J. New York Entomol. Soc. 102(3):310–317, 1994

A NEW CASE OF PARTHENOGENESIS IN BEETLES: *LONGITARSUS MELANURUS* (MELSHEIMER) (COLEOPTERA: CHRYSOMELIDAE)

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Abstract.—Parthenogenesis as previously known in five genera of Chrysomelidae (Leaf Beetles) is reviewed. Evidence is presented for a new case of parthenogenesis in Chrysomelidae, *Longitarsus melanurus* (Melsheimer), recorded feeding on an introduced plant, *Echium vulgare* Linnaeus (Boraginaceae), in Massachusetts, New York, Pennsylvania, and Virginia.

Parthenogenetic reproduction (egg development without fertilization) is a kind of genetic polymorphism which occurs sporadically in insects with relatively few cases in beetles. In Coleoptera, especially Polyphaga, the most common parthenogenesis is developmentally apomictic or ameiotic, producing all females, usually referred to as thelytoky. These parthenogenetic species often have geographical differences, thus some populations may be parthenogenetic while populations of the same species from a different geographic area may be bisexual. There are some advantages of thelytoky in that females can spend all of their time feeding and reproducing rather than searching for mates, thus, the reproductive potential of the population is higher. A disadvantage of thelytoky is that the long-term effect may be loss of the ability to adapt to changing environments (Chapman, 1971). Considering the large number of species of Coleoptera, parthenogenesis has been discovered in relatively few families or species, but certainly many await discovery (Smith and Virkki, 1978). Probably the best studied case of thelytoky in Coleoptera is that of the polyploid weevils such as *Otiorhynchus* (Curculionidae) in which many species demonstrate this phenomenon (see Suomalainen and Saura, 1973; Saura et al., 1976; Smith and Virkki, 1978).

In the Chrysomelidae, however, there are only ten reported cases, including six in one genus, of parthenogenesis and two of these are Alticinae. Petitpierre (*in litt.*) also mentioned possible instances of polyploidy (as yet unproven) in *Aulacophora femoralis* (Motschulsky) (Galerucinae) and *Dicladispa armigera* (Olivier) (Hispinae). The first reported case of parthenogenesis in Chrysomelidae, possibly the first of any beetle, was in *Gastrophysa raphini* Herbst (=*viridula* DeGeer) (Chrysomelinae) by Osborne (1879, 1880a, b). However, apparently little further cytogenetic research has been conducted on *G. viridula* (see Petitpierre et al., 1988). Another chrysomeline genus, *Calligrapha,* has 36 known species recorded in North America and another 37 recorded from Central and South America (Wilcox, 1975). After examining 17 *Calligrapha* species cytologically, Robertson (1964a) first reported that six of these species were parthenogenetic (*vicina* Schaeffer, *virginea* Brown, *alnicola* Brown, *apicalis* Notman, *ostryae* Brown, and *scalaris* (LeConte)). *C. scalaris* had parthenogenetic or bisexual populations depending on the location (Robertson, 1964a), but the parthenogenetics were all tetraploid. Robertson (1966) studied *Calligrapha* further and in greater detail, including the foodplants, distribution, sex ratios, egg production, and chromosome configuration of both bisexual and parthenogenetic species. He also discovered supernumerary chromosomes in *C. philadelphica* L. (Robertson, 1964b).

Smith (1971) referred to the situation in *Calligrapha* as studied by Robertson (1964a, 1966) as "pseudoparthenogenesis" apparently because he interpreted Robertson's data as indicating a type of facultative (i.e., that some populations or some generations produced only females and others were bisexual) rather than the usual obligatory parthenogenesis. It seems that further genetic study of *Calligrapha* species and their populations is warranted.

The best known case of chrysomelid parthenogenesis is *Bromius* (formerly *Adoxus*) *obscurus* (L.) (Eumolpinae). This case represents a geographical parthenogenesis where the North American populations of *B. obscurus* are diploid (bisexual) and the European populations are apomictic triploids (females only) (Smith, 1971). Although parthenogenetic *B. obscurus* was first reported long ago (Jobert, 1881; Jolicoer and Topsent, 1892), it has been studied quite thoroughly by Suomalainen (1965) and Lokki et al. (1976). Jobert (1881) examined over 3700 specimens without finding any males. In the early 1900s there were a few reports of rare *B. obscurus* males in Europe; however, Lokki et al. (1976) cytologically confirmed parthenogenesis in this species, but stated that even obligatory parthenogenetic species may occasionally produce a few males.

In North America *B. obscurus* feeds on grapes (*Vitis*), whereas the populations in Europe feed on *Chamaenerion* or *Epilobium* (Onagraceae) (Suomalainen et al., 1987; Mohr, 1966). Lokki et al. (1976) pointed out that in all parthenogenetic animals the bisexual race is assumed to be the ancestral one from which the parthenogenetic one evolved, thus the North American populations are ancestral for *B. obscurus*. Lokki et al. (1976) also stated that, compared to other parthenogenetic insects they had studied (e.g., the flightless moth, *Solenobia triquetrella* (Hübner) and the flightless weevil, *Otiorhynchus scaber* (L.)), *B. obscurus* was genetically very monomorphic, i.e., less polymorphic. They explained this as caused by the active dispersal capability of *B. obscurus*. Study of genetic polymorphism in parthenogenetic insects with differing dispersal capabilities should shed light on the relationship between mutation and selection (Lokki et al., 1976).

Only two species of Alticinae have been reported as parthenogenetic. The first was *Altica lazulina* LeConte which is distributed in Washington, Oregon and Idaho (Hatch, 1971), and reported from Montana and Colorado (Wilcox, 1975) as well as from British Columbia (Smith and Virkki, 1978). This *Altica* was reported by Smith (1960, 1971), Smith and Virkki (1978) and Suomalainen et al. (1987) as producing triploid thelytokous parthenogenesis (in the laboratory only). This species is apparently bisexual in nature, Hatch (1971) gives aedeagus characters in his key and male specimens are present in the LeConte and Horn collections in the Museum of Comparative Zoology at Harvard University (MCZ). Robertson (1966) said that Smith (unpubl.) found *A. tombacina* (Mannerheim) to be a triploid parthenogenetic; however, probably this was the preliminary determination for *A. lazulina*. Smith (1960) listed chromosome information for 8 species of *Altica*, all normal diploid bisexuals, but there was no mention of *A. tombacina* or *lazulina*. However, this genus is extremely difficult taxonomically and it has never been revised in this century; therefore, the identity of specimens are usually suspect.

The second Alticinae reported as parthenogenetic was *Chaetocnema perplexa* Blake

(Virkki et al., 1989). Even though Blake (1941) described *C. perplexa* as bisexual, she stated that "although there were many specimens, there were very few males in any collection." S. Clark (in Virkki et al., 1989 and pers. comm.) says that all specimens he has examined from the West Indies have been females. Virkki et al. (1989) sampled hundreds of *C. perplexa* from sweet potatoes (*Ipomoea* spp.) in Puerto Rico and all were females; they reasoned that absence of males was an indication of parthenogenesis. Many of these *C. perplexa* were infested by a nematode (*Howardula* sp.) and Virkki et al. (1989) found that this infestation suppressed oogenesis in over one half of the beetle populations. They speculated that this pressure, possibly in combination with other unexplained factors, may be enough to produce the observed parthenogenetic populations.

The present study concerns parthenogenesis in a third Alticinae, *Longitarsus. Longitarsus* is the most biodiverse genus in the Chrysomelidae with between 600–700 described species worldwide; it is also the most difficult taxonomically and, like most insect groups, relatively little is known about the biology of most species. Furth (1980b) reported that, more than any other chrysomelid group, *Longitarsus* had a significant percentage of species with intra-specific wing length polymorphism (flightlessness). Even though many species of *Longitarsus* have been examined cytogenetically (Petitpierre et al., 1988; Segarra and Petitpierre, 1988), as yet none have been found with any unusual characteristics.

METHODS AND RESULTS

In 1983 E. R. Hoebeke (Cornell University) sent the author 9 female specimens of a *Longitarsus* species for determination that he had collected in New York (Onondaga Co., Solvay railroad yards, 14 May 1983) feeding on *Echium vulgare* L., a Boraginaceae introduced to North America a very long time ago (see Discussion). After comparison with specimens in the author's extensive Palearctic *Longitarsus* collection and with the literature, and dissection and study of the female spermatheca, the author determined that this *Longitarsus* species was not a Palearctic species but rather a Nearctic species. At that time the author did not attempt to determine the exact species name.

On 7 July 1991 the author collected 55 specimens of the same *Longitarsus* feeding on *E. vulgare* along Memorial Drive in Cambridge, Massachusetts (Middlesex Co.) near the city border with Watertown. Like many borage-feeding *Longitarsus* which the author has collected in the Palearctic, this species was feeding on both surfaces of *E. vulgare* leaves, especially on the rosette leaves. These specimens were kept alive on their foodplant under ambient conditions at the MCZ and were observed to be actively feeding and laying eggs. After one week the specimens were killed with ethyl acetate and examined, including spermatheca, and found to be all females. With the aid of the MCZ's historical collections of J. L. LeConte, G. Horn, F. V. Melsheimer, H. C. Fall, etc., this species was determined to be *L. melanurus* (Melsheimer). Based on the author's extensive field experience in the Palearctic with many borage-feeding *Longitarsus* (Furth, 1980a), if females are abundantly ovipositing, males should be present. The author returned to the same site 10 days later (17 July) and collected 41 more specimens—all proved to be females of *L. melanurus*; therefore, all 96 specimens from this site were females. An attempt was made to collect more spec-

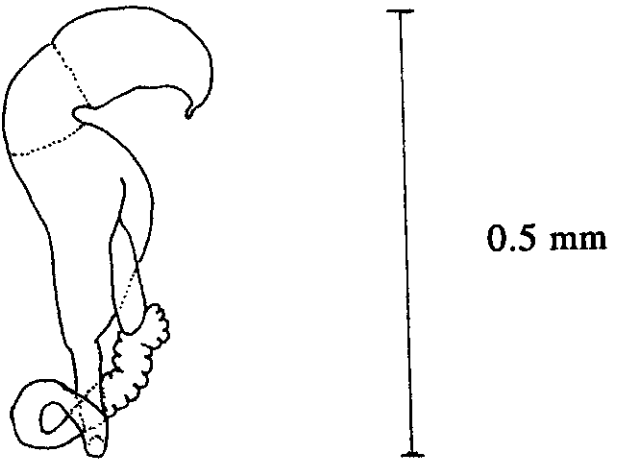

Fig. 1. Spermatheca of *Longitarsus melanurus* (Melsheimer), lateral view.

imens from the same site in Cambridge on 7 July 1993; however, the *E. vulgare* plants had been cut down apparently several weeks previously and only a few rosettes remained. As a result only 5 specimens were collected in 1993, all females; therefore, the population of *L. melanurus* still exists at the Cambridge site.

L. melanurus spermathecae from the Massachusetts and New York populations were examined. The spermatheca (Fig. 1) is typical for *Longitarsus*; however, preliminary study indicates more than the normal amount of morphological variability in the coiling pattern of the spermathecal duct. In this genus the coiling pattern of the duct is normally quite constant with little variability; however, there are some exceptions (Leonardi, 1973).

Longitarsus melanurus (Melsheimer) was originally described from Pennsylvania, but more recently recorded from the eastern USA and Canada (Wilcox, 1975). Blatchley (1910) figured *L. melanurus* and recorded it as frequent in southern and rare in northern Indiana, taken from roadside vegetation. With the aid of E. R. Hoebeke, the author was able to examine and determine the following series of *L. melanurus* collected recently from *E. vulgare* and deposited in the insect collection at Cornell University: Pennsylvania, Schuylkill Co., Port Carbon, 18 July 1985, A. G. Wheeler, Jr. (13 specimens); Virginia, Rockbridge Co., I-81 S. Natural Bridge exit, 2 July 1987, A. G. Wheeler (106 specimens); Pennsylvania, Dauphin Co., Harrisburg, 6 July 1987, E. R. Hoebeke (27 specimens). All of these specimens are females; most are deposited at Cornell University with samples of each in the author's collection. The author has also carefully examined and redetermined all of the specimens of *L. melanurus* in the collections of the MCZ (LeConte, Horn, Melsheimer-Zeigler, Fall, and general). In the MCZ collections there were true *L. melanurus* from: Quebec, Maine; New Hampshire; New York; Pennsylvania; West Virginia; North Carolina; Michigan; Illinois; "Dakota"; Kansas; Missouri; Texas; Iowa; and Colorado—all of these specimens are also females. No apparent type specimen or type series was found in any of the MCZ collections, including the Melsheimer material. With the assistance of

A. Provansha, the author was able to examine the collection at Purdue University, including the W. S. Blatchley collection, which contains 10 specimens of *L. melanurus* from 8 counties of Indiana—all are females. Thanks to the late Edward Balsbaugh, Jr., the author examined a small series of *L. melanurus* from the North Dakota State University insect collection which contains 11 specimens from North Dakota, Minnesota and Pennsylvania—all females.

DISCUSSION

This study provides quite convincing evidence of the parthenogenesis in *Longitarsus melanurus,* the sixth genus and eleventh species of Chrysomelidae reported with this phenomenon. As with the case of parthenogenesis in *Chaetocnema perplexa* reported by Virkki et al. (1989) from Puerto Rico, the evidence for parthenogenesis in *L. melanurus* is circumstantial and statistical (i.e., absence of males) rather than cytogenetic. Because *Longitarsus* have root feeding larvae, fairly elaborate controlled facilities would be required to rear them in order to verify that all progeny are female. Also cytogenetic techniques necessary to prove parthenogenesis are rather complicated (Virkki, *in litt.,* Petitpierre, *in litt.*) and are beyond the scope of the present study.

The all-female samples from *E. vulgare* at the Cambridge, Massachusetts site together with the same from New York, Pennsylvania, Virginia in the collections of Cornell University and of the author, as well as the few smaller museum samples listed above, indicate quite strongly that most and probably all populations of *L. melanurus* are parthenogenetic, probably thelytokous polyploidy as known in other chrysomelids such as *Calligrapha* and *Bromius.* Of course, it remains to be proven whether the parthenogenesis in *L. melanurus* has a geographical bisexual component as do the European and North American populations of *Bromius obscurus.*

Because *Echium vulgare* (Viper's Bugloss) is an introduced plant in North America, it is interesting to speculate as to the true foodplant for *L. melanurus.* Leighton (1986) indicates that *E. vulgare* was present in New England early in the seventeenth century; therefore, it was introduced more than 350 years ago and *L. melanurus* could have been using *E. vulgare* as a foodplant since then. Also Gray (1848) lists *E. vulgare* as "rare in the Northern States, a troublesome weed in Virginia." There are relatively few native Boraginaceae in eastern North America, especially any that may be related, including chemically, to *Echium,* the most likely may be native species of *Lithospermum* or *Onosmodium* which are in the same tribe as *Echium* (Riedl, 1968; Feinbrun-Dothan, 1978). Another possibility may be native species of *Cynoglossum,* in a closely related tribe. All three of these other genera share some chemical substances with *Echium,* for example, bornesit, fructane and allantoin, but the known chemistry of *Echium* seems much less diverse than that of *Lithospermum* (Hegnauer, 1964, 1989).

Virkki et al. (1989) speculate that heavy infestation by a nematode may have caused parthenogenesis in *Chaetocnema perplexa.* If *L. melanurus* is actually bisexual in some populations, then switching to a non-native foodplant may be a synergistic contributing factor to parthenogenesis in this species. However, the evidence suggests that all populations of *L. melanurus* are parthenogenetic and, therefore, this type of genetic polymorphism apparently also is reflected in its ability to switch to a non-native foodplant. The Massachusetts population of *L. melanurus* is macropterous and fully able to fly and to disperse to other stands of *E. vulgare* or to its native foodplant. Part of the theory of thelytokous parthenogenesis is that an all-female population can concentrate its energy on reproduction, i.e., increased fecundity. A similar principle pertains to the theory of intra-specific wing polymorphism present in many species of *Longitarsus,* in which wing reduction allows increased fecundity (Furth, 1980b).

Chapman's (1971) definition of thelytokous parthenogenesis states that the disadvantageous long-term effect is loss of ability to adapt to changing environments; however, the present study demonstrates that *L. melanurus* has been able to establish at least several widely disjunct populations feeding on a non-native foodplant. If *L. melanurus* is indeed a totally parthenogenetic species, then, contrary to the principle mentioned above, it does seem to be able to adapt to changing environments such as a new foodplant in disjunct regions. Although it may seem that the switch of *L. melanurus* to the introduced *E. vulgare* may be recent in evolutionary time, other genetic phenomena such as wing polymorphism apparently occur rather rapidly in this beetle genus and others (Furth, 1980b).

The purpose of this study is primarily to report the existence of parthenogenesis in *Longitarsus melanurus* and to encourage further research concerning its genetics as well as its foodplant switching. The existence of these phenomena in *L. melanurus* should provide a variety of interesting topics for future investigation.

ACKNOWLEDGMENTS

I am primarily and especially indebted to E. Richard Hoebeke (Cornell University) who provided early and recent access to the *Longitarsus* material at Cornell as well as help with literature. I also would like to express gratitude to Dr. Niilo Virkki (University of Puerto Rico) and to Dr. Eduard Petitpierre (Universitat de les Illes Balears, Spain) for information and comments concerning cytogenetics. I am also indebted to the following: Dr. Shawn Clark (West Virginia Department of Agriculture) for information concerning *Chaetocnema perplexa* from the West Indies; the late Dr. Edward U. Balsbaugh, Jr. (North Dakota State University), and Arwin Provonsha (Purdue University) for access to specimens at their respective institutions; and Emily Wood (Harvard University Herbaria) for determination and information about *Echium vulgare.*

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Received 20 January 1994; accepted 10 August 1994.

APPENDIX

After this manuscript was submitted, the author was contacted by Mr. Andrew H. Williams (Department of Entomology, University of Wisconsin, Madison) concerning his survey of *Onosmodium molle* Michx. (Boraginaceae), a plant listed by the Wisconsin Bureau of Endangered Resources as a species of Special Concern. Mr. Williams found adults of *L. melanurus* (determined by E. Riley, Texas A&M University, College Station, and later confirmed by the author) feeding on leaves of *O. molle* at several localities in Wisconsin (Dane, Grant and Iowa counties) on dates ranging from May 13 to July 22. In addition, he found one adult feeding on a leaf of *Cynoglossum officinale* L. (a Boraginaceae introduced from Europe). This discovery of *L. melanurus* feeding on a native *Onosmodium* confirms the author's prediction made in the Discussion of this paper.