#### References

- 1. C. L. Hull, Principles of Behavior (Appleton-
- Century-Crofts, New York, 1943).
  K. W. Spence, Behavior Theory and Condi-tioning (Yale Univ. Press, New Haven, Conn., Control of the Control of 2. 1956).
- W. K. Estes, in Nebraska Symposium on Moti-3.
- 5.
- 6. F. D. Sheffield, T. B. Roby, B. A. Campbell,
- *ibid.* 47, 349 (1954). E. Stellar and J. H. Hill, *ibid.* 45, 96 (1952).
- E. Stellar and J. H. Hill, *iola.* 43, 96 (1952). This study was supported in part by a grant from the Rockefeller Foundation to the arts and sciences division of the American Uni-versity of Beirut. The data were collected at the University of Illinois.

6 March 1959

# **Control of Oöcyte Development**

### in Cockroaches

Abstract. Development of ovarian eggs and secretory activity of colleterial glands are inhibited by the oötheca in the oöthecal chamber of Blattella germanica (L.) and by the oötheca in the uterus of Pycnoscelus surinamensis (L.). The inhibition is due to nervous stimuli from pressure of the oötheca. Removing the oötheca or severing the ventral nerve cord eliminates inhibition of the corpora allata and results in premature development of the oöcytes and resumption of activity of the colleterial glands.

Oöthecal eggs in the uterus of the cockroach Leucophaea maderae (Fab.) are said to release a substance which causes the brain to inhibit secretion of the corpora allata and, thus, maturation of oöcytes (1). Differences in ovipositing behavior among various species of cock-

roaches (2) indicate that this mechanism would operate only in species carrying their oöthecae internally throughout embryogenesis.

Blattella germanica carries its oötheca externally during embryogenesis, and the oötheca inhibits development of the oöcytes and secretion of the colleterial glands. Removal of the egg case from the female results in an increase in the rate of oötheca production (3). The oötheca is carried an average of 30 days (4). During this time the oöcytes increase in length only slightly, from 0.34 to 0.52 mm. Ten days after the first oötheca is dropped the oöcytes have grown to an average length of 2.55 mm, and a second oötheca is formed. The corpora allata were shown to be necessary for development of the oöcytes of B. germanica; allatectomized adult females did not oviposit. Implantation of corpora allata into allatectomized females resulted in oviposition within 2 weeks. An allatectomized female with four implanted corpora allata produced three oöthecae in 61 days; another produced four in 58 days. When imitation wax "oöthecae" were inserted into the oöthecal chamber of adult females 1 day old or less, the oöcytes remained undeveloped. When the ventral nerve cord was severed in a female carrying an oötheca, the oöcytes grew rapidly and colleterial glands accumulated secretion in spite of the presence of an attached oötheca [Fig. 1 (1 and 2)]. Nineteen females from which oöthecae were removed 3 to 5 days after oviposition formed new oöthecae in  $19.8 \pm 0.5$  days (5). Similarly, 11 females whose nerve cords were



**31 JULY 1959** 

Fig. 1. (1, 2) Reproductive tracts of B. germanica females that carried oöthecae for 26 days. (about  $\times 4.8$ ). (1) Unoperated female; the ovaries (arrows) are undeveloped and the colleterial glands lack secretion; (2) female whose ventral nerve cord was severed 6 days after oviposition; the basal oöcytes are almost mature, and the colleterial glands are full of secretion. (3, 4) Reproductive tracts of P. surinamensis females that have oöthecae in their brood sacs. (about ×4.1). (3) Unoperated female 37 days after oviposition; the ovaries (arrows) are small, and the colleterial glands lack secretion; (4) female whose ventral nerve cord was severed just after oviposition; 29 days later the basal oöcytes have matured and the colleterial glands are full of secretion.



Fig. 2. Blattella germanica whose ventral nerve cord was severed 4 days after oviposition; 19 days after the operation it had formed a second oötheca, to which the first adhered. (×2.4). [E. R. Willis]

cut 3 to 5 days after oviposition formed new oöthecae in  $19.5 \pm 0.5$  days. The original oötheca may adhere to the new one, as shown in Fig. 2. One female with a severed nerve cord formed four oöthecae over a period of 82 days, essentially doubling the rate of oöthecal production.

Pycnoscelus surinamensis incubates its eggs in a uterus, like Leucophaea maderae (2). During gestation, which averaged 55.5 days in our parthenogenetic strain of Pycnoscelus (4), the oöcytes increased slightly in length, from 0.56 to 0.75 mm. About 2 weeks after parturition, oviposition again occurs, when the oöcytes average 3.2 mm in length. Usually about 70 days elapse between the formation of the first and second oöthecae. Allatectomized adult females failed to oviposit, but when corpora allata were implanted, these females oviposited 2 or more weeks later. The presence of an oötheca in the uterus inhibited ovarian development; the interval between the production of successive oöthecae was decreased from about 70 to 27 days when oöthecae were removed between 1 and 7 days after oviposition. The presence of parts of oöthecae implanted into the body cavity of adult females 1 day old or less failed to inhibit development of the oöcytes. Parts of young oöthecae were implanted into the body cavities of six females 1 day old or less; after 11 days the oöcytes of these six females were  $2.91 \pm 0.06$  mm long—a length similar to that  $(2.93 \pm 0.06 \text{ mm})$  of oöcytes of normal 11-day-old females.

The oötheca was removed from the uterus of each of ten females 1 to 16 days after oviposition, and one half of each oötheca was implanted into the body cavity of the donor female. Twentythree days after the operation the oöcytes averaged  $2.70 \pm 0.10$  mm in length. However, substitution of a wax oötheca for a real oötheca in the uterus inhibited oöcyte development. Ten females whose nerve cords were cut either 0, < 1, or 4 days after oviposition had well-developed oöcytes 2.74 ± 0.18 mm long and

full colleterial glands 24 to 31 days after the operation [Fig. 1 (3 and 4)]. When real or wax oöthecae were present in the uterus, oöcytes developed only after the nerve cord was severed.

In both Blattella germanica and Pycnoscelus surinamensis, inhibition of oöcyte development during pregnancy appears to be due to nervous stimuli resulting from pressure of the oötheca-on the uterus in P. surinamensis and on the oöthecal chamber in B. germanica. There was no indication that any substance released by the eggs in the oötheca acted through the brain to inhibit secretion of the corpora allata, as has been reported for Leucophaea maderae (1).

# LOUIS M. ROTH\*

# BARBARA STAY<sup>†</sup>

Pioneering Research Laboratories, U.S. Army Quartermaster Research and Engineering Center, Natick, Massachusetts

### **References and Notes**

- M. Lüscher and F. Engelmann, Rev. suisse zool. 62, 649 (1955); F. Engelmann, J. Insect. Physiol. 1, 257 (1957).
  L. M. Roth and E. R. Willis, Smithsonian Misc. Collections 122, 1 (1954); Trans. Am. Entomol. Soc. 83, 221 (1958).
  B. M. Parker and F. L. Campbell, J. Econ. Entomol. 33, 610 (1940).
  Insects were kept at 24° to 25°C and at about 50 to 70 percent relative humidity.

- 50 to 70 percent relative humidity.
- The numbers following ± represent standard 5.
- Present address: Central Research Labora-tories, United Fruit Co., Upland Road, Norwood Mass
- Present address: Biological Laboratories, Har-vard University, Cambridge, Mass. ţ

11 March 1959

### Fault Zone along Northern **Boundary of Western** Snake River Plain, Idaho

Abstract. Gravity, seismic, and geologic studies indicate that at least 9000 ft of aggregate throw along a zone of northwest-trending, high-angle faults has displaced the western Snake River Plain downward relative to highlands on the north. At least 5000 ft of movement occurred between the early and middle Pliocene. Progressively diminishing movement since then amounts to 4000 ft.

Movement within a northwest-trending zone of high-angle faults, producing the abrupt escarpment that rises along the northern boundary of the western Snake River Plain in Idaho, was first recognized during reconnaissance surveys 60 years ago (1) but was disregarded in subsequent discussions that attributed the Snake River Plain to downwarping (2). Recently published gravity and seismic studies support the role of faulting as a cause of the escarpment, and current geologic mapping by the U.S. Geological Survey helps to date

the times of movement. The fault zone aligns middle Pliocene and younger rocks of the Snake River Plain against a variety of older rocks in highlands to the north, including granite of the Idaho batholith north of Mayfield and silicic volcanics of early Pliocene age north of Mountain Home.

The pertinent gravity measurements are in a network of 800 locations that embraces southern Idaho and adjacent parts of neighboring states. In this network the greatest change in gravity is across the northern boundary of the Snake River Plain, amounting to a difference of 166 milligals between a high in the Snake River Plain 10 mi southwest of Mountain Home and the low in the Idaho batholith (3). This difference in gravity is opposite to that associated with high-angle faults elsewhere in western United States and indicates that rocks in the downthrown block of the Snake River Plain are heavy compared with the Idaho batholith. From analysis of a 50-milligal residual anomaly associated with the steep gravity gradient near Mountain Home, it is calculated that from 13,000 to 38,000 ft of rocks about as dense as Columbia River basalt have been dropped down against the Idaho batholith (4), the thickness of the displaced rocks depending on the density contrast assumed  $(0.3 \text{ and } 0.1 \text{ g/cm}^3, \text{ respectively}).$ 

The crustal break implied by the gravity measurements is possibly expressed by a line of earthquake epicenters that extends diagonally from Puget Sound, across the Columbia River Plateau, along the northern boundary of the western Snake River Plain, and thence across the plain to northern Utah (5). In Idaho, these earthquakes originate principally at average depths of 61 and 38 km (38 and 24 mi), the shallower earthquakes being near the base of the crust (6). The displacement calculated from the gravity measurements therefore ranges from one-tenth to onethird of the local crustal thickness.

Geologic evidence of intermittent crustal adjustment has been found near King Hill along the zone of faulting inferred from the geophysical observations, indicating that rocks of early Pliocene and younger age are dropped downward toward the Snake River Plain in progressively diminishing amounts. Thus, the bounding escarpment is formed by a large displacement of the silicic volcanics of early Pliocene age; basalt of middle Pliocene age that overlaps these faulted volcanics is offset a lesser amount; sedimentary rocks of late Pliocene age overlying the faulted basalt are somewhat offset and disarrayed by faulting; deposits of early Pleistocene age resting on the disturbed late Pliocene rocks are dropped down only a few hundred feet; and, finally, the deposits of middle Pleistocene and younger age are fractured, but not measurably offset, along the fault zone. The detailed paleontologic evidence by which this rock sequence has been dated will be described elsewhere, but the amounts of progressive crustal displacement can be summarized briefly.

The faulted silicic volcanics north of the fault zone are part of an eroded highland as much as 7500 ft above sea level, whereas drilling in the Snake River Plain 15 mi south of the fault zone reached a depth of 1200 ft below sea level without encountering these volcanics (7); this seemingly demonstrates a minimum displacement of about 9000 feet. The basalt of middle Pliocene age forms an upland 3800 ft above sea level north of the fault zone, but at King Hill, near the southern margin of the zone, drilling reached a depth of 1600 feet above sea level without penetrating this basalt (8); this suggests an offset of about 2200 feet. Displacement of the sedimentary rocks of upper Pliocene age is shown by exposures mainly along the northern margin of the fault zone, where one prominent fault offsets these rocks 600 ft, but tilting, no doubt caused by concealed faults within the fault zone, accounts for an equal amount of additional displacement, aggregating about 1200 ft. The deposits of early Pleistocene age along the fault zone are stepped down by a series of faults whose combined throw is about 600 ft. As the sum of all the measurable displacements in rocks younger than the silicic volcanics (4000 ft) accounts for less than half the minimum total displacement along the fault zone (9000 ft), most of the movement must have occurred before deposition of the middle Pliocene and younger rocks, but after eruption of the early Pliocene silicic volcanics (9).

HAROLD E. MALDE U.S. Geological Survey,

Denver, Colorado

#### **References** and Notes

- W. Lindgren, U.S. Geol. Survey Ann. Rept. No. 18 (1898), part 3, p. 631; I. C. Russell, U.S. Geol. Survey Bull. 199 (1902), pp. 42-0012 43, 47.
- 3.
- 4. 1959). G. P. Woollard, Trans. Am. Geophys. Union
- 5. 39, 1137, Fig. 5 (1958). , *ibid.* 39, 1146 (1958).
- W. Youngquist and T. H. Kiilsgaard, Bull. Am. Assoc. Petrol. Geologists 35, 90 (1951). H. T. Stearns, Lynn Crandall, W. G. Steward, U.S. Geol. Survey Water Supply Paper No.
- U.S. Geol. Survey water Survey, and 774 (1938), p. 52. Publication of this report is authorized by the director of the U.S. Geological Survey. This report has benefited from critical reading by L. C. Pakiser and W. E. Bonini.

22 May 1959