

ly different at experimental photoperiods less than, equal to, or greater than the minimum field photoperiod (experiments A and B, Table 1). In experiment C, lizards received illumination for $\frac{3}{4}$ to 1 hour on Mondays, Wednesdays, and Fridays, or an average experimental photoperiod of less than $\frac{1}{2}$ hour per day, considerably less than the average minimum field photoperiod (4 hours per day). At autopsy, 67 percent of the experimental lizards had enlarged yolked follicles, whereas gonadal development had begun in only one of ten controls.

The reproductive cycle of most female *U. stansburiana* is refractory to environmental stimulation until early December. Although none of 57 females was reproductive at the end of experiment A, 12 of 22 females were reproductive at the end of experiment B two months later. Photoperiods were the same in both experiments, indicating a temporal difference in reproductive capability. In experiment D, one year later, 1 of 13 females became reproductive between September and November while between October and December, 4 of 16 became reproductive with the same photoperiod.

That temperature has greater influence than photoperiod in initiating the reproductive cycle has been suggested for at least one other temperate-zone reptile (4); however, photoperiod is generally considered more important. While careful studies (2, 3) have established the predominant influence of photoperiod in some species, other studies (8, 9) had inadequate controls.

The refractory period in birds is probably controlled by the neurosecretory system (5), and apparently provides time for resynthesis of neurohormonal substances depleted by reproductive activity of the previous season (10). We do not know the physiological basis or adaptive significance of the refractory period of *U. stansburiana*. However, because fat-body cycling parallels the reproductive cycle and is directly related to reproductive potential (12), the refractory period may provide time for enlargement of the corpora adiposa and may be controlled by factors other than those which affect refractoriness in birds.

Environmental factors affecting reproductive cycles are of obvious evolutionary interest. Varying responses among different species of the same genus (9) may indicate that the rela-

tive importance of environmental stimuli is evolutionarily labile. Asplund and Lowe (12) have reported sympatric populations of *Urosaurus ornatus* and *Uta stansburiana* with contrasting reproductive cycles and suggest that the species have had different macroclimatic evolutionary histories.

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29 March 1965

Chilocorus similis Rossi:

Disinterment and Case History

Abstract. *Cytological proof is presented that the Asiatic predator Chilocorus similis (Coleoptera, Coccinellidae), liberated in California sometime between the years 1923 and 1947, has since been masquerading there under the name C. orbus.*

On page two of his "Biological Control of Insect Pests in the Continental United States," Clausen (1) states: "*Chilocorus similis* Rossi, the predator of the white peach scale [*Pseudaulacaspis pentagona* (Targ.)] and of the San Jose scale (*Aspidiotus perniciosus* Comst.), imported from Japan in 1901 and 1902 and extensively colonized in Georgia, showed a marked increase the following year and was still common in 1905, but eventually died out." On page 31 he continues: "The San Jose scale, which originated in Asia and was first

observed in the United States about 1870, quickly spread over the entire country. . . ." "A coccinellid beetle, *Chilocorus similis*, is an abundant enemy of the scale in Japan, and efforts were made to import and establish it from 1895 to 1923, but without success." Further, on page 32, he concludes as follows: "Several shipments were made to the United States, but only two individuals survived. However, they proved sufficient for rearing purposes, and large numbers were produced in the insectary at Washington, D.C., for release in several States. The field colonies appeared to thrive, especially those in Georgia, where recoveries were made for several years, but the species did not persist beyond 1905."

According to Marlatt (2), the predator species introduced from China and Japan between 1895 and 1902 was *C. similis* Rossi. In 1923, material under this name was released in Santa Barbara County, California, but Clausen is of the opinion (3) that the species involved in these various importations was *Chilocorus kuwanae* Silvestri and that *C. similis* has, in fact, never been introduced into North America.

In 1948, I understand, specimens received from China labeled *Chilocorus renipustulatus* Scriba were cultured in large numbers at the Citrus Experiment Station, Riverside, California, and liberated in that State. In connection with these later releases Clausen (2) comments on page 32: "Several attempts have been made to establish this predator on various other scale insects in California, but they likewise were not successful." It is my purpose herein to present evidence for at least one exception to this generalization.

Three species in the genus *Chilocorus* Leach are native to California: *Chilocorus cacti* (Linnaeus), *Chilocorus orbus* Casey, and *Chilocorus fraternus* Leconte. The first is easily recognized, but the last two can be distinguished from each other only with much difficulty (4), although their taxonomic separation is greatly facilitated over most of their range by their almost complete geographic isolation. On the other hand, *C. orbus* and *C. fraternus* are well characterized cytologically, not by chromosome number, for both have 22 chromosomes, but in the morphology of the autosomes; those of *C. orbus* are reasonably uniform in size and shape, whereas those of *C. fraternus*

are comparatively variable, especially in the size of the free arms of the rod-shaped bivalents (see Fig. 1, *a* and *d*). The chromosome complement of *C. fraternus* is actually indistinguishable from that of *C. cacti* (Fig. 1*b*), and unlike *C. orbus* with *C. fraternus* or *C. cacti*, these two species can be crossed in the laboratory with the production of viable hybrids (5, 6).

During 1957 I had occasion to visit the southern part of California on a collecting expedition. At the Citrus Experiment Station, Riverside, I was directed to Carpinteria, which is situated in Santa Barbara County, on the coastal side of the Santa Ynez Mountains, east of Santa Barbara, where *C. orbus* was believed to be abundant on a neglected citrus farm. There, on 31 October, at the Moore Ranch, scale-infested lemon trees yielded 19 adult, 1 pupal, and 5 larval *Chilocorus*; at the nearby Ellery Ranch, which was under cultivation, 63 adults were taken off unsprayed avocados. The collecting took no longer than a couple of hours.

Cytological examination of 11 of the adults at once revealed a situation entirely novel in the Chilocorini (7). Although the diploid chromosome number of the beetles from Carpinteria is 20, as it is in *Chilocorus tricyclus* Smith, the 20 chromosomes have a total of only 24 arms in females [23 in males (8)], as against 40 in female *C. tricyclus* (39 in males): in other words, 16 autosomes are one-armed in Carpinteria females, but none of the autosomes are one-armed in *C. tricyclus* females. Furthermore, in maturation divisions, the autosomes associate to form one large ring-shaped bivalent and eight rod-shaped bivalents, rather than the three rings and six rods observed in *C. tricyclus* (Fig. 1, *e* and *f*). Since the invariable rule for native North American species of *Chilocorus* is that in meiosis, with reduction in chromosome number downward from 26, one ring replaces two pairs of rods (9), the cytological evidence proves that the Carpinteria beetles must be phylogenetically distinct from North American species.

Twenty adults obtained from Carpinteria were paired in various combinations with native species, but even though copulation was noticed occasionally, all attempts to hybridize proved unsuccessful. Thus, since all native North American species can be hybridized one way or another (5),

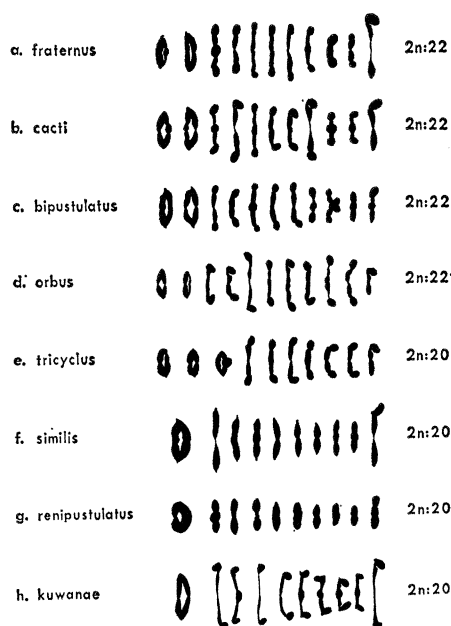


Fig. 1. First metaphase of meiosis (side view) in males of four North American (*a*, *b*, *d*, and *e*) and four exotic (*c*, *f*, *g*, and *h*) species of *Chilocorus* (\times about 1050). Homologous chromosomes are associated either through both arms, to form "rings" (left), or through only one, to form "rods" (right). At the extreme right is the sex-determining bivalent, XY.

the genetical evidence confirms the cytological evidence that these Carpinteria beetles are derivationally exotic. A nomenclatural problem had then to be faced: whether, in reporting on their establishment, they should be designated *C. similis*, *C. renipustulatus*, or *C. kuwanae*.

According to Hagen (10), who has wide experience in coccinellid taxonomy, the insects are, on morphological grounds, clearly not indigenous to North America. He readily separated them from native species and from the Palearctic *Chilocorus bipustulatus* (Linnaeus), all of which I had in culture at that time. Finding the Carpinteria adults indistinguishable in general form and in the sculpture of the siphon from pinned specimens of Chinese *C. renipustulatus* that he had obtained from Riverside in 1948, Hagen was at first inclined to adopt this name. However, he then found that they did not agree with Silvestri's interpretation of adult European *C. renipustulatus* Scriba, nor their larvae with Van Emde's description of *C. renipustulatus* larvae found in England. On the other hand, the Carpinteria adults fit more closely Silvestri's description of *C.*

kuwanae and the adults and larvae strongly resemble those of *C. similis* figured and photographed by Marlatt (2, figs. 2 and 3 and plate XVII). With *C. renipustulatus* thus seemingly disposed of, it still remained a moot point as to whether it was *C. similis* or *C. kuwanae* (3) that had been introduced or whether, in fact, both had been introduced on different occasions. This uncertainty, it seemed, might be resolved if *C. kuwanae* were available for cytological comparison.

In July 1958, two male progeny reared at Riverside from *C. kuwanae* Silvestri parents collected in Japan by personnel of the U.S. Department of Agriculture were provided for cytological examination. Since the autosomes and Y chromosomes of the males were two-armed, they could be immediately distinguished from Carpinteria material (see Fig. 1, *f* and *h*), *C. kuwanae* thus being eliminated as a possible designation for the latter population. It nevertheless still remained to examine the chromosomes of undoubted *C. renipustulatus*, preferably from Europe.

In June 1961, eight living adults labeled *Chilocorus renipustulatus* Scriba were airmailed to Sault Ste. Marie, Ontario, by Esko Suomalainen of the Institute of Genetics, University of Helsinki, Finland. Their resemblance to the Carpinteria specimens was, to me, unmistakable. Cytologically they proved to be identical (Fig. 1*g*) and therefore distinct from the 1958 Japanese *C. kuwanae* Silvestri. This would appear to have established beyond doubt that the Japanese *C. kuwanae* and European *C. renipustulatus* are biologically valid species, leaving *C. similis* as the true identity of the beetles, introduced during 1895–1902, 1923, or 1948, that initiated the Carpinteria colony. However, since larvae were unavailable and since I had expected *C. renipustulatus* to be chromosomally similar to Palearctic *C. bipustulatus* (Fig. 1*c*), and particularly because *C. similis* was originally described from Italy, I hesitated to accept Suomalainen's taxonomic identification unreservedly.

Recently, however, Suomalainen's determination has, not surprisingly, been confirmed by Zaslavskij, who specializes in the systematics of Chilocorini at the Leningrad Academy of Sciences (11). He writes: "The material you received from Finland is the true *Ch. renipustulatus*." However, he continues: "I know no valid characters

distinguishing this species from *Ch. kuwanae* and I doubt that in this case we deal with distinct species." In the light of their diagnostic chromosome differences, it thus becomes clear that we are here concerned with sibling species; these are tolerably common in the Chilocorini (5, 6, 12).

The accumulated cytological evidence immediately exempts *C. kuwanae* Silvestri and *C. renipustulatus* Scriba from synonymy, and, accepting the morphological differences between the Carpinteria material and Silvestri's and Van Emden's descriptions as taxonomically valid, it must be granted that, along with *C. kuwanae* and *C. renipustulatus*, *C. similis* Rossi also occurs in Asia, either allopatrically or sympatrically. With *C. kuwanae* disqualified cytologically and *C. renipustulatus* excluded on morphological grounds, I therefore consider it reasonable to apply the name *C. similis* to the population that by 1957 had perpetuated itself in California over a period of some 10 or perhaps even 35 years and has there been masquerading under the name *C. orbus* Casey. Whether a similar state of affairs exists in Georgia or elsewhere in the east, with *C. similis* now being confused with *C. stigma*, remains an intriguing possibility worthy of investigation.

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25 March 1965

Particle Sorting and Stone Migration by Freezing and Thawing

An account of the relative migration of particles of various sizes caused by alternate freezing and thawing of earth was given some time ago in these pages by Corte (1), along with experiments he suggests may be helpful in interpreting the phenomenon. However, there is another mechanism (2) that explains in a compelling, plausible manner the gradual lifting of a relatively large particle (or boulder or fence post) through the surrounding smaller particles.

Consider a spherical body as in Fig. 1, embedded in an aqueous slurry of finer particles which is being frozen from above, the freezing line having descended to the level A. If the body is a grain of a few milligrams or a stone of a few grams or even kilograms, the adhesion of the ice to the top of the sphere will be strong enough to be capable of supporting its weight. If it is a boulder of several tons, it may be necessary for it to be embedded in a block of frozen slurry down to level B before lifting can occur. With the body adhering to the frozen block, consider the subsequent freezing of a layer of thickness dz . Since water expands on freezing, a mixture of water and particles has an average coefficient of expansion on freezing—here denoted by α —which is somewhat less than that of pure water. The layer of thickness dz then expands by an amount αdz on freezing, lifting the entire thick layer of frozen slurry above it by that amount and the sphere with it. Because of the rigidity of the sphere, a cavity would be left beneath it, except for the fact that the still unfrozen slurry beneath flows in to equalize pressure and fill the void. The extent to which this flow may consist of water filtering through the soil rather than mass movement of the slurry may depend on the porosity and effective viscosity of the slurry and on the time available, which depends on the rate of freezing. (This can explain some of the observed dependence of the migration distance per cycle on the rate of freezing.) The sphere is lifted by a total amount of the order of magnitude of α times the diameter, which may be one or a few percent of the diameter. Some particles and some water move into a space of this thickness below the sphere, as indicated schematically by the curved arrows in Fig. 1.

Consider now the reverse process, thawing from above. When thawing has progressed to level B, for example, the sphere is still firmly supported by the frozen slurry beneath it (including that which flowed in just before freezing). As the thawing surface advances a distance dz , the contraction permits the whole mass of soil above it to fall by αdz . However, the solid dome of the sphere protrudes into this descending mass, forcing some of the fluid slurry above it to flow sideways around the obstruction and help fill in the space being provided above the thawing layer. Thus particles move away from the top of the sphere, and the net result of the whole cycle is that the sphere rests higher with more soil beneath it and less above.

Freezing and subsequent thawing from beneath transport the stone downward by this mechanism, as is easily seen by repeating the argument for this case. The direction of motion is determined by the direction of the freezing and subsequent thawing, not by the direction of gravity, because gravity serves merely to supply a pressure to fill in the voids and thus acts as a scalar, not a vector.

In the case of horizontal motion of a vertical plane of freezing and thawing, as near a steep bank, gravity plays its role not only as a scalar but possibly more prominently as a vector causing a slope of the stone's net motion. An upward slope can be explained as follows: When the nascent cavity is being filled by both rheological flow of the slurry and by porous seeping of the water, the tendency should be for a denser mixture, richer in soil particles, to settle to the bottom of the "cavity" under one side of the stone, thus causing a net lift. On the other hand, an explanation can also

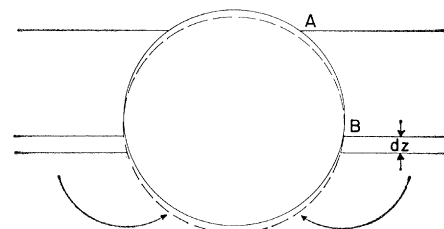


Fig. 1. The spherical stone may be raised by adhesion to the frozen block as the freezing line descends from level A to B and beyond, because of the expansion of the surrounding mud on freezing.