

BIOSYSTEMATICS OF NORTH AMERICAN *IPS* (COLEOPTERA: SCOLYTIDAE)

HOPPING'S GROUP IX

G. N. LANIER

Forest Research Laboratory, Department of Fisheries and Forestry, Edmonton, Alberta

Abstract

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Controlled mating experiments demonstrating total reproductive isolation, together with consistent differences in morphological and cytological detail, confirmed the validity of the closely related group IX *Ips*: *grandicollis*, *cribricollis*, *lecontei*, *montanus*, *confusus*, *paraconfusus*, and *hoppingi*. The latter two species, new to science, were formerly considered to be *confusus*.

Matings between *grandicollis* from eastern Canada and North Carolina were subnormally fertile; other intraspecific matings between individuals of the same population or distant populations produced fully fertile progeny. Interspecific pairings usually resulted in insemination and normal-appearing egg galleries, but, with one exception, none of the eggs hatched.

One *montanus* and two *confusus*, each mated by males of the same species, produced all-daughter broods. This "sex-ratio" condition appeared to be the result of a matrilineally transferred cytoplasmic factor lethal to male embryos only.

At first meiotic metaphase all species had the karyotypic formula $15AA + Xy$, and only *grandicollis* was easily differentiated by bivalent configuration or size sequence. Most other species showed diagnostic differences at meiotic prophase or second meiotic metaphase. Pairing disruptions and anaphase bridges occurred in *grandicollis* interpopulational hybrids; meiosis was normal in progeny from interpopulational pairings of *confusus*, *paraconfusus*, and *montanus*.

In *grandicollis* the median struts of the male genitalia were 1.5 times longer than the median lobe. The struts/lobe ratios for other species approximated 1.00 but differences for most comparisons between species were statistically significant. The shape of the pars stridens on females was different for most species and mean widths of striations thereon ranged from 0.517μ for *paraconfusus* to 0.876μ for *lecontei*. This character provided absolute discrimination of females of *confusus* from those of *paraconfusus* and *hoppingi* but the latter two species were most easily separated by differences in the density of punctures in the elytral declivity.

It is hypothesized that contiguous allopatry and differences in host and ecological specialization, evidenced in species of group IX, is maintained by their high propensity for interspecific mating which fails completely to produce progeny.

Introduction

Because of their economic importance and conspicuous occurrence in most coniferous forests, the bark beetles of the genus *Ips* and their parasites have been intensively studied biologically and reviewed taxonomically. In addition, certain species have been important in studies of aggregation behaviour, host selection, sex pheromones, sound production, and muscle regeneration.

Hopping (1963a-d, 1964, 1965a-e) revised the North American members of this genus, dividing them into 10 subgeneric groups. Lanier's (1966) mating and chromosomal studies supported Hopping's "natural" groups and confirmed the validity, with respect to each other, of three pairs of extremely similar species. The present paper is the first of a series presenting results of further biosystematic studies. *Ips* species of group IX are investigated in detail and three species (two new), heretofore considered to be *I. confusus* (Leconte), are described.

Review of Group IX

Hopping (1963b) placed *I. grandicollis* (Eichhoff), *I. chagnoni* Swaine, *I. cribricollis* (Eichhoff), *I. confusus*, *I. montanus* (Eichhoff), and *I. lecontei* Swaine

in group IX. Characteristics he used to define this group are pine-feeding, 5 spines on each lateral margin of the elytral declivity, antennal club sutures strongly angled in the middle, and a median tubercle on the frons of males which is usually obsolete or reduced in females.

These 5-spined *Ips* have a history of taxonomic controversy.¹ Schedl (1955) proposed the synonymy of *I. cloudcrofti* Swaine, *lecontei*, *vancouveri* Swaine, *montanus*, and *confusus*. S. L. Wood (1957) replied that *montanus*, *lecontei*, and *confusus* were valid because they could be segregated by morphological characters and their distributions overlapped. However, he synonymized *vancouveri* with *montanus* and *cloudcrofti* with *cribricollis*.² Schedl (1960) insisted that *montanus* was a synonym of *confusus* and suggested that *cribricollis* might be synonymous with *lecontei*. Hopping (1965c) accepted Wood's arrangement and also synonymized *chagnoni* with *grandicollis* on the grounds that size variation between these species was clinal (increasing from south to north) and other differences noted by Swaine (1918) were within the variability of specimens from one locality. Lanier (1966) found that *confusus* from the California mountains and *montanus* would readily mate, but no eggs hatched even though their karyotypes were nearly identical.

Lindquist (1969) supported Hopping's concept of group IX by considering host-specific tarsonemid mites on *confusus*, *montanus*, *grandicollis*, and *lecontei* all to be subspecies of *Iponemus confusus* (Lindquist and Bedard). *Iponemus nahua* Lindquist, a parasite of *cribricollis*, was given full species status, partly on the basis of its morphological differences from the *Iponemus confusus* subspecies, and partly because these mites and their respective hosts, *cribricollis* and *lecontei*, are sympatric in Mexico and may occur together in the same host material. Other group IX species are completely isolated (*grandicollis*)³ or contiguously allopatric (Figs. 1, 2). However, adjacent species show different ecological and (or) host preferences (Hopping 1965c; Lanier 1966; Lindquist 1969).

*I. confusus*⁴ and *grandicollis* are not attracted to sex pheromones in the frass of species of other groups with which they are sympatric. However, strong attraction of *grandicollis* to *confusus* frass (Vité *et al.* 1964) and cross attraction between *confusus*, *montanus*, and *lecontei* has been demonstrated (D. L. Wood and Lanier, unpub. data; Pitman, pers. comm.). Being sympatric, *cribricollis* and *lecontei* presumably are not cross attractive, but this supposition has not been tested.

I. confusus (sensu Hopping) includes two conspicuously distinct ecological races: one attacks *Pinus ponderosa* Laws. and other pines along the Pacific-facing slopes of the mountains of California and Oregon; the other, in southeastern California and the interior southwestern states, infests only pinyon pines (*P. monophylla* Torr. & Frem. and *P. edulis* Engelm.) even though *P. ponderosa* is present (Chansler 1964). Biological information given by Schwerdtfeger (1956) and records listed by Schedl (1955) for "*confusus*" in central America actually refer to *lecontei* (Schedl 1960; Hopping 1965c). In Mexico *confusus* is known only from *Pinus cembroides* Zucc.; both the insect (Thomas 1966 and personal communication) and its host (Critchfield and Little 1966; Mirov 1967) appear to be biologically similar to the interior race. Hopping (1965c) was unable to find

¹Hopping (1965c), Schedl (1955), and Swaine (1909) list complete synonymy.

²Hopkins (1905, p. 77) misquoted Eichhoff (1868, p. 273) in referring to this species as "*Toxus cribricollis* Eichh." — herein considered to be a *nomen nudum*.

³*I. grandicollis* (sensu Hopping) is the only group IX species in eastern North America. It has also been introduced into pine plantations in Australia (Hopping 1965c; Morgan 1967).

⁴Populations from montane California; described as a new species herein.

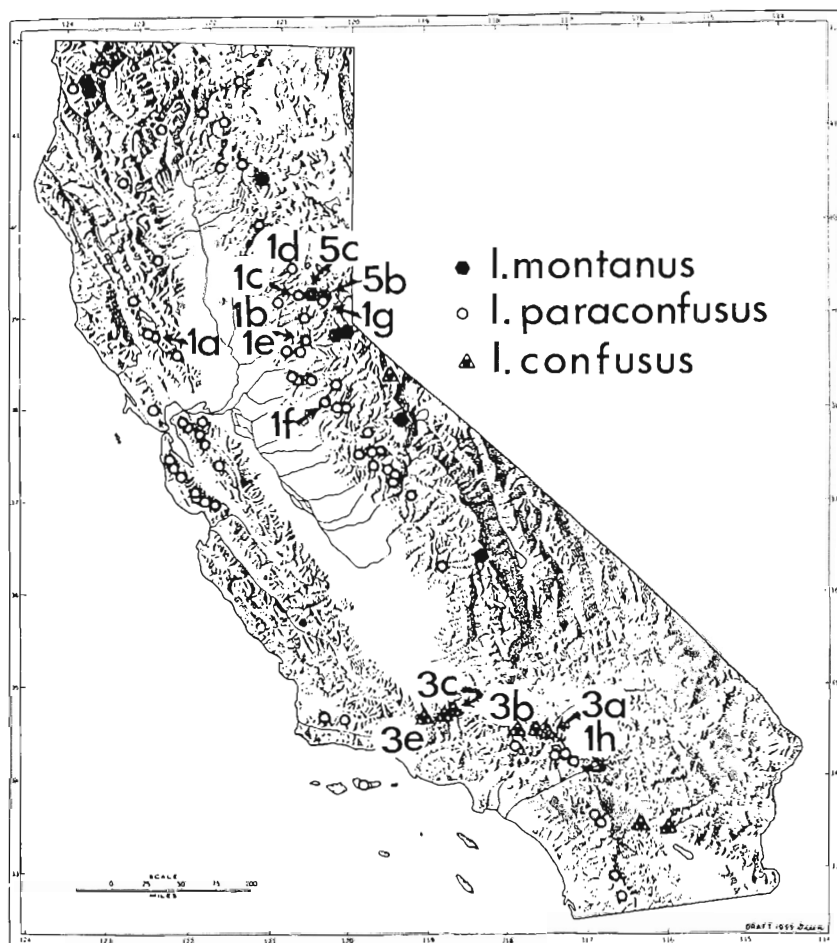


FIG. 1. Collection localities for *Ips montanus*, *paraconfusus*, and *confusus* illustrating their contiguously allopatric distribution in California. Populations used in breeding experiments and/or cytological study are indicated as listed in Table I. Base map courtesy of the California Insect Survey, Berkeley.

morphological differences between the *confusus* races. Subsequently, differences were discovered on the pars stridens of females (Barr 1969).

Although cross-attractive, response of the races to sex pheromones is slightly different (D. L. Wood and Lanier, unpub. data). Lindquist (1969) reported no dissimilarities in the *Iponemus* mites in *Ips confusus* from various areas. However, Nickle (1963a, b) found striking differences between the parasitic nematodes from the two races. The present study demonstrates the reality of three species in the *confusus* complex while supporting the validity of Hopping's (1965c) concepts of *cribricollis*, *lecontei*, *montanus*, and *grandicollis*.

Methods

This study employed controlled matings, karyology, and examination and measurement of morphological characters. Insects used in pairings were taken as callow adults from pupal chambers in naturally infested material or laboratory colonies (Table I). Beetles were sexed with characters summarized by Lanier and Cameron (1969) and placed in corked 8-dr shell vials (10–20 per vial) with strips of fresh pine phloem. After feeding for 1–2 weeks they were used in experiments or stored (ca. 3°C) for later use. Procedures for making and

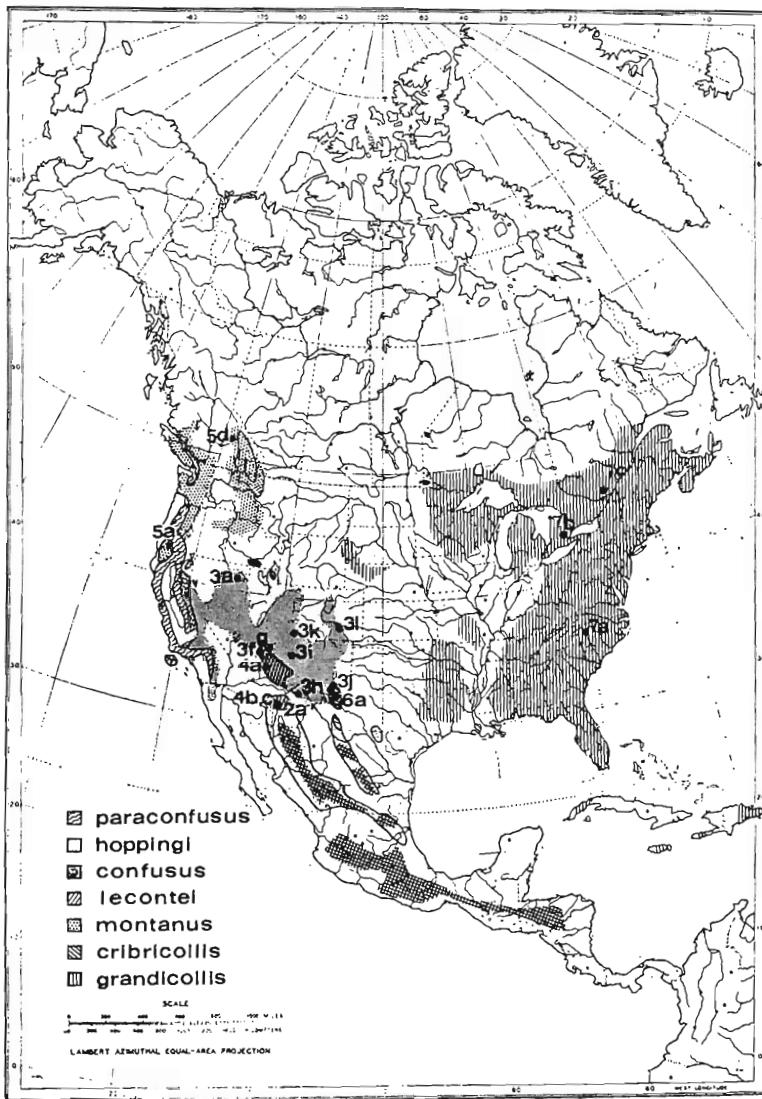


FIG. 2. Distribution of *Ips* species of group IX in North America. Populations used in breeding experiments and/or cytological study are indicated as listed in Table I. The isolated midwestern occurrence of *grandicollis* is based on two series, one recently taken by the author from *Pinus ponderosa* in the Black Hills of South Dakota and the other taken by L. G. Baumhofer from planted *P. banksiana* at Halsey, Neb. After (in part) Hopping (1965) and Lindquist (1969).

evaluating pairings were similar to those described previously (Lanier 1966), except that incubation was at 30°–35°C and maturation of broods required less than 25 days. The term "pairing" denotes the act of placing insects of the opposite sex together to induce mating; "mating" denotes sperm transfer.

Karyotypic determinations were made exclusively from acteo-orecin squashes of testes taken from fresh adults, 2–7 days after ecdysis. Usually, testes were squashed immediately upon dissection. To obtain clearly spread spermatogonial and second meiotic metaphase (MII) cells, testes were soaked (at the expense of staining) for 2 minutes in distilled water.

Measurements of male genitalia were made from microslide mounts ca 100×. Drawings were traced from photographs in consultation with the original object.

TABLE I

Host and collection locality for *Ips* species of group IX used in controlled mating and cytological studies*

Species	Collection locality	Host pine	♀ paired with ♂ of:	No. examined cytologically
1. <i>paraconfusus</i> †	a. Calif., Whispering pines	<i>ponderosa</i>	1e;5a,b	4
	b. Calif., Nevada City	<i>ponderosa</i>	—	7
	c. Calif., Cisco	<i>jeffreyi</i>	1a;5b	—
	d. Calif., Downieville	<i>ponderosa</i>	5a	2
	e. Calif., 10 mi NW. Georgetn.	<i>ponderosa</i>	3a,f;4a	8
	f. Calif., Avery	<i>ponderosa</i>	1g,h;2a;3c,d,g, h,j,l;6a;7a	5
	g. Calif., Old Soda Springs	<i>monticola</i>	—	—
	h. Calif., Lake Arrowhead	<i>ponderosa</i>	1f;3c	1
2. <i>hoppingi</i>	a. Ariz., 20 mi S. Chiricahua Nat. Mon.	<i>cembroides</i>	1f;3h;4b,c	4
3. <i>confusus</i>	a. Nev., Pequop Pass	<i>monophylla</i>	1e;3c;4a;5c	—
	b. Calif., Valyermo	<i>monophylla</i>	1e;3a,e,f;4a;5c	—
	c. Calif., Fraser Park	<i>monophylla</i>	1f;3e	—
	d. Calif., Wrightwood	<i>monophylla</i>	1f	—
	e. Calif., Chuchupate Ranger Sta.	<i>monophylla</i>	1f;2a;3h,i,j,l	4
	f. Ariz., Seligman	<i>edulis</i>	1h;2c;5b	6
	g. Ariz., Williams	<i>edulis</i>	1e,h;3a,c,d,e;4a;5b	5
	h. N.M., 15 mi W. Kingston	<i>edulis</i>	1f;2a;3e,l	—
	i. N.M., Grants	<i>edulis</i>	2a;3l	—
	j. N.M., Capitan	<i>edulis</i>	2a	—
	k. Colo., Cortez	<i>edulis</i>	—	—
	l. Colo., Crestone	<i>edulis</i>	1f;2a;3h	—
4. <i>lecontei</i>	a. Ariz., Prescott	<i>ponderosa</i>	1e;3a,e;5c	7
	b. Ariz., 20 mi S. Chiricahua Nat. Mon.	<i>arizonica</i>	2a;3h,k;4c	1
	c. Ariz., 20 mi S. Chiricahua Nat. Mon.	<i>cembroides</i>	2a;4b	—
5. <i>montanus</i> (= <i>vancouveri</i>)	a. Ore., Lake of the Woods	<i>monticola</i>	1a,c	1
	b. Calif., Soda Springs	<i>monticola</i>	1a,c,f,g;2f;4a	2
	c. Calif., Kingvale	<i>monticola</i>	1c,e;3a,f;4a	4
	d. B.C., Sicamous	<i>monticola</i>	5b	2
6. <i>cribricollis</i> (= <i>cloudcrofti</i>)	a. N.M., Ruidoso	<i>ponderosa</i>	1f;4b,c;7a	4
7. <i>grandicollis</i> (= <i>chagnoni</i>) (= <i>c. chagnoni</i>)	a. N.C., Research Triangle Park	<i>elliottii</i>	1f;6a;7b,c	6
	b. Ontario, Midhurst	<i>sylvestris</i>	7a	5
	c. Quebec, Aylmer	<i>resinosa</i>	7a	—

*Material studied morphologically only is listed in "Description of species."

†Part of the data for *paraconfusus* and *montanus* are resummarized from a previous paper (Lanier 1966) in which the name "*confusus*" is applied to *paraconfusus*.

Measurements of pronotal width and total body length were made with a binocular microscope at 40×. To determine density of punctuation in the elytral declivity, the punctures within, or intersected by, the lines of an ocular grid covering approximately 0.27 mm² on one elytron (80×) were counted. The mean of counts for the two elytra was taken as the punctuation index for the specimen involved. To measure width of striations on the pars stridens of the females, this part of the stridulating organ was removed from the vertex of the head, mounted in Permout® on a microslide, and photographed at 1250×. The aggregate width of four striations was measured (40×) on contact prints, and this measurement was converted to *u*/striation, actual scale. The width of the whole pars stridens was measured on photographs with a millimeter scale.

Samples of the insect material (voucher specimens) have been deposited in the California Academy of Science (San Francisco) and in the Canadian National Collection (Ottawa).

Taxonomy

In redescribing *I. confusus*, Hopping (1965c) had before him specimens of the three sibling species listed below. As external morphology is essentially identical for each species, repetition of that description is unnecessary. Recently discovered differences, described in detail in the text of this paper, are cited below.

Ips confusus (Leconte)

TAXONOMIC LITERATURE

Tomicus confusus Leconte 1876, p. 364; Swartz 1886, p. 42.

Ips confusus, Swaine 1909, p. 122, 1918,* 1924,* pp. 69-70; Schedl 1955,* pp. 40-41; S. L. Wood 1957,† p. 397; Schedl 1960,* p. 7; Hopping 1963b,† pp. 514-516, 1965c,† pp. 425-429.

BIOLOGICAL LITERATURE

Tomicus confusus, Hopkins 1905.

Ips confusus, Keen 1933; Little 1943; Massey 1957, 1960, 1952; Nickle 1963a,* b,* c*; Chansler 1964, 1966; Struble 1966†; Kinn 1967a, 1968*; Lindquist 1969†; Barr 1969 ("pinyon form"); Lanier and Cameron 1969 ("*confusus* A").

DIAGNOSIS. Females of this species differ from those of *hoppingi* and *paraconfusus* by having a narrower pars stridens with wider striations. In males of *confusus*, the median struts of the genitalia are shorter than the median lobe, whereas in *hoppingi* and *paraconfusus* they are equal to, or longer than, the median lobe. The declivities of both sexes are more densely punctate than those of *paraconfusus*. The second largest autosome of *confusus* is heterobrachial rather than cephalobrachial as in *hoppingi* and *paraconfusus*.

TYPES. The holotype (female — "Type 1025", Leconte collection, Museum of Comparative Zoology, Harvard University) was examined and its pars stridens was mounted on a slide to permit positive identification. Type locality is "southern California" (Leconte 1876; Swaine 1924; Hopping 1965c) but original host was not recorded.

Twenty-two homotypes were dispersed as follows: 4 ♀ ♀ and 4 ♂ ♂ — Valyermo, Los Angeles Co., Calif., X-65, *Pinus monophylla*, G. N. Lanier, collector — Canadian National Collection, Ottawa; 1 ♀ and 1 ♂ — Joshua Tree Nat. Mon., Calif., I-16-58, Hopk. U.S. 34092A, *Pinus monophylla*, R. C. Hall, collector — Pacific Southwest For. & Range Exp. Sta., Berkeley; 2 ♀ ♀ and 2 ♂ ♂ — Seligman, Coconino Co., Ariz., X-65, *Pinus edulis*, G. N. Lanier, collector — California Academy of Science, San Francisco; 2 ♀ ♀ and 2 ♂ ♂ — same data — U.S. National Museum, Washington, D.C.; 2 ♀ ♀ and 2 ♂ ♂ — Pequop Pass, 5 mi W. Oasis, Elko Co., Nev., VIII-65, *Pinus monophylla*, G. N. Lanier, collector — California Insect Survey, Berkeley.

MATERIAL EXAMINED. Over 1000 specimens.

UNITED STATES

Arizona: Flagstaff, Seligman and Williams, Coconino Co.; Prescott, Yavapai Co.; Window Rock, Apache Co.; Coconino Nat. For.; Grand Canyon. **California:** Frazier Park and 10 mi W. Frazier Park, Kern Co.; Wrightwood, San Bernardino

*Refers in part to *paraconfusus* n. sp.

†Refers in part to *paraconfusus* and *hoppingi* n. sp.

Co.; Joshua Tree Nat. Mon. and 16 mi SW. Palm Desert, Riverside Co.; Gorman and Valyermo, Los Angeles Co.; Coleville, Mono Co.; Chuchupate Ranger Sta., Ventura Co.; Inyo Nat. For.; Death Valley Nat. Monument. **Colorado:** Mesa Verde Nat. Park, Mancos, and Cortez, Montezuma Co.; Canyon City, Fremont Co.; Crestone, Sagucho Co.; Grand Junction, and Colorado Nat. Monument, Mesa Co.; Norwood, San Miguel Co.; Turkey Cr., El Paso Co.; Uncompahgre Nat. For. **Nevada:** Baker, White Pine Co.; Pequop Pass and Charleston, Elko Co. **New Mexico:** Cloudcroft and Capitan, Lincoln Co.; 5 mi W. Magdalena, Socorro Co.; Grants, Valencia Co.; 15 mi W. Kingston, Grants Co.; Los Alamos, Sandoval Co.; Datin Mts. **Utah:** La Sal Mts., San Juan Co.; Mercur and Lofgreen, Tooele Co.; Panguitch, Garfield Co.; Beaver, Beaver Co.; Parowan Cyn.; Iron Co.; Gooseberry, Fish Lake Nat. For.; Mt. Carmel; San Isabel Nat. For. **Wyoming:** Atlantic City, Fremont Co. (see "Remarks").

MEXICO

Baja California: Tecate.

REMARKS. Usual hosts are the pinyon pines including *P. monophylla* and *edulis* in the interior southwestern United States and *P. quadrifolia* in Baja California (Figs. 1, 2). Occasionally collected in *P. ponderosa* (3 records) and *P. flexilis* James (2 records). However, one record in the latter host is dubious as it is based upon a single specimen among a large series of a distantly related *Ips* taken at Atlantic City, Wyo., more than 100 miles north of the range of pinyon pines. This species shows unique (for *Ips*) tolerance to pine resin and may produce large pitch tubes in killing vigorous trees. I have found *I. confusus* in cohabitation with *I. latidens* (Leconte) and *I. pini* (Say).

Ips hoppingi n. sp.

LITERATURE

Ips confusus, S. L. Wood 1957*; Hopping 1963b,* 1965c*; Struble 1966*; Thomas 1966; Lindquist 1969.*

DIAGNOSIS. Females of this species differ from *confusus* in having wider pars stridens with narrower striations. Males of *hoppingi* have genitalia with median struts longer than the median lobe while the struts are equal to or shorter than the lobe on the *confusus* genitalia. The declivities of both sexes are more densely punctured than those of *paraconfusus*. The second largest autosome is cephalo-brachial in *hoppingi* rather than heterobrachial as in *confusus*.

TYPES. Holotype: female: Ariz. Cochise Co. 20 mi S. Chiricahua Nat. Mon., 19-X-68, *Pinus cembroides*, G. N. Lanier, collector — deposited in the Canadian National Collection (CNC), Ottawa.

Allotype: male: same data as holotype, also in CNC.

Paratypes: 76 in aggregate. 40 — same data as holotype, 10 in CNC, 10 in California Academy of Science (CAS), 10 in U.S. National Museum (USNM), 10 in Forest Research Laboratory, Edmonton, Alta. 10 — Texas, Big Bend Nat. Park, Chisos Mts., *Pinus cembroides*, E. H. Lampi, collector — in CNC. 26 — Mesa del Huracan, Chih. Mex. *Pinus cembroides*, J. B. Thomas, collector — 10 in CNC, 10 in USNM, 3 in CAS, and 3 in California Insect Survey, Berkeley.

MATERIAL EXAMINED. 167 specimens.

UNITED STATES

Arizona: Chiricahua Nat. Monument; 20 mi S. Chiricahua Nat. Monument, Cochise Co. **Texas:** Chisos Mts., Big Bend Nat. Park; Davis Mts.; Big Bend Nat. Park.

MEXICO

Chihuahua: Mesa del Huracan. **Hidalgo:** Zimapan. **Mexico:** Temascaltepec.

REMARKS. This species is named for George R. Hopping, Canada Department of Fisheries and Forestry (retired), in recognition of his extensive and outstanding work on the genus *Ips*.

I. hoppingi apparently follows the range of its usual host, *Pinus cembroides* in Mexico and southern parts of Arizona, New Mexico, and Texas (Fig. 2) but it probably does not occur in isolated remnant trees (Mirov 1967) in southern California. I have seen two specimens from *P. ponderosa*.

Ips paraconfusus n. sp.

TAXONOMIC LITERATURE

Ips confusus, Swaine 1918,* p. 113, 1924,* pp. 69, 70; Craighead 1930, p. 6; Chamberlin 1939, pp. 411, 419; Schedl 1955,* pp. 40, 41; S. L. Wood 1957,† p. 397; Chamberlin 1958, pp. 163, 167; Schedl 1960,* p. 7; Hopping 1963b,† pp. 514–516, 1965c,† pp. 425–429; Lanier 1966.

BIOLOGICAL LITERATURE

Ips confusus, Chamberlin 1917, p. 328; Doane *et al.* 1936, pp. 55, 88, 89, 448; Graham 1952, pp. 263, 264, 331; Keen 1953, pp. 146–148; Lyon 1955; Struble and Hall 1955; Struble 1955; Moore 1957; Hall 1958; Lyon 1959; Berryman and Stark 1961; D. L. Wood 1961; Lindquist and Bedard 1961; D. L. Wood and Vité 1961; D. L. Wood 1962a, b; Vité and Gara 1962; Gara and Vité 1962; Nickle 1963a,* b,* c*; D. L. Wood 1963; Vité *et al.* 1963; Gara 1963; D. L. Wood and Bushing 1963; Pitman 1965; Pitman *et al.* 1965; Vité 1965; Bedard 1966; Pitman 1966; Pitman *et al.* 1966; Renwick *et al.* 1966; D. L. Wood and Stark 1966; D. L. Wood *et al.* 1966; Borden and D. L. Wood 1966; Silverstein, Rodin, and D. L. Wood 1966; Silverstein *et al.* 1966; Struble 1966†; Cameron and Borden 1967; D. L. Wood *et al.* 1967; Lyon and Shea 1967; Thomas 1967; Kinn 1967b, 1968*; Borden 1967, 1968; D. L. Wood and Stark 1968; D. L. Wood *et al.* 1968; Vité and Pitman 1968; Borden and Slater 1968, 1969; Lindquist 1969†; Barr 1969; Lanier and Cameron 1969 ("*confusus* B"); Bedard and Browne 1969; Bhakthan *et al.* 1969; Rice 1969; Borden *et al.* 1969; Bhakthan *et al.* 1970.

DIAGNOSIS. Females of this species differ from *confusus* in having wider parastridens with narrower striations. Males of *paraconfusus* have genitalia with median struts longer than the median lobe while struts are equal to or shorter than the lobe on the *confusus* genitalia. The declivities of both sexes are more sparsely punctured than those of *hoppingi*. The second largest autosome is cephalo-brachial in *paraconfusus* rather than heterobrachial as in *confusus*.

TYPES. Holotype: female: Calif., Calaveras Co., Avery, I-67, *Pinus ponderosa*, G. N. Lanier, collector — deposited in the Canadian National Collection, Ottawa.

Allotype: male: same data as holotype, also CNC.

Paratypes: 100 — same data as holotype; 20 in CNC, 20 in U.S. National Museum, 20 in California Academy of Science, 20 in California Insect Survey, 20 in Forest Research Laboratory, Edmonton, Alta.

MATERIAL EXAMINED. Over 1000 specimens.

*Refers in part to *I. confusus* (Leconte).

†Refers in part to *I. confusus* and *I. hoppingi* n. sp.

UNITED STATES

California: Happy Camp, Bartle, McCloud, and Medicine Lake, Siskiyou Co.; Hat Creek P.O. and Montgomery, Shasta Co.; Trinity Center and Hayfork, Trinity Co.; Belden, Plumas Co.; Downieville, Sierra Co.; Challenge, Yuba Co.; Grass Valley and Nevada City, Nevada Co.; Gold Run and Old Soda Springs, Placer Co.; Greenwood, Pilot Ridge, Blodgett Forest, Pollock Pines, and Placerville, El Dorado Co.; Angels Camp, Murphies, Avery, Arnold, Big Trees, Dorrington, and West Point, Calaveras Co.; Strawberry, Pinecrest, and Mather, Tuolumne Co.; Bass Lake and North Fork, Madera Co.; Dinky Creek, Huntington Lake, and Miramonte, Fresno Co.; Camp Nelson, Tulare Co., Whittier Springs, Midtown, and Whispering Pines, Lake Co.; Corte Madera, Marin Co.; Berkeley, Oakland, and Sunol, Alameda Co.; Mt. Diablo, Contra Costa Co.; Stanford U. (Buckhorn Cyn.) and San Mateo, San Mateo Co.; San Jose and Mt. Hamilton, Santa Clara Co.; Santa Cruz, Santa Cruz Co.; Santa Barbara and Figuero Mtn., Santa Barbara Co.; San Dimas Exp. For., Los Angeles Co.; Blue Jay, Crestline, and Lake Arrowhead P.O., San Bernardino Co.; Mtn. Center, Riverside Co.; Descanso, San Diego Co.; Cleveland Nat. For.; Santa Cruz Island. **Oregon:** Ashland, Central Point, and Jacksonville, Jackson Co.; 10 mi SW. Dallas, Polk Co.; Corvallis and 4 mi S. Brownsville, Linn Co.; Black Rock.

REMARKS. This species breeds in all pines within its range including *P. ponderosa*, *lambertiana*, *monticola*, *contorta*, *jeffreyi*, *coulteri*, *sabinianae*, *attenuata*, *radiata*, and *murricata*. It ranges from northern Oregon to southern California west of the crests of the Sierra Nevada and Cascade Mts. (Figs. 1, 2). It is not known from the desert-facing "Great Basin" timber type even though *P. ponderosa*, its principal host, is present. Owing to its polyphagia, it may co-exist with *I. pini*, *calligraphus* (Germar), *plastographus* (Leconte), *mexicanus* (Hopkins), *emarginatus* (Leconte), *latidens*, *sabinianae* (G. Hopping), and rarely *montanus*. During periods of drought this species is a serious tree killer either singularly, or in association with *Dendroctonus* (Scolytidae) species.

Results

Pairing Experiments

Intraspecific (control) pairings of each species produced brood (Table II) although results varied between species. Significantly, *confusus* from five western states were highly interfertile as were *montanus* from California, Oregon, and British Columbia (Figs. 1, 2). *I. paraconfusus* from the central Sierra Nevada (1f) interbred freely with populations from the Sierra Nevada summit (1g) and the San Bernardino Mountains (1h) where this species is contiguously allopatric with *montanus* and *confusus*, respectively. However, fertility for matings between *grandicollis* from North Carolina (7a) and eastern Canada (7b, 7c) was reduced. Some fully developed larvae did not penetrate the chorion and others hatched but failed to feed. Thus, the ratios of larval mines to egg niches (L/E) for *grandicollis* × "*chagnoni*" pairings (Table II) are quite lower than actual per cent hatch.

Hatchability for *hoppingi* control pairings was also low. At least two of the females that produced subnormal galleries were heavily infested with nematodes — a condition known to reduce fecundity and fertility in *Ips* (Massey 1960; Nickle 1963c).

Only 29 of 59 eggs laid by one *montanus* hatched and all 11 D₁ which developed from these were females. Matings of 2 D₁ also showed a reduced egg

TABLE II
Results of pairing *Ips* species of group IX

Females	Males	Pairings	Females ovipositing	Broods	Positively inseminated females	Egg niches	Larvae per egg niche
<i>lecontei</i>	<i>lecontei</i>	12	12	12	12	343	.90
	<i>confusus</i>	15	8	0	4	140	.00
	<i>paraconfusus</i>	4	2	0	3	37	.00
	<i>hoppingi</i>	4	3	0	1	20	.00
	<i>montanus</i>	6	1	0	1	4	.00
	<i>cribricollis</i>	2	0	0	0	0	.00
<i>confusus</i>	<i>confusus</i>	57	47	45	45	1774	.81
	<i>paraconfusus</i>	22	18	0	11	525	.00
	<i>hoppingi</i>	25	14	0	11	571	.00
	<i>montanus</i>	16	6	1*	3	238	.03
	<i>lecontei</i>	11	5	0	3	112	.00
<i>paraconfusus</i>	<i>paraconfusus</i>	22	18	17	17	812	.85
	<i>confusus</i>	38	27	0	18	942	.00
	<i>hoppingi</i>	10	10	0	9	526	.00
	<i>montanus</i>	19	13	0	7	442	.00
	<i>lecontei</i>	4	3	0	3	61	.00
	<i>cribricollis</i>	5	3	0	2	67	.00
	<i>grandicollis</i>	10	8	0	2	261	.00
<i>hoppingi</i>	<i>hoppingi</i>	10	9	9	9	183	.68
	<i>confusus</i>	14	8	0	5	176	.00
	<i>paraconfusus</i>	6	3	0	3	105	.00
	<i>lecontei</i>	4	3	0	1	79	.00
<i>montanus</i>	<i>montanus</i>	19	12	12	12	333	.78
	<i>confusus</i>	9	2	0	2	96	.00
	<i>paraconfusus</i>	17	10	0	9	231	.00
	<i>lecontei</i>	8	1	0	1	31	.00
<i>cribricollis</i>	<i>cribricollis</i>	8	7	7	7	224	.89
	<i>grandicollis</i>	9	7	0	2	249	.00
	<i>paraconfusus</i>	3	2	0	0	11	.00
	<i>lecontei</i>	4	1	0	0	14	.00
<i>grandicollis</i>	<i>grandicollis</i>	8	6	6	6	254	.84
	"chagnoni"	5	5	4	4	235	.52
	Hybrid†	5	5	5	5	220	.60
	<i>cribricollis</i>	10	8	0	1	190	.00
	<i>paraconfusus</i>	7	4	0	0	52	.00
"chagnoni"	"chagnoni"	3	1	1	1	15	.87
	<i>grandicollis</i>	7	7	7	7	432	.59
	Hybrid	5	2	2	2	92	.94
Hybrid	Hybrid	7	4	3	3	160	.48
	<i>grandicollis</i>	10	6	6	6	230	.76

*Larvae died in first and second instars.

†Progeny of ♂♂ *chagnoni* × ♀♀ *grandicollis*.

hatchability and again only daughters were produced. When other D₁ were mated by *paraconfusus* or *confusus* males none of the eggs hatched. Similarly, 2 *confusus* pairings showed an L/E of 0.50 and produced broods of 10 and 22 daughters. This appears similar to a condition reported in *I. latidens* (Leconte) in which a maternally transmitted cytoplasmic factor is lethal to male but not to female embryos (Lanier and Oliver 1966).

In most interspecific pairings, beetles behaved as if they were the same species. Females placed at the entrance to the males' galleries stridulated vigorously and

were quickly admitted to nuptial chambers where they mated and initiated construction of egg galleries. Normal numbers of eggs were laid *but none hatched* except in one pairing of *confusus* \times *montanus* (Table II). Here, 57 egg niches yielded eight larvae which mined about 2 cm, then died. Many of the unhatched eggs from pairings among *montanus*, *confusus*, *paraconfusus*, and *hoppingi* contained head capsules of larvae. No head capsules were seen in eggs produced in interspecific pairings involving *lecontei*, *cribricollis*, and *grandicollis*.

Fewer egg galleries resulted from interspecific pairings than from intraspecific (control) pairings. This was most evident from pairings involving *lecontei*. In *lecontei* \times *montanus*, only 14% of the pairings resulted in egg galleries whereas egg galleries were produced in 100% and 63% of the controls, respectively. Females in reciprocal pairings involving *lecontei* often had difficulty in gaining entrance and sometimes bored irregular galleries adjacent to the nuptial chamber. In interspecific pairings involving *grandicollis* sensu lato, most females oviposited but insemination was weak or could not be confirmed. Egg-laying females in all other combinations usually held abundant sperm in their spermathecae.

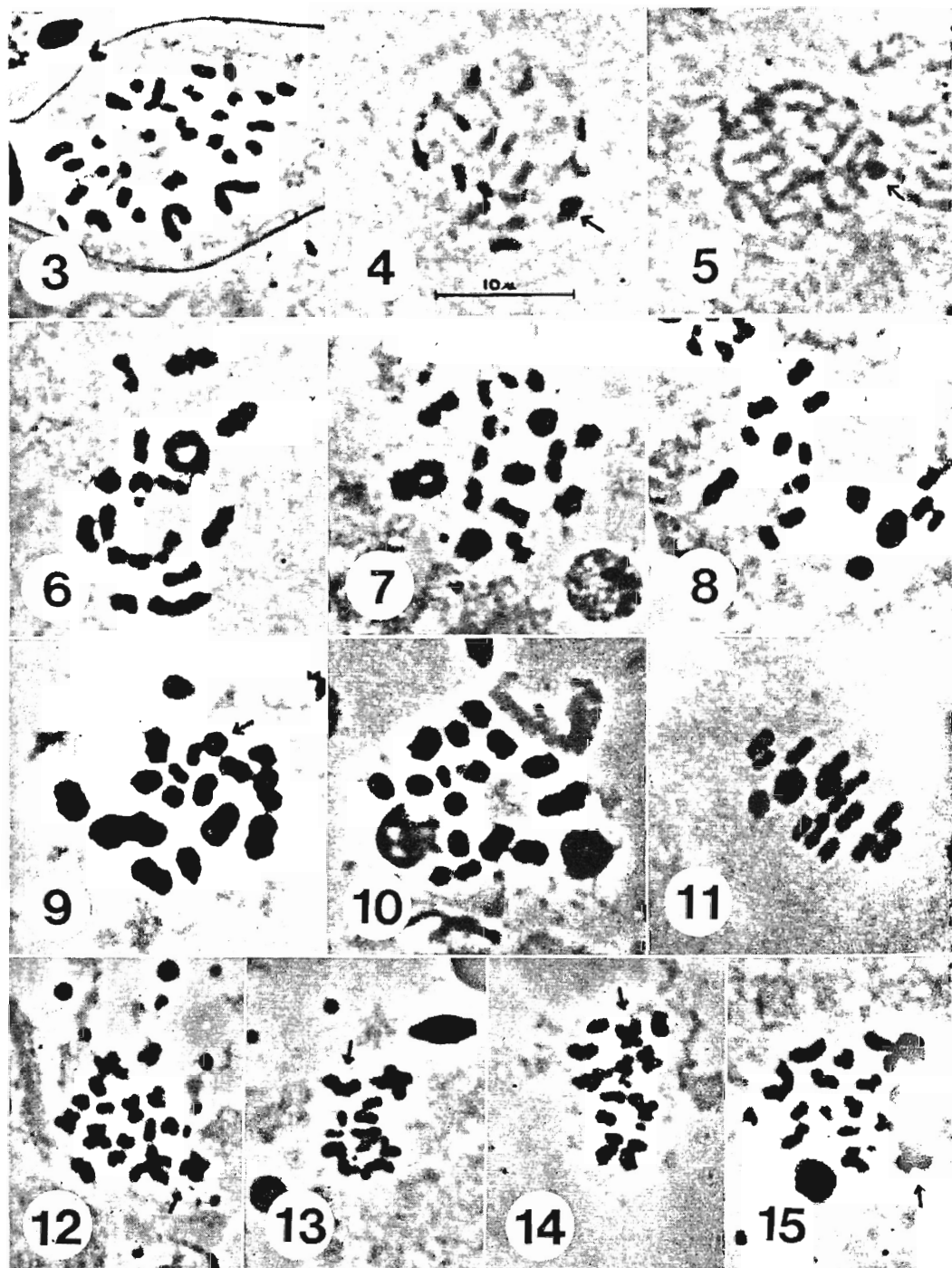
Especially notable are pairings involving three male *paraconfusus* (1g: Fig. 1; Table I) taken among 200 *montanus* (5b) attacking a *Pinus monticola* in an area where the distributions of these beetles meet. After the identity of these males was confirmed by successful crossing to *paraconfusus* (1f), they were paired with virgin *montanus* (5b) which resulted in three galleries with an aggregate of 90 inviable eggs. A single female putative *paraconfusus*, also among the *montanus*, laid 26 inviable eggs when reintroduced without a male. Mating in the original host was certain as her spermatheca was filled with sperm. The identity of her original mate is unknown but results of the mating indicate that he was a *montanus*.

Karyotypes

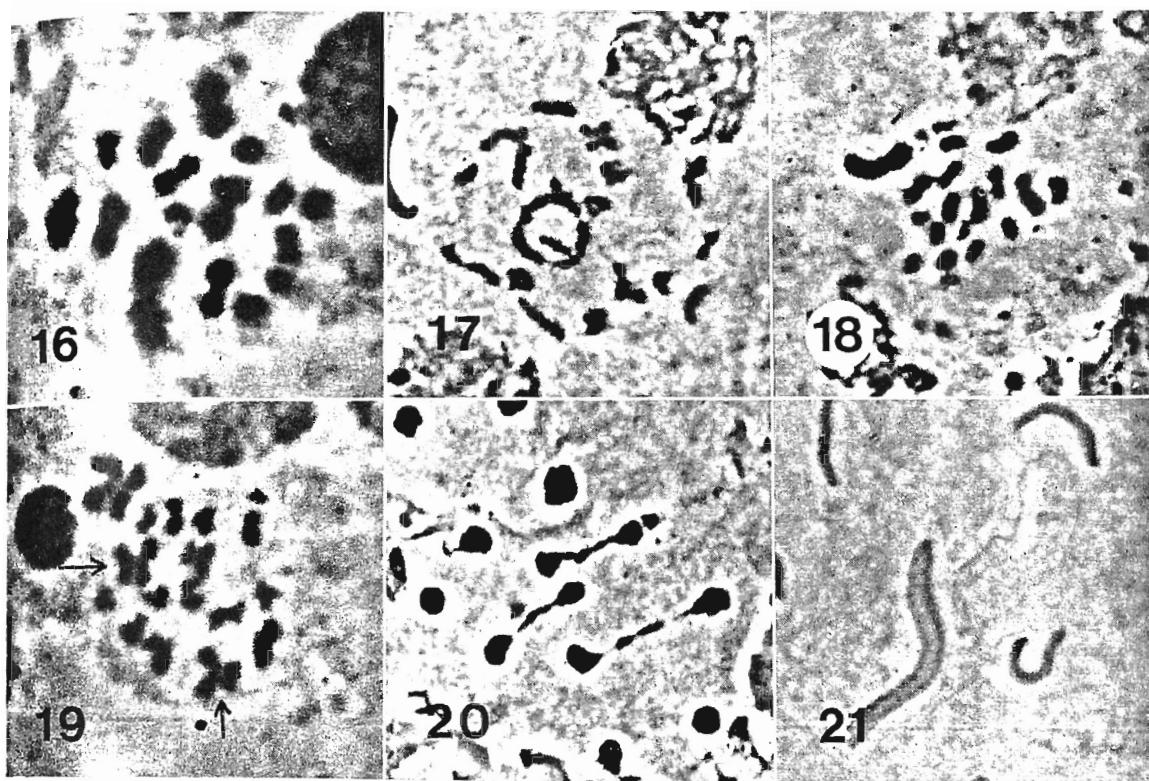
A previous paper (Lanier 1966) described and illustrated the first pro-metaphase (PMI) karyotypes of *montanus* and *paraconfusus* ("*confusus*"). *I. confusus*, *hoppingi*, *lecontei*, *cribricollis*, and *grandicollis* have the same karyotypic formula ($15AA + Xy_r$) and only *grandicollis* is easily differentiated. However, examination of prophase (pachytene) and second metaphase (MII) revealed diagnostic differences among other species. Spermatogonial (mitotic) cells contained 32 chromosomes (Fig. 3) and lacked conspicuous characters differentiating species.

At pachytene the X and y surround the nucleolus (John and Lewis 1960) while the autosomes are intimately paired, diffuse, and tangled in a "bouquet." In *montanus* (Fig. 4), each autosomal bivalent is marked by a darkly stained heterochromatic segment approximately one-third as large as the $Xy_r +$ nucleolus. In *cribricollis*, these segments are no larger than one-quarter the size of the $Xy_r +$ nucleolus while in *confusus* (Fig. 5), *paraconfusus*, *hoppingi*, *grandicollis*, and *lecontei* they are relatively tiny or missing.

At MI in *montanus* (Fig. 6), *paraconfusus*, *confusus* (Fig. 7), *hoppingi* (Fig. 8), *lecontei*, and *cribricollis* (Fig. 11) autosomal bivalent No. 1 (in order of decreasing size) is conspicuously largest; other bivalents showed a gradual reduction in size with noticeable breaks behind Nos. 2, 3, 5, 6, and 10. In at least 90% of the cells, No. 1 is ring-shaped, the chromosomes being attached by two terminal chiasmata. In the remaining cells, No. 1 is a cross, indicating a single interstitial attachment. In *confusus* and *montanus*, both Nos. 2 and 3 may form rings, crosses, or rods while only one of these bivalents (presumably No. 3) is ring-



FIGS. 3-15. Chromosomes of *Ips* species of group IX. 3, spermatogonium (mitosis) of *grandicollis*, $2n = 32$. 4-5, pachynema (meiotic prophase) of *montanus* (4) and *confusus* (5) (sex bivalent + nucleolus indicated by arrows). 6-10, prometaphase I of *montanus* (6), *confusus* (7), *hoppingi* (8), and *grandicollis* (9, 10); all $15AA + Xy_n$, except cell from aberrant individual with $14AA + 2A + Xy_n$ (10). 11, metaphase I of *cribricollis*; $15AA + Xy_n$. 12-15, metaphase II of *montanus* (12), *paraconfusus* (13), *confusus* (14), and *grandicollis* (15); all $n = 16$. Note that the largest chromosome (No. 1) is similar in all species while position of centromere varies in second largest chromosome (arrows).

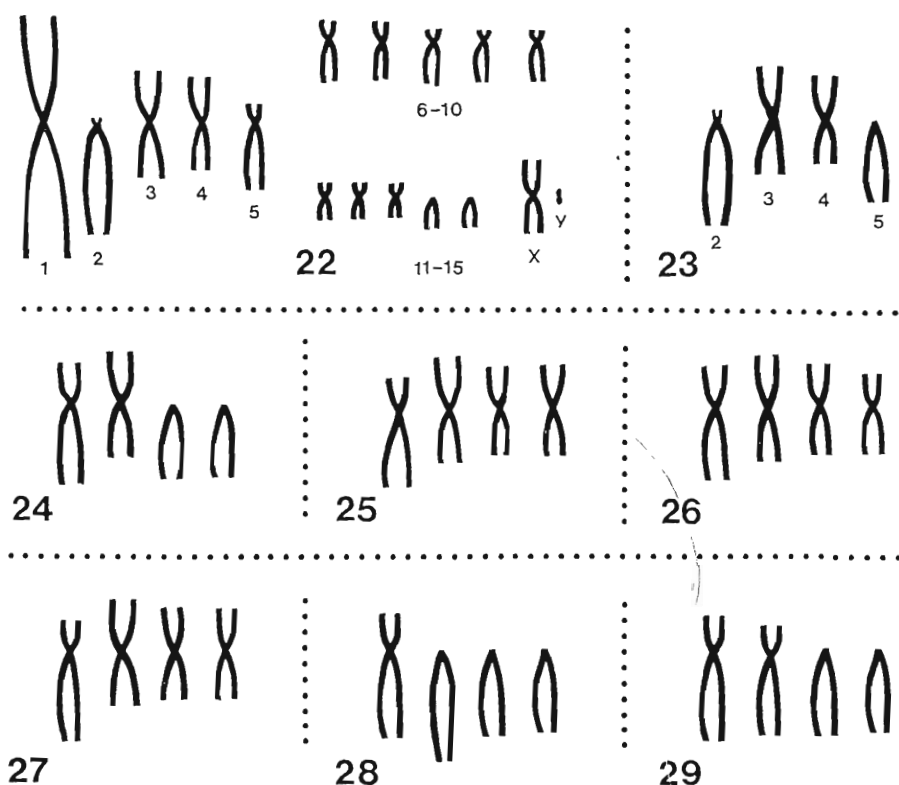


FIGS. 16-21. Chromosomes and spermatids of *Ips* "chagnoni" and its hybrid with *grandicollis*. 16, prometaphase in "chagnoni", 15AA + X_Y. 17-18, diakinesis (17) and prometaphase (18) of hybrid; 15AA + X_Y and 14AA + 2A + X_Y, respectively. 19, second metaphase in "chagnoni"; note the autosome Nos. 2 and 3 (arrows) are heterobrachial. 20, hybrid telophase nuclei with chromatin bridges. 21, normal and abnormally large spermatids in hybrid.

shaped in *paraconfusus*, *hoppingi*, *lecontei*, and *cribricollis*. Other bivalents form crosses, rods, or occasionally, rings.

In *grandicollis* (Fig. 9) and "chagnoni" (Fig. 16), bivalent No. 1 was also conspicuously large while other breaks in size sequence occur behind Nos. 2, 5, 6, 11, and 13. Bivalent No. 1 may be circular but it was predominantly rod- or cross-shaped. Other bivalents were cross- or rod-shaped, but never circular. In addition to these differences, many cells in one *grandicollis* s. str. contained two univalents resulting from precocious separation of a bivalent at PMI (Fig. 10). Two univalents also occurred in some MI cells of *grandicollis* × "chagnoni" hybrids (Fig. 18) although most cells were normal (Fig. 17).

At MII the two chromatids ($\frac{1}{2}$ chromosomes) were attached only at their centromeres. Configurations of chromosomes similar in size sequence provided an objective basis for comparing different species. In all species except *grandicollis*, the three largest autosomes could be individually identified by their size and the five smallest autosomes were, in aggregate, usually recognizable. In each species, the largest autosome was heterobrachial with an arm ratio of approximately 4:5. Autosome No. 2 was diagnostic for some species; in *montanus* (Figs. 12, 22), *confusus* (Figs. 14, 24), *lecontei* (Fig. 26), *cribricollis* (Fig. 27), and *grandicollis* sensu lato (Figs. 15, 19, 28, 29) it was heterobrachial, while in *hoppingi* (Fig. 22) and *paraconfusus* (Figs. 13, 23) it was cephalobrachial. No. 3 was isobrachial except in "chagnoni" where it was heterobrachial and in *grandicollis* (Figs. 15, 28) where it was cephalobrachial. The arm ratios (AR's) of



Figs. 22-29. Idiograms of second metaphase chromosomes of *Ips* species of group IX. 22, autosomes 1-15 plus X and y of *hoppingi*. 23-29, autosomes 2-5 of *paraconfusus* (23), *confusus* (24), *montanus* (25), *lecontei* (26), *cribricollis* (27), *grandicollis* (28), and "*chagnoni*" (29). Confluence of arms indicates position of centromeres.

other autosomes may have differed among species but these were not completely analyzed owing to their smallness and the rarity of well spread cells. The X-chromosome was not identified in *grandicollis* sensu lato but sex chromosomes in all other species were similar, the y's being tiny dots and the X's isobrachial, about the size of No. 3, but less distinct in outline and slightly more darkly stained.

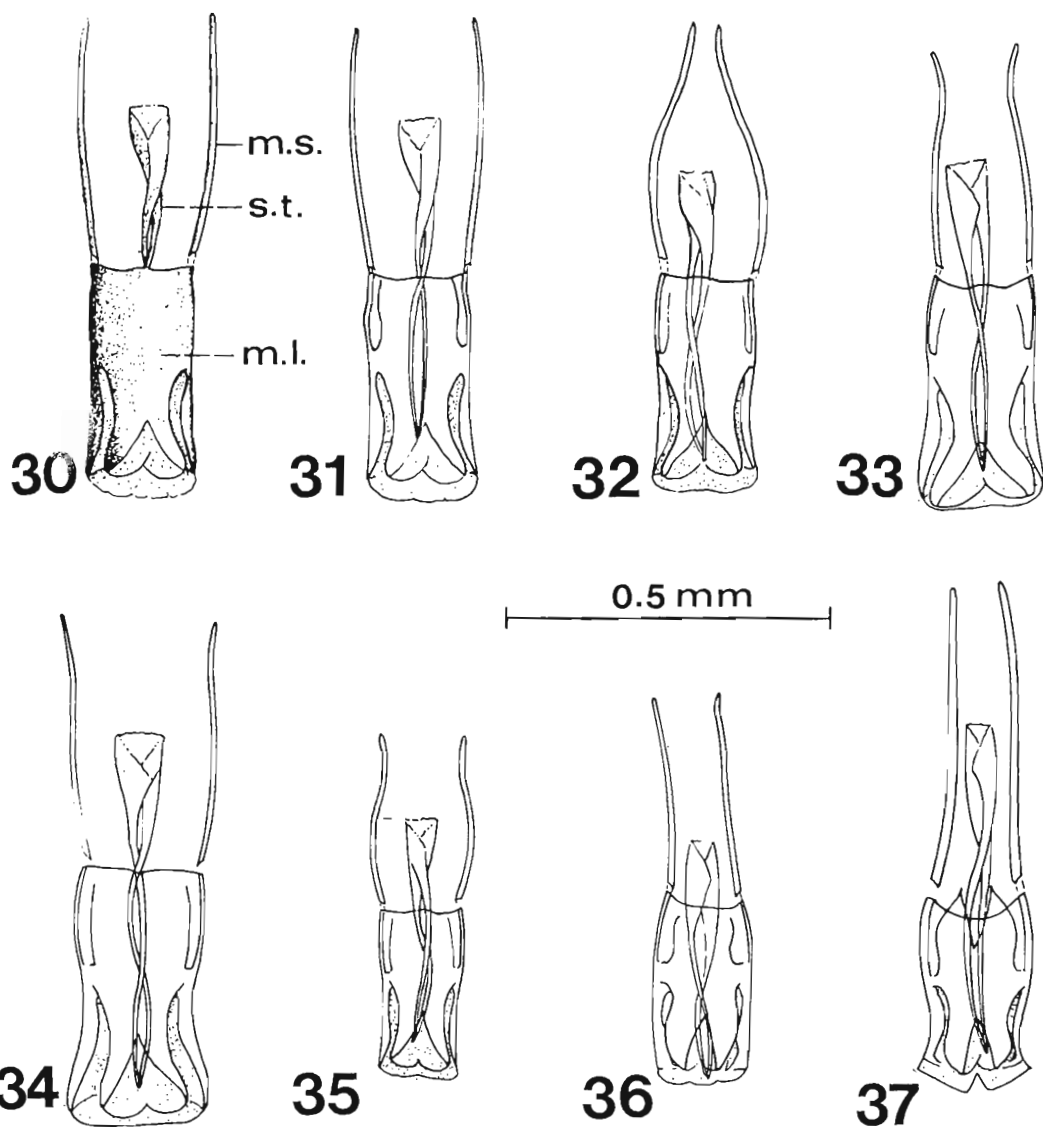
Chromatin bridges were common at first telophase of the hybrid of *grandicollis* and "*chagnoni*" (Fig. 20). These were probably a result of a pericentric inversion in No. 3 and possibly other chromosomes. Some bridged nuclei apparently never separated, but developed into a relatively huge spermatid (Fig. 21).

Morphological Examinations

External morphological characters described and illustrated by Hopping (1965c) proved adequate for separation of group IX species, sensu Hopping. However, *confusus* s. str. and its sibling species, *hoppingi* and *paraconfusus*, could be differentiated only by male genitalia, female pars stridens, and by statistical analysis of pronotal width and density of punctation in the elytral declivity.

Male Genitalia

Hopping's (1963b) analysis of a genitalia of group IX species is unfortunately based upon that of *I. grandicollis* which is unique for its long median struts, bilobed median lobe, and urn-shaped internal sac. The ratio of length of median struts to median lobe (S/L) for *grandicollis* approximates 1.50 while the S/L for



Figs. 30-37. Male genitalia of *Ips* species of group IX: *paraconfusus* (30, 31), *hoppingi* (32), *confusus* (33), *montanus* (34), *cribricollis* (35), *lecontei* (36), and *grandicollis* (37); median struts, m.s.; median lobe, m.l., seminal trough, s.t.

all other species are near 1.00 (Table III; Figs. 30-37). However, all comparisons except *paraconfusus* vs. *cribricollis* and *lecontei* vs. *confusus* are significantly different. The S/L easily separates *confusus* from *paraconfusus* and *hoppingi* but differences between the latter two were slight.

Pars stridens

On *confusus*, *hoppingi*, *paraconfusus*, *lecontei*, and *grandicollis* (= *chagnoni*) the *pars stridens* of the female was elongate; on *grandicollis* and *cribricollis* it was elliptical (Figs. 38-45; Table III). Among species of the first type, *confusus* was distinguished at 40 \times by its very narrow *pars stridens*. Differences among other species within the two types were not readily apparent at less than 200 magnifications. Within species, variation in over-all length of the *pars stridens* appeared to be directly related to pronotal width.

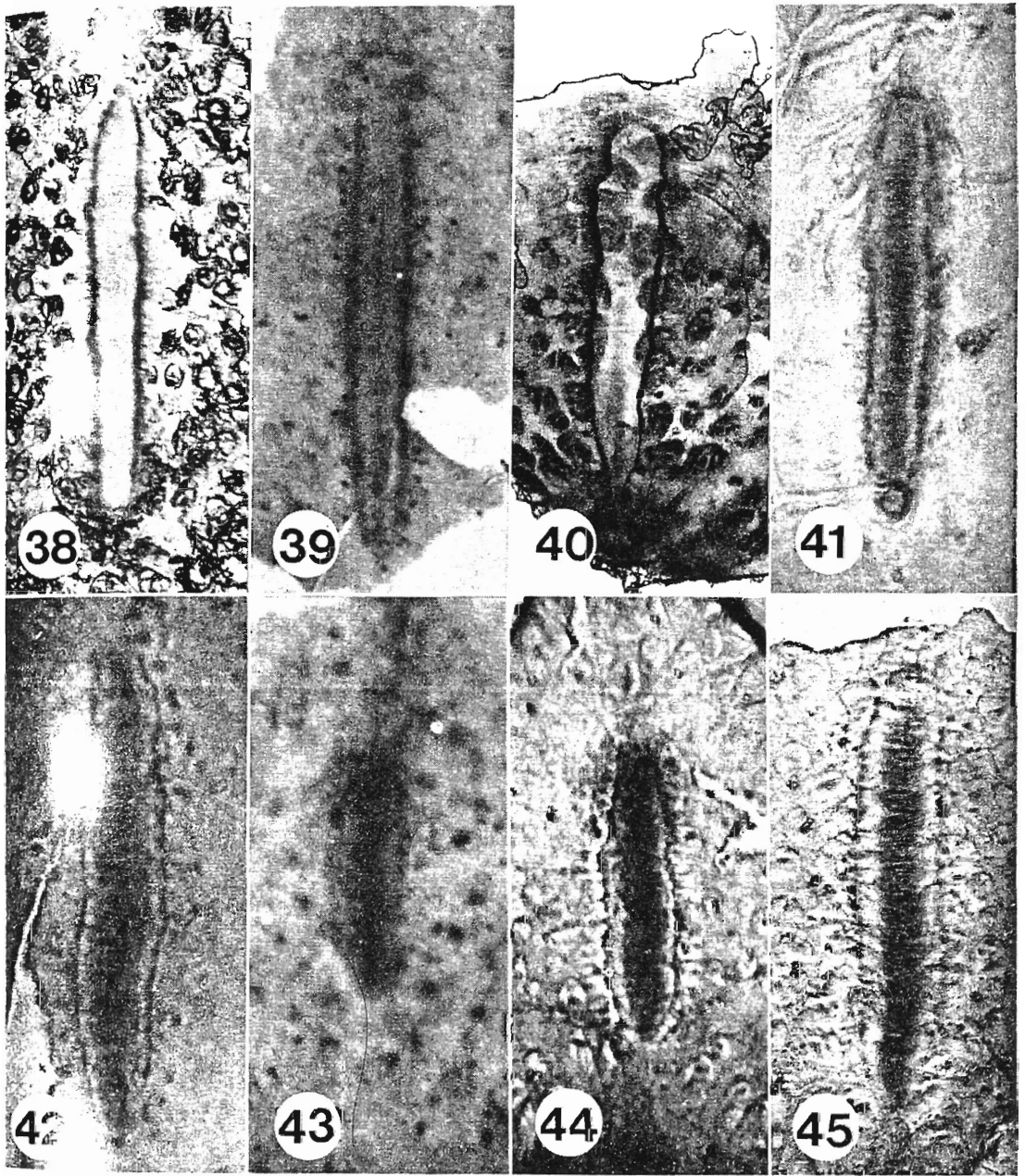
Striations were remarkably uniform throughout the length of the *pars stridens* from any specimen (Figs. 46-51). Variation between specimens of the same

TABLE III
Comparisons of male genitalia, female pars stridens, and pronotal widths of *Ips* species of group IX

Species	Male genitalia (struts/lobe)*			Female pars stridens			Pronotal width (mm)		
	No.	Range	\bar{X}	Striation width (μ)†		\bar{X}	Total width (μ)‡		\bar{X}
				No.	Range		Range	No.	
<i>paraconfusus</i>	22	.97-1.29	1.12±.082	23	.492-.573	.517±.0230	45.0-62.5	72	1.40-1.76
<i>confusus</i>	36	.74-1.07	.93±.060	54	.638-.786	.698±.0360	27.5-50.0	139	1.50-1.92
<i>hoppingi</i>	19	1.05-1.25	1.16±.056	23	.492-.606	.545±.0370	42.5-50.0	63	1.30-2.00
<i>montanus</i>	9	.94-1.06	1.02±.043	10	.524-.590	.566±.0207	50.0-67.5	8	1.97-2.17
<i>lecontei</i>	9	.86-1.00	.92±.054	10	.819-.949	.876±.0407	52.5-70.0	8	1.60-1.90
<i>cricbricollis</i>	10	1.00-1.10	1.07±.042	10	.606-.688	.658±.0244	50.0-57.5	9	1.23-1.40
<i>grandicollis</i>	17	1.27-1.58	1.49±.087	9	.655-.704	.692±.0298	57.5-67.5	23	1.07-1.53
" <i>chagnoni</i> " §	6	1.37-1.66	1.56±.106	4	.688-.752	.720±.0258	70.0-90.0	40	1.43-1.97

Differences in genitalia and pars stridens all significant ($P < .05$) except:

- *S/L — *grandicollis* vs. "*chagnoni*", *confusus* vs. *lecontei*, and *paraconfusus* vs. *cricbricollis*.
- †Striation width — *montanus* vs. *hoppingi*, *grandicollis* vs. "*chagnoni*", and *confusus* vs. *grandicollis* and "*chagnoni*".
- ‡Pars stridens, total width — *lecontei* vs. *montanus*, and *cricbricollis* vs. *paraconfusus* and *montanus*.
- §The synonymy *chagnoni* = *grandicollis* (Hopping 1965c) is considered valid but the entities are separated here to recognize morphological differences between northern and southern populations.



FIGS. 38-45. Whole pars stridens of *Ips* species of group IX: *confusus* (38), *hoppingi* (39), *paraconfusus* (40), *montanus* (41), *lecontei* (42), *cribricollis* (43), *grandicollis* (44), "*chagnoni*" (45).

species was always less than 15% of the mean and did not appear to be correlated with beetle size or collection locality. This character separates *lecontei* from other group IX species and provides absolute discrimination between *confusus*, and *paraconfusus* or *hoppingi*. The width of striations overlaps for some of the species, but differences in all comparisons except *hoppingi* vs. *montanus* and *cribricollis* vs. *grandicollis* are statistically very significant (Table III).

Pro. 1 Width

Pronotal width is used here as an index of size as it is easily and accurately measured with an ocular micrometer. Total length is more difficult to determine

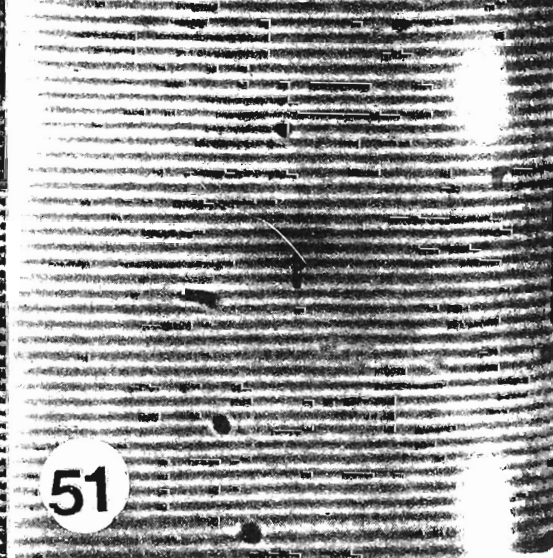
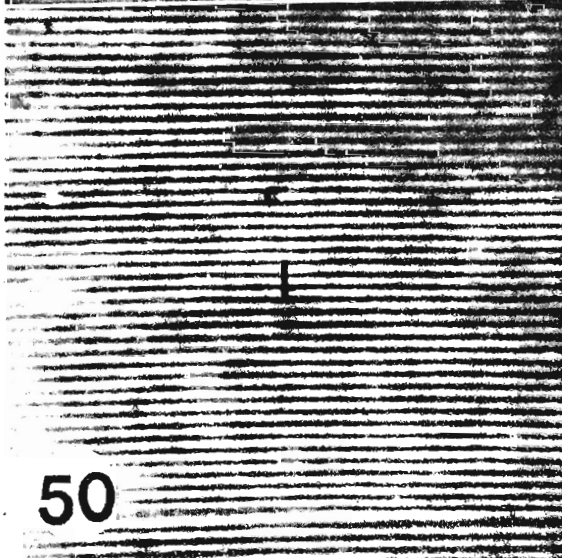
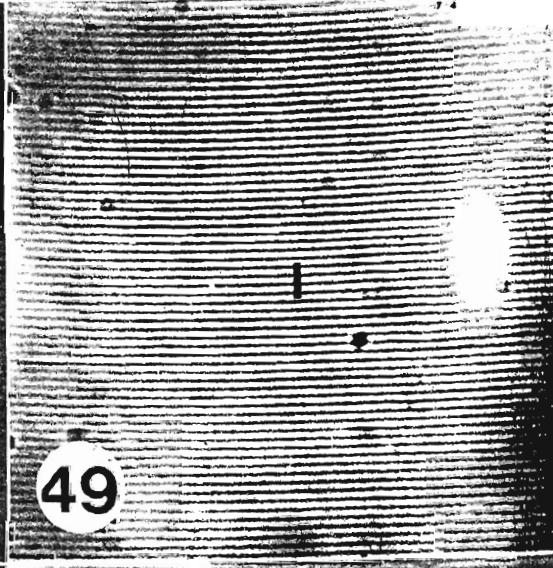
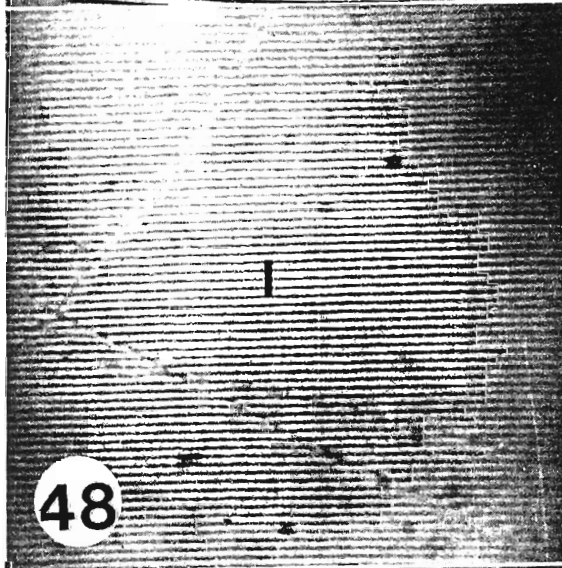
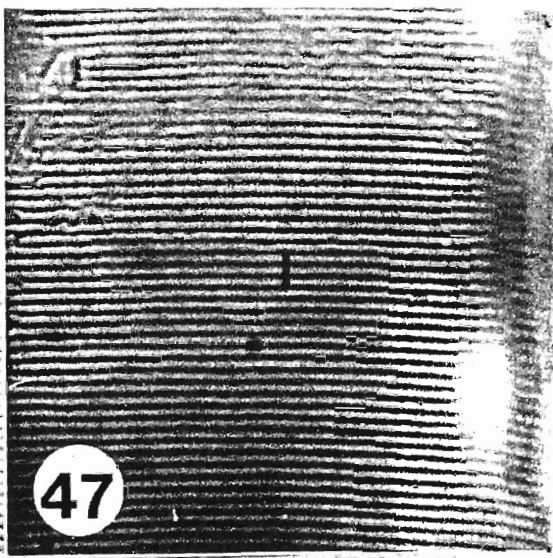
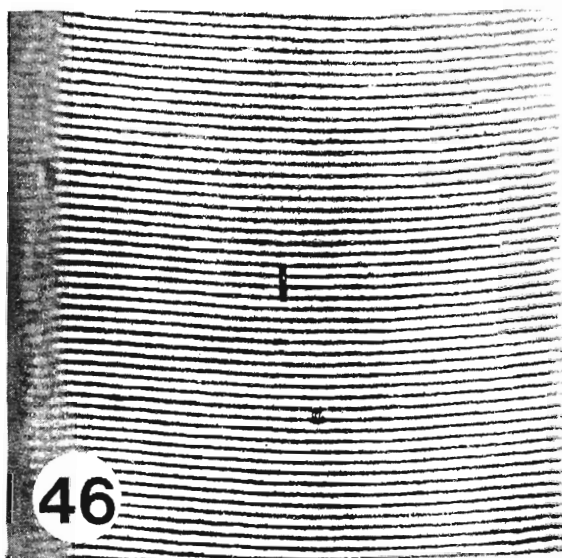


TABLE IV

Punctures per 1/10 mm² in elytral declivity of *Ips paraconfusus*, *confusus*, and *hoppingi*

Species	Females			Males		
	No.	Range	\bar{X}	No.	Range	\bar{X}
<i>paraconfusus</i>	42	2.59-4.26	3.36 ± .47*	32	1.85-2.78	2.28 ± .37*
<i>confusus</i>	35	2.95-5.00	4.01 ± .56	33	2.24-3.70	2.89 ± .39
<i>hoppingi</i>	30	2.82-5.56	3.83 ± .64	25	2.24-3.70	2.87 ± .47

*Significantly less than values for *confusus* and *hoppingi*.

and varies with the degree of separation at the articulation between the pronotum and the mesonotum. All group IX *Ips* are approximately 2.7 times longer than wide (Hopping 1965c) although the species differ considerably in size (Table III). The larger size of *montanus* easily distinguishes it from *paraconfusus*, provided that a sufficient number (about five) of specimens are examined. Similarly, size alone is sufficient criteria for differentiating the sympatric *lecontei* and *cribricollis*. *I. confusus* is statistically larger than *hoppingi* and *paraconfusus* but overlap is too great to rely on this character for identification. There is no significant difference in size between the sexes.

As already noted, size of *grandicollis* sensu lato increases from south to north (Hopping 1965c). Series of *grandicollis* s. str. and "*chagnoni*" available to me scarcely overlapped in size but laboratory hybrids were clearly intermediate. Series within other species may differ significantly in pronotal width, but variation appears to be associated with condition of the host rather than geographic range. For example, a group of *hoppingi* collected from a small very desiccated *P. cembroides* in the Chiricahua Mts. of Arizona had a mean pronotal width of 1.50 mm while the mean for their laboratory-reared progeny was 1.67. In laboratory rearings qualitative factors such as growth rate and moisture content of the individual host appeared to affect beetle size but host species did not.

Punctuation in the Elytra

The density of punctuation in the elytral declivity of *paraconfusus* males is noticeably less than in females (S. L. Wood, pers. comm.).⁶ This secondary sex character also occurs in *confusus* and *hoppingi* but the difference between sexes is less apparent owing to greater overlap. Objective measurement proved that the declivities of both sexes of *paraconfusus* were less densely punctured than those of the same sexes of *confusus* and *hoppingi*, but the latter two species were not different (Table IV). Subjective identification of 57 *paraconfusus* and 46 *confusus* using puncture density alone was 76% correct.⁷

Discussion

Species Validity

Complete infertility of all interspecific pairings (except for one *montanus* × *confusus*), together with morphological and karyological differences, confirms the

⁶Department of Zoology and Entomology, Brigham Young University.

⁷A group of specimens bearing only code labels was prepared by Miss B. A. Barr (Division of Entomology, Berkeley) to test the author's ability to separate *paraconfusus* and *confusus* using externally visible characters.

Figs. 46-51. Segments of pars stridens of *Ips* species of group IX: *confusus* holotype (46), *confusus* (47), *hoppingi* (48), *paraconfusus* (49), *grandicollis* (50), and *lecontei* (51). Vertical line in each figure = 2 μ.

validity, with respect to each other, of *lecontei*, *montanus*, *confusus*, *hoppingi*, *paraconfusus*, *cribricollis*, and *grandicollis*. Conversely, free intraspecific breeding and morphological homogeneity of adjacent and distant populations confirm the synonymy *vancouveri* = *montanus* and illustrate the soundness of the concepts of *confusus* and *paraconfusus*. The synonymy *cloudcrofti* = *cribricollis* was not tested but this investigation revealed no morphological, ecological, or distributional anomalies that question it.

Reduced interfertility as well as difference in size and a pericentric inversion in chromosome No. 3 indicate incipient speciation of *grandicollis* and "*chagnoni*." However, this evidence is inadequate for resurrection of "*chagnoni*," and insufficient material was seen to consider according "*chagnoni*" the status of subspecies. These entities probably do interbreed in nature and may merely represent extremes of a cline. The univalent chromosome observed in one "*pure*" *grandicollis* (Fig. 10) may indicate that the "*chagnoni*"-type inversion occurs in the southeastern United States.

Species Relationships

The great commonalty in morphology, karyology, biology, sex pheromones, and parasitic mites demonstrates the authenticity of group IX. Within this group the *confusus* sibling species appear to be most closely related and, of these, *hoppingi* and *paraconfusus* are extremely alike morphologically. *I. confusus* is most similar to *hoppingi* while *montanus* seems closest to *confusus*. *I. lecontei* and *grandicollis* are, each in a different way, apparently closest to *cribricollis*. *I. cribricollis* is probably nearest to the progenitor of group IX whose origin was most likely in the Mexican highlands during the mid-Tertiary when this area served as a secondary centre of evolution and speciation of pines (Mirov 1967).

Group IX has no known representatives from the Old World (Hopping 1963*b*) and no direct relationship with other North American groups. However, this group shows most affinities with groups III, IV, and X which also probably originated in Mexico (Lindquist 1969).

Interspecific Mating in Nature

Sympatry of *Ips* of different groups (Lanier 1966; Lindquist 1969) is possible because such species have their particular sex pheromone (Vité *et al.* 1964; Wilkinson 1964; D. L. Wood and Lanier, unpub. data). Conversely, lack of specificity of sex pheromones theoretically renders sympatry impossible. Cross attraction discussed earlier must promote interspecific mating between contiguously allopatric species such as *paraconfusus* and *montanus* or *lecontei* and *confusus*. Interspecific mating did occur between wild *paraconfusus* females and males of *montanus* and *confusus* that were introduced into small bolts and set out in an area where only *paraconfusus* occurred (D. L. Wood and Lanier, unpub. data). An incident of natural co-existence and probable mating of *montanus* and *paraconfusus* is documented herein and Lindquist (1969) described a mixed series of *paraconfusus* ("*confusus*") and *montanus* taken from *P. monticola* near Caribou Lake, Calif. (I have examined this series and agree with Lindquist's determinations). There is no reason to believe the results of natural interspecific matings would be different from those for laboratory pairings — the net effect would be the utilization of host material and genetic death of the individuals involved. Thus, the propensity of closely related, cross attractive, species to mate and the consequent inviability of these matings may prohibit sympatry and reinforce host and ecological specialization.

The collection of teneral adults of *lecontei* and *hoppingi* in cohabitation (3a, 4c Table I) indicates successful assortment of these species and detracts from the generality made in the previous paragraph. However, cross attraction between *lecontei* and *confusus*, *montanus*, and *paraconfusus* is relatively weak (D. L. Wood and Lanier, unpub. data). *I. hoppingi* has not been tested for response to sex pheromone, but it is expected to be very similar to those of the other *confusus* sibling species. In addition to pheromones, stridulation may enforce breeding isolation of *lecontei* from *hoppingi*, *confusus*, and *cribricollis* because it serves as a courtship call which induces the male to allow the female to enter the nuptial chamber (Wilkinson *et al.* 1967; Barr 1969). Striations on the *lecontei* pars stridens are quite wider than those on other group IX *Ips*, so sounds made may not be fully effective in seducing the male *hoppingi*, *confusus*, or *cribricollis*. This supposition is supported by the relatively low success of interspecific pairings involving *lecontei*.

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References

- Barr, B. A. 1969. Sound production in Scolytidae (Coleoptera) with emphasis on the genus *Ips*. *Can. Ent.* **101**: 636-672.
- Bedard Jr., W. D. 1966. A ground phloem medium for rearing immature bark beetles (Scolytidae). *Ann. ent. Soc. Am.* **59**: 931-938.
- Bedard, W. D., and L. E. Browne. 1969. A delivery-trapping system for evaluating insect chemical attractants in nature. *J. econ. Ent.* **62**: 1202-1203.
- Berrigan, A. A., and R. W. Stark. 1961. Studies on the effect of temperature on the development of *Ips confusus* (Leconte) using radiographic techniques. *Bull. ecol. Soc. Am.* **42**: 61.
- Bhakthan, M. M. G., K. K. Nair, and J. H. Borden. 1969. Occurrence of a fat body layer around the testes of *Ips confusus* (Coleoptera: Scolytidae). *Ann. ent. Soc. Am.* **62**: 1495-1496.

- Bhakthan, N. M. G., J. H. Borden, and K. K. Nair. 1970. Fine structure of degenerating and regenerating flight muscles in a bark beetle, *Ips confusus*. I: Degeneration. *J. Cell Sci.* **6**: 807-819.
- Borden, J. H. 1967. Factors influencing the response of *Ips confusus* (Coleoptera: Scolytidae) to male attractant. *Can. Ent.* **99**: 1164-1193.
- 1968. Antennal morphology of *Ips confusus* (Coleoptera: Scolytidae). *Ann. ent. Soc. Am.* **61**: 10-13.
- Borden, J. H., K. K. Nair, and C. E. Slater. 1969. Synthetic juvenile hormone: induction of sex pheromone production in *Ips confusus*. *Science* **166**: 1626-1627.
- Borden, J. H., and C. E. Slater. 1968. Induction of flight muscle degeneration by synthetic juvenile hormone in *Ips confusus* (Coleoptera: Scolytidae). *Z. Vergl. Physiol.* **61**: 366-368.
- 1969. Flight muscle volume change in *Ips confusus* (Coleoptera: Scolytidae). *Can. J. Zool.* **47**: 29-32.
- Borden, J. H., and D. L. Wood. 1966. The antennal receptors and olfactory response of *Ips confusus* (Coleoptera: Scolytidae) to male sex attractant in the laboratory. *Ann. ent. Soc. Am.* **59**: 253-261.
- Cameron, E. A., and J. H. Borden. 1967. Emergence patterns of *Ips confusus* (Coleoptera: Scolytidae) from ponderosa pine. *Can. Ent.* **99**: 236-244.
- Chamberlin, W. J. 1917. An annotated list of the scolytid beetles of Oregon. *Can. Ent.* **49**: 321-328.
- 1939. The bark and timber beetles of North America. Ore. State Coll. Coop. Assoc., Corvallis.
- 1958. The Scolytoidea of the Northwest: Oregon, Washington, Idaho, British Columbia. *Ore. St. Monog. Stud. Ent.*, No. 2.
- Chansler, J. F. 1964. Overwintering habits of *Ips lecontei* Sw. and *Ips confusus* (Lec.) in Arizona and New Mexico. *U.S. For. Serv. Res. Note* RM27.
- 1966. Cold hardiness of two species of *Ips* beetles. *J. For.* **64**: 622-624.
- Craighead, F. C. 1930. An annotated list of the important North American forest insects. *Misc. Publs U.S. Dep. Agric.*, No. 74.
- Critchfield, W. B., and E. L. Little Jr. 1966. Geographic distributions of the pines of the world. *Misc. Publs U.S. Dep. Agric.*, No. 991.
- Doane, R. W., et al. 1936. Forest insects. McGraw-Hill, N.Y., London.
- Eichhoff, W. 1868. Neue Amerikanische Borkenkäfer — Gattung und Arten. *Ber. ent. Z.* **12**: 273-280.
- Gara, R. I. 1963. Studies on the flight behavior of *Ips confusus* (Lec.) (Coleoptera: Scolytidae) in response to attractive material. *Contr. Boyce Thompson Inst. Pl. Res.* **22**: 51-66.
- Gara, R. I., and J. P. Vité. 1962. Studies on the flight patterns of bark beetles (Coleoptera: Scolytidae) in second growth ponderosa pine forests. *Contr. Boyce Thompson Inst. Pl. Res.* **21**: 275-289.
- Graham, S. A. 1952. Forest entomology. 3rd ed. McGraw-Hill, N.Y., Toronto, London.
- Hall, R. C. 1958. Environmental factors associated with outbreaks by the western pine beetle and the California five-spined engraver in California. *Proc. 10th int. Congr. Ent.*, Vol. 4, p. 341.
- Hopkins, A. D. 1905. Notes on some Mexican Scolytidae with descriptions of some new species. *Proc. ent. Soc. Wash.* **7**: 71-79.
- Hopping, G. R. 1963a. Generic characters in the tribe Ipinini (Coleoptera: Scolytidae), with a new species, a new combination and new synonymy. *Can. Ent.* **95**: 61-68.
- 1963b. The natural groups of species in the genus *Ips* De Geer (Coleoptera: Scolytidae) in North America. *Can. Ent.* **95**: 508-516.
- 1963c. The North American species in group I of *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **97**: 159-172.
- 1963d. The North American species in groups II and III of *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **95**: 1202-1210.
- 1964. The North American species in groups IV and V of *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **96**: 970-978.
- 1965a. The North American species in group VIII of *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **97**: 159-172.
- 1965b. The North American species in group VII of *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **97**: 193-198.

- . 1965c. North American species in group IX of *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **97**: 422-434.
- . 1965d. The North American species of group VI of *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **97**: 533-541.
- . 1965e. The North American species in group X of *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **97**: 803-809.
- John, B., and K. R. Lewis. 1960. Nucleolar controlled segregation of sex chromosomes in beetles. *Heredity* **15**: 431-439.
- Keen, F. P. 1933. A note on the hibernation habits of some engraver beetles of the genus *Ips*. *J. econ. Ent.* **26**: 297-298.
- . 1953. Insect enemies of western forests. *Misc. Publ. U.S. Dep. Agric.*, No. 273. 2nd ed.
- Kinn, D. N. 1967a. A new species of *Cercomegistus* (Acari: Mesostigmata) from California. *Acarologia* **9**: 488-496.
- . 1967b. Notes on the life cycle and habits of *Digamasellus quadrisetus* (Megostigmata: Digamasellidae). *Ann. ent. Soc. Am.* **60**: 862-865.
- . 1968. A new species of *Pleuronectocelaeno* (Acarina: Celaenopsidae) associated with bark beetles in North and Central America. *Acarologia* **10**: 191-205.
- Lanier, G. N. 1966. Interspecific mating and cytological studies of closely related species of *Ips* De Geer and *Orthotomicus* Ferrari (Coleoptera: Scolytidae). *Can. Ent.* **98**: 175-188.
- Lanier, G. N., and A. E. Cameron. 1969. Secondary sex characters in the North American species of the genus *Ips* De Geer (Coleoptera: Scolytidae). *Can. Ent.* **101**: 862-870.
- Lanier, G. N., and J. H. Oliver. 1966. "Sex-ratio" condition: Unusual mechanisms in bark beetles. *Science* **153**: 208-209.
- Leconte, J. L. 1876. Family IX. Scolytidae. In: J. L. Leconte and G. H. Horn, The Rhynchophora of America north of Mexico. *Proc. Am. philos. Soc.* **15**: 341-391.
- Lindquist, E. E. 1969. Review of holartic tarsenemid mites (Acarina: Prostigmata) parasitizing eggs of Ipine bark beetles. *Mem. ent. Soc. Can.*, No. 60.
- Lindquist, E. E., and W. D. Bedard. 1961. Biology and taxonomy of mites of the genus *Tarsonemoides* (Acarina: Tarsonemidae) parasitizing eggs of bark beetles of the genus *Ips*. *Can. Ent.* **93**: 982-999.
- *Little, E. L. 1943. Common insects on pinyon (*Pinus edulis*). *Jl N.Y. ent. Soc.* **51**: 239-252.
- Lyon, R. L. 1955. A secondary sex character on the male of the California five-spined engraver, *Ips confusus* (Lec.) (Coleoptera: Scolytidae). *Can. Ent.* **87**: 482-483.
- . 1959. Toxicity of several residual-type insecticides to selected western bark beetles. *J. econ. Ent.* **52**: 323-327.
- Lyon, R. L., and P. J. Shea. 1967. Chemosterilants to control bark beetles . . . tepa shows promise in preliminary test. *U.S. For. Ser. Res. Note* 139.
- Massey, C. L. 1957. Four new species of *Aphelenchulus* (Nematoda) parasitic in bark beetles in the United States. *Proc. helminth. Soc. Wash.* **24**: 29-34.
- . 1960. Nematode parasites and associates of the California five-spined engraver, *Ips confusus* (Lec.). *Proc. helminth. Soc. Wash.* **27**: 14-22.
- . 1962. Life history of *Aphelenchulus elongatus* Massey (Nematoda) an endoparasite of *Ips confusus* LeConte, with a description of the male. *J. Insect Pathol.* **4**: 95-103.
- Mirov, N. T. 1967. The genus *Pinus*. Ronald Press, New York.
- Moore, A. D. 1957. The relative toxicity of DDT, toxaphene, lindane and isodrin to *Dendroctonus brevicornis* Lec. and *Ips confusus* (Lec.). *J. econ. Ent.* **50**: 548-550.
- Morgan, F. D. 1967. *Ips grandicollis* in South Australia. *Aust. Forestry* **31**: 137-155.
- Nickle, W. R. 1963a. Notes on the genus *Contortylenchus* Ruhm, 1956 with observations on the biology and life history of *C. elongatus* (Massey, 1960) n. comb., a parasite of a bark beetle. *Proc. helminth. Soc. Wash.* **30**: 218-223.
- . 1963b. *Bovienema* (Nematoda: Allantonematidae), a new genus parasitizing bark beetles of the genus *Pityogenes* Bedel, with notes on other endoparasitic nematodes of scolytids. *Proc. helminth. Soc. Wash.* **30**: 256-262.
- . 1963c. Observations on the effect of Nematodes on *Ips confusus* (LeConte) and other bark beetles. *J. Insect. Pathol.* **5**: 386-389.
- Pitman, G. B. 1965. Certain factors affecting colonization of ponderosa pine by *Ips confusus* (LeConte) (Coleoptera: Scolytidae). *Diss. Abstr.* **26**: 598.
- . 1966. Studies on the pheromone of *Ips confusus* (LeConte) III. The influence of host material on pheromone production. *Contr. Boyce Thompson Inst. Pl. Res.* **23**: 147-158.

- Pitman, G. B., R. A. Kliefth, and J. P. Vité. 1965. Studies on the pheromone of *Ips confusus* (LeConte). II: Further observations on the site of production. *Contr. Boyce Thompson Inst. Pl. Res.* **23**: 13-17.
- Pitman, G. B., J. A. A. Renwick, and J. P. Vité. 1966. Variation in olfactory behavior of *Ips confusus* (Lec.) (Coleoptera: Scolytidae) between laboratory and field bioassays. *Naturwissenschaften* **53**: 46-47.
- Renwick, J. A. A., G. B. Pitman, and J. P. Vité. 1966. Detection of a volatile compound in hindguts of male *Ips confusus* (LeConte) (Coleoptera: Scolytidae). *Naturwissenschaften* **53**: 83-84.
- Rice, R. E. 1969. Response of some predators and parasites of *Ips confusus* (LeC.) (Coleoptera: Scolytidae) to olfactory attractants. *Contr. Boyce Thompson Inst. Pl. Res.* **24**: 189-194.
- Schedl, K. E. 1955. Die Kiefern-Borkenkafer Guatemalas. *Z. angew. Ent.* **38**: 1-48.
- . 1960. Synonymies of bark beetles (Scolytidae) IV. *Coleopt. Bull.* **14**: 5-12.
- Schwerdtfeger, F. 1956. Scolytidae (Col.) on *Pinus*-Arten in Mittelamerika. I. Das C. n. *Ips* De Geer. *Z. angew. Ent.* **39**: 34-57.
- Silverstein, R. M., J. O. Rodin, and D. L. Wood. 1966. Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. *Science* **154**: 509-510.
- Silverstein, R. M., et al. 1966. Identification of two new terpene alcohols from frass produced by *Ips confusus* in ponderosa pine. *Tetrahedron* **22**: 1929-1936.
- Struble, G. R. 1955. California five-spined engraver beetle. *U.S. Dep. Agric. Forest Pest Leaflet*, No. 4.
- . 1966. California five-spined *Ips*. *U.S. Dep. Agric. Forest Pest Leaflet*, No. 102.
- Struble, G. R., and R. C. Hall. 1955. The California five-spined engraver. Its biology and control. *U.S. Dep. Agric. Circ.*, No. 964. 21 pp.
- Swaine, J. M. 1909. Catalogue of the described Scolytidae of America, north of Mexico. Appendix B in 24th report of the State Entomologist on injurious and other insects of the state of New York. *N.Y. St. Mus. Bull.* **134**: 76-159.
- . 1918. Canadian bark beetles. II: A preliminary classification, with an account of the habits and means of control. *Tech. Bull. Can. Dep. Agric.*, No. 14.
- . 1924. The allies of *Ips confusus* LeC. in western America. Family Ipidae, Coleoptera. *Can. Ent.* **56**: 69-72.
- Swartz, E. A. 1886. Remarks on North American Scolytids. *Entomologica* **2**: 40-42, 54-56.
- Thomas, J. B. 1966. Some Scolytidae from the Sierra Madre Occidental in Mexico. *Can. Ent.* **98**: 871-875.
- . 1967. A comparative study of gastric caeca in adult and larval stages of bark beetles (Coleoptera: Scolytidae). *Proc. ent. Soc. Ont.* **97**: 71-90.
- Vité, J. P. 1965. Die Wirkung pflanzen-und isekteneigener Lockstoffe auf *Pityophthorus* und *Pityogenes* (Coleoptera: Scolytidae). *Naturwissenschaften* **52**: 267.
- Vité, J. P., and R. I. Gara. 1962. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera: Scolytidae). *Contr. Boyce Thompson Inst. Pl. Res.* **21**: 251-273.
- Vité, J. P., and G. B. Pitman. 1968. Bark beetle aggregation: effects of feeding on the release of pheromones in *Dendroctonus* and *Ips*. *Nature* **218**: 169-170.
- Vité, J. P., R. I. Gara, and R. A. Kliefth. 1963. Collection and bioassay of a volatile fraction attractive to *Ips confusus* (LeC.) (Coleoptera: Scolytidae). *Contr. Boyce Thompson Inst. Pl. Res.* **22**: 39-50.
- Vité, J. P., R. I. Gara, and H. D. von Scheller. 1964. Field observations on the response to attractants of bark beetles infesting southern pines. *Contr. Boyce Thompson Inst. Pl. Res.* **22**: 461-470.
- Wilkinson, R. C. 1964. Attraction and development of *Ips* bark beetle populations in artificially infested pine bolts exposed on fire-tower and turntables in Florida. *Fla Ent.* **47**: 57-64.
- Wilkinson, R. C., et al. 1967. Stridulation and behavior in two southeastern *Ips* bark beetles (Coleoptera: Scolytidae). *Fla Ent.* **50**: 185-195.
- Wood, D. L. 1961. Stridulation in the genus *Ips* De Geer. *Pan-Pacif. Ent.* **37**: 187-188.
- . 1962a. Experiments on the interrelationship between oleoresin exudation pressure in *Pinus ponderosa* and attack by *Ips confusus* (LeC.) (Coleoptera: Scolytidae). *Can. Ent.* **94**: 473-477.
- . 1962b. The attraction created by males of a bark beetle *Ips confusus* (LeConte) attacking ponderosa pine. *Pan-Pacif. Ent.* **38**: 141-146.

1963. Studies on host selection by *Ips confusus* (LeConte) (Coleoptera: Scolytidae) with special reference to Hopkins' host selection principle. *Univ. Calif. Publ. Ent.* **27**: 241-282.
- od, D. L., and R. W. Bushing. 1963. The olfactory response of *Ips confusus* (LeConte) (Coleoptera: Scolytidae) to the secondary attraction in the laboratory. *Can. Ent.* **95**: 1066-1078.
- od, D. L., and R. W. Stark. 1966. The effects of gamma radiation on the biology and behavior of adult *Ips confusus* (LeConte) (Coleoptera: Scolytidae). *Can. Ent.* **98**: 1-10.
- 1968. The life history of *Ips calligraphus* (Coleoptera: Scolytidae) with notes on its biology in California. *Can. Ent.* **100**: 145-151.
- od, D. L., and J. P. Vité. 1961. Studies on the host selection behavior of *Ips confusus* (LeConte) (Coleoptera: Scolytidae) attacking *Pinus ponderosa*. *Contr. Boyce Thompson Inst. Pl. Res.* **21**: 79-95.
- od, D. L., et al. 1966. Sex pheromones of bark beetles. I: Mass production, bio-assay, source, and isolation of the sex pheromone of *Ips confusus* (LeC.). *J. Insect Physiol.* **12**: 523-536.
- 1967. Unique synergistic effects produced by the principal sex attractant compounds of *Ips confusus* (LeConte) (Coleoptera: Scolytidae). *Nature* **215**: 206.
- 1968. Response of *Ips confusus* to synthetic sex pheromones in nature. *Science* **159**: 1373-1374.
- od, S. L. 1957. Distributional notes on and synonymies of some North American Scolytidae (Coleoptera). *Can. Ent.* **89**: 396-403.

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THE HISTOLOGY OF THE GIANT FIBRE SYSTEM IN THE ABDOMINAL VENTRAL NERVE CORD OF THE DESERT LOCUST

W. D. SEABROOK¹

Department of Zoology and Applied Entomology,
Imperial College of Science and Technology, London, S. W. 7, England

Abstract

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Schistocerca gregaria possess four neurones of giant fibre proportions within the abdominal ventral nerve cord. These fibres arise from single cell bodies in the terminal ganglionic mass and pass without interruption to the metathoracic ganglion. Fibres become reduced in diameter when passing through a ganglion. Branching of the giant fibres occurs in abdominal ganglia 6 and 7.

Résumé

Schistocerca gregaria possède quatre neurones de type géant dans la chaîne nerveuse ventrale abdominale. Ces fibres proviennent de cellules individuelles de la masse ganglionique terminale et passent sans interruption au ganglion métathoracique. Le diamètre de ces fibres est réduit lorsqu'ils passent à travers un ganglion. Les fibres géants branchent dans le sixième ainsi que le septième ganglion abdominal.

Introduction

The insect abdominal giant fibre system has been investigated in *Periplaneta* (Pumphrey and Rawdon Smith 1937; Roeder 1948), in *Locusta* (Cook 1951), in *Nauphotho cinerea* (Hughes 1953), and in *Aeschna* (Mill 1964). However some questions remain concerning the location of the giant fibre cell bodies, the location of synaptic areas, and the possible syncytial nature of these fibres. It is hoped that these findings from the desert locust may shed light on these points.

The morphology and structure of the abdominal central nervous system of *Schistocerca gregaria* have been reported by Seabrook (1968a, b, 1970).

¹Present address: Department of Biology, The University of New Brunswick, Fredericton, Canada.