *Coccinella* in his World revision (Crotch 1874). Crotch's vacillating perspective was probably due to the conflicting impressions provided by *C. munda*'s external color pattern (very like that of *C. sanguinea*) and the external topology (more elongated and depressed than most of its congeners). The similarity in the form of the genitalia of *C. sanguinea* and *C. munda* (Gordon 1985) resolve this apparent dilemma and support the view of a very close systematic relationship.

Casey (1899) described *Cycloneda ater* (later corrected to *atra*) from an unlabeled specimen found in the Levette cabinet. While Casey later expressed some doubt regarding the proper generic placement of the unusual all black species (Casey 1908), he felt certain it was a member of the North American fauna because the cabinet contained "little or no foreign material." Other revisions, confined to the Nearctic fauna (Leng 1903, 1920; Gordon 1985), skirted the issue of classification by declaring the specimen to be of probable foreign origin; a not unreasonable assumption considering the species failed to reappear in any other collected samples. Recent dissection and examination of the male holotype ("atra Csy[handwritten]/bequest 1925/TYPE USNM 35528 [red label]") reveal it to be a wholly typical example of *Cycloneda munda* in all respects except for the aberrant coloration. Not only are the chitinous external structures and genitalia deeply pigmented, but the internal ligaments and fat body are sooty and oddly decomposed. Thus, it would seem that the black coloration

tion is more likely due to some sort of post-mortem treatment than an expression of genetics. Backlighting the elytra with a strong light reveals a ruddy glow, suggesting the presence of the orange pigmentation found in typical examples of the species.

Iablokoff-Khnzorian described *Coccinella krikkeni* from a male specimen deposited in Naturalis, Nationaal Natuurhistorisch Museum, Leiden, and published the description, along with illustrations of the habitus and male genitalia, in a large volume on Palearctic and Oriental Coccinellinae (Iablokoff-Khnzorian 1982). While the genitalia of some *Coccinella* species are not very different from those of *Cycloneda*, the pronotal color patterns of *C. krikkeni* are highly aberrant for *Coccinella*, yet typical of *Cycloneda*. The genitalia illustrations and description of leg coloration suggest the species *Cycloneda munda*, which is restricted to the eastern United States and parts of Canada. Subsequent examination of the holotype ("Museum Leiden, S. INDIA = Madras State, Coimbatore, 1400 ft, X.1961 P.Susai Nathan/Holotypus Coccinella Krikkeni Khnz [handwritten label]") confirmed the suspected synonymy, but provided no insight as to how it came to bear such an unexpected locality label. This unique record may be the result of accidental transport through commerce, or, more likely, an accident of mislabeling.

Cycloneda polita Casey
(Figs. 4–6)

Cycloneda polita Casey 1899: 93; Timberlake 1943: 24; Mader 1958: 241 (in key); Hatch 1961: 181; Belicek 1976: 330; Gordon 1985: 820 (in key, distribution, diagnosis, genitalia, adult habitus); Gordon and Vandenberg 1993: 309 (description of 4th instar larva, larval key).

Coccinella (*Cycloneda*) *sanguinea* var. *polita*: Leng 1903: 203.

Coccinella (*Cycloneda*) *sanguinea*: Palmer 1914: 232 (not *sanguinea* Linnaeus) (description larval instars, color habitus late instar).

Cycloneda munda ab. *polita*: Leng 1920: 216; Korschefsky 1932: 285.

Cycloneda polita flava Timberlake 1943: 24.

Remarks.—Gordon synonymized the subspecies *Cycloneda polita flava* Timberlake with the nominate subspecies because it has identical genitalia, and differs only in possessing a paler elytral coloration. Although I disagree with the reasons for the synonymy, the action is still supportable. Specimens of *Cycloneda polita* with bright orange or scarlet elytra also occur within the specified range of *C. polita flava* (Alameda Co. and Santa Cruz Mountains, California); therefore, it is probably little more than an aberration which occurs at higher frequencies in some areas.

ACKNOWLEDGMENTS

I am grateful to the following individuals and institutions for their kind assistance: G. House, Department of Entomology, Smithsonian Institution, National Museum of Natural History, Washington, DC (Casey collection) (USNM) for access to the holotypes of *Cycloneda atra* Casey and *Cycloneda hondurasica* Casey; R. de Jong and J. van Tol, Naturalis, Nationaal Natuurhistorisch Museum, Leiden (RMNH) for loan of the holotype of *Coccinella krikkeni* Iablokoff-Khnzorian; M. Elgueta, Museo Nacional de Historia Natural, Santiago for loan of the syntype of *Coccinella reflexa* Germain; D. Kavanaugh, Department of Entomology, California Academy of Sciences, California for access to type material of *Adalia galapagoensis* Van Dyke; R. Pope, Department of Entomology, The Natural History Museum, London (BMNH) and Roger Booth, CAB International Institute of Entomology, London for access to type material of *Cycloneda sanguinea caymana* Casey; J. Obrycki, Department of Entomology, Iowa State University, and D. Nickle, J. Brown, E. Roberts, and R. Gordon (emeritus), Systematic Entomology Laboratory, Washington, DC for making

corrections and supplying useful comments on earlier versions of the manuscript; E. Roberts also prepared the genitalia drawings, as well as digital photographs and sketches used in making the illustrations.

LITERATURE CITED

- Arioli, M. C. S. 1985. Coccinellini no Rio Grande do Sul, Brazil (Coleoptera, Coccinellidae). *Revista do Centro de Ciências Rurais, Brazil* 15(1): 5–35.
- Belicek, J. 1976. Coccinellidae of western Canada and Alaska with analyses of the transmontane zoogeographic relationships between the fauna of British Columbia and Alberta (Insecta: Coleoptera: Coccinellidae). *Quaestiones Entomologicae* 12: 283–409.
- Berg, F. G. C. 1874. Noticias criticas sobre algunas publicaciones entomológicas. *Boletín de la Academia Nacional de Ciencias Exactas Existente en la Universidad de Córdoba* 1: 274–293.
- Blatchley, W. S. 1910. An illustrated catalogue of the Coleoptera or beetles (exclusive of the Rhynophora) known to occur in Indiana. *Bulletin, Indiana Department of Geology and Natural Resources* 1: 1–1386.
- Blackwelder, R. E. 1945. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part III. *Bulletin of the United States National Museum* 185: 343–550.
- Brèthes, J. 1923. Catalogue synonymique des Coccinellides du Chili. *Revista Chilena de Historia Natural*, XXV, 1921(1923): 453–456.
- Bruch, C. 1915. Catálogo sistemático de los coleópteros de la República Argentina. *Revista del Museo de La Plata, pars IX*, 19: 346–400.
- Casey, T. L. 1899. A revision of the American Coccinellidae. *Journal of the New York Entomological Society* 7: 71–169.
- . 1908. Notes on the Coccinellidae. *The Canadian Entomologist* 40: 393–421.
- Chapin, E. A. 1941. Lady-beetles belonging to the genus *Procula* Mulsant. *Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey"* 15: 165–168.
- . 1949. New beetle records for Florida. *Coleopterists' Bulletin* 3: 23.
- . 1957. Records of coccinellid beetles from the Cayman Islands, with descriptions of new species from the West Indies. *The Entomologist's Monthly Magazine* 93: 89–91.
- . 1969. New synonymy and generic reassignment in South American *Coccinellina* (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington* 71(3): 467–469.
- Chapin, J. B. 1974. The Coccinellidae of Louisiana (Insecta: Coleoptera). *Bulletin of the Louisiana State University Experiment Station* 682: 1–87.
- Chapius, F. 1876. *Histoire naturelle des insectes. Genera des Coléoptères*, Paris 12: 1–424.
- Crotch, G. R. 1871. *List of Coccinellidae*. Cambridge, 8 pp.
- . 1873a. Revision of the Coccinellidae of the United States. *Transactions of the American Entomological Society* 4: 363–382.
- . 1873b. Check List of the Coleoptera of America, North of Mexico. Salem, 136 pp.
- . 1874. A Revision of the Coleopterous Family Coccinellidae. London, 311 pp.
- Erichson, W. F. 1842. Beitrag zur Insecten-Fauna von Vandiemensland, mit besonderer Berücksichtigung der geographischen Verbreitung der Insecten, von Herausgeber. *Archiv für Naturgeschichte* 8: 238–241.
- Fabricius, J. C. 1792. *Entomologia Systematica*. Hafniae, Vol. 1, part 1, 330 pp., part 2, 538 pp.
- Germain, P. 1854. Descripcion de 21 especies nuevas de Coleópteros de Chile. *Anales de la Universidad, Chile* 11: 326–336.
- Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society* 93: 1–912.
- . 1987. A catalogue of the Crotch collection of Coccinellidae (Coleoptera). *Occasional Papers on Systematic Entomology No. 3*. London, 46 pp.
- Gordon, R. D. and N. J. Vandenberg 1993. Larval systematics of North American *Cyclonedra* Crotch (Coleoptera: Coccinellidae). *Entomologica Scandinavica* 24: 301–312.
- Gorham, H. S. 1892. *Biologia Centrali-Americana, Insecta, Coleoptera, Coccinellidae* 7: 161–176.
- Hampe, C. 1850. Beschreibung einiger neuen Kafer-Arten. *Stettiner Entomologische Zeitung* 11: 346–358.
- Hodek, I. et al. 1973. *Biology of Coccinellidae*. Academia, Czechoslovak Academy of Sciences, Prague, 260 pp.
- Handlirsch, A. 1906–1908. *Die fossilen Insecten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen*. Engelmann, Leipzig, 1430 pp.
- Hatch, M. H. 1961. *Beetles of the Pacific Northwest, part III: Pselaphidae and Diversicornia*. University of Washington Press, Seattle, 503 pp.
- Iablokoff-Khnzorian, S. M. 1990. About the classification of the Coccinellini. *Coccinella* 2: 58–60.
- . 1982. Les Coccinelles, Coléoptères-Coccinellidae, Tribu Coccinellini des régions Paléarctique et Orientale. Paris, 568 pp.
- International Commision of Zoological Nomenclature. 1999. *International code of zoological nomenclature, fourth edition*. London, 306 pp.
- Korschefsky, R. 1932. *Coleopterorum Catalogus, Pars 120, Coccinellidae II*. Berlin, 659 pp.
- Leng, C. W. 1903. Notes on Coccinellidae. II. *Journal*

- of the New York Entomological Society 11: 193–213.
- . 1920. Catalogue of the Coleoptera of America, North of Mexico. Mount Vernon, New York, 470 pp.
- Linnaeus, C. 1763. *Centuria Insectorum Rariorum*. Uppsala, 32 pp.
- Mader, L. 1958. Die amerikanischen Coccinelliden der Gruppe *Synonychini*. *Annalen des Naturhistorischen Museums in Wien* 62: 236–249.
- Mulsant, M. E. 1850. Species des Coléoptères trimères sécuripalpes. *Annales des Sciences Physiques et Naturelles, d'Agriculture et d'Industrie*, Lyon 2: 1–1104.
- . 1866. Monographie des coccinellides. *Mémoires de l'Académie Sciences, Belles-lettres et Arts de Lyon* 15: 1–112.
- Palmer, M. A. 1914. Some notes on life history of lady-beetles. *Annals of the Entomological Society of America* 7: 213–238.
- Phuoc, D. T. and F. W. Stehr. 1974. Morphology and taxonomy of the known pupae of Coccinellidae (Coleoptera) of North America, with a discussion of phylogenetic relationships. *Contributions of the American Entomological Institute* 10(6): 1–126.
- Rivera, M. J. 1904. Biología des eos coleopteros Chilenos cuyas larvas atacan al trigo. *Revista Chilena de Historia Natural* 8: 241–254.
- Saini, E. D. 1983. Clave para estadios larvales de Coccinellidos. *Revista de la Sociedad Entomologica Argentina* 42: 397–403.
- . 1985. Identificación práctica de “vaquitas” beneficiosas. Parte I. Departamento Publicaciones, Prensa y Difusión, Instituto Nacional de Tecnología Agropecuaria, 22 pp.
- Say, T. 1835. Descriptions of new American coleopterous insects, and observations on some already described. *Boston Journal of Natural History* 1: 151–203.
- Timberlake, P. H. 1943. The Coccinellidae or ladybeetles of the Koebele collection. Part I. Bulletin of the Experiment Station of the Hawaiian Sugar Planters' Association, Entomological Series 22: 1–67.
- Vandenberg, N. J. 1987. A systematic study of *Olla* Casey and allied genera of the New World (Coleoptera: Coccinellidae), Ph.D. dissertation, University of California, Berkeley (unpublished for nomenclatorial purposes).
- . 1992. Revision of the New World lady beetles of the genus *Olla* and description of a new allied genus (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* 85: 370–392.
- . 1997. Beetle economics. In Hoagland, K. E. and A. Y. Rossman, eds. *Global Genetic Resources: Access, Ownership, and Intellectual Property Rights*. Association of Systematics Collections. Washington, 348 pp.
- Vandenberg, N. and R. D. Gordon. 1988. The Coccinellidae (Coleoptera) of South America, part I. A revision of the genus *Erythroneda* Timberlake, 1943. *Revista Brasileira de Entomologia* 32: 31–43.
- . 1996. A new genus of Neotropical Coccinellini (Coleoptera: Coccinellidae) related to *Olla* Casey and allies. *Proceedings of the Entomological Society of Washington* 98(3): 541–550.
- Van Dyke, E. 1953. The Coleoptera of the Galapagos Islands. Occasional papers of the California Academy of Sciences, XXII, 181 pp.
- Weise, J. 1898. Coccinellen aus Südamerika. *Deutsche Entomologische Zeitschrift* 1898: 125–126.
- . 1902. Coccinelliden aus Südamerika. III. *Deutsche Entomologische Zeitschrift* 1902: 161–176.
- . 1904a. Coccinellidae in Argentina, Chili et Brasilia e collectione domini Caroli Bruchi. *Revista del Museo de La Plata* 11: 193–198.
- . 1904b. Synonymische Bemerkungen zu Gorham, *Biologia Centrali-Americana*, vol. VII, Coccinellidae. *Deutsche Entomologische Zeitschrift* 1904: 433–452.
- . 1906. Hispinae, Coccinellidae et Endomychidae Argentina et vecinitate e collectione Bruchiana. *Revista del Museo de La Plata* 12: 219–231.
- . 1922. Coleoptera e collectione Bruchiana. *Annales de la Sociedad Científica Argentina* 94: 30–40.
- Wilson, J. W. 1926. The genitalia of some of the Coccinellidae. *Journal of the Elisha Mitchell Scientific Society* 42(1 & 2): 63–74.
- Wingo, C. W. 1952. The Coccinellidae (Coleoptera) of the upper Mississippi Basin. *Iowa State Journal of Science* 27: 15–53.
- Zelený, J. 1969. A biological and toxicological study of *Cycloneda limbifer* Casey (Coleoptera, Coccinellidae). *Acta Entomologica Bohemoslovaca* 66: 333–344.



Vandenberg, Natalia J. 2002. "The new world genus *Cycloneda* Crotch (Coleoptera: Coccinellidae: Coccinellini): Historical review, new diagnosis, new generic and specific synonyms, and an improved key to North American species." *Proceedings of the Entomological Society of Washington* 104, 221–236.

View This Item Online: <https://www.biodiversitylibrary.org/item/54767>

Permalink: <https://www.biodiversitylibrary.org/partpdf/54878>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Smithsonian

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Entomological Society of Washington

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.