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BIOLOGY AND RELATIONSHIPS OF *PTEROSTICHUS ADSTRICTUS*
ESCHSCHOLTZ AND *PTEROSTICHUS PENNSYLVANICUS* LÉCONTE
(COLEOPTERA: CARABIDAE)

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Some ecological, behavioural and structural characteristics of two structurally similar species, Pterostichus adstrictus Eschscholtz and P. pensylvanicus LeConte, are compared. P. adstrictus, a more northern species ranges from the forest litter to open meadow habitats; females oviposit in logs over a wide moisture range; development is rapid in Alberta. P. pensylvanicus, a more southern species, is restricted to forest litter habitats; females oviposit mostly in very moist soil; development is slower. Population fluctuations are probably weather controlled through temperature and moisture level at the oviposition sites, and by the behaviour of immature stages whereby they remain in these sites. Northern limits of distribution are probably strongly affected by the temperature where eggs and larvae occur. Mechanisms preventing hybridization are precopulatory; males recognize females of their own species, but the method of recognition was not established. The phyletic relationships of both species as well as other North American species in the subgenus are discussed. The subgenus Bothriopterus is redefined to include the species previously placed in the subgenus Dysidius. The past history of the North American species is reconstructed.

Nous comparons l'écologie, les moeurs et la morphologie de deux espèces très similaires: Pterostichus adstrictus Eschscholtz et P. pensylvanicus LeConte. P. adstrictus, une espèce plus nordique, se rencontre sous les feuilles en forêt et dans les champs; les femelles pondent leurs oeufs dans le bois pourri qui peut être humide à mouillé; le développement des stades larvaires est rapide en Alberta. P. pensylvanicus, une espèce à distribution moins nordique, se trouve sous les feuilles en forêt seulement; les femelles pondent surtout dans le sol très humide; le développement est plus lent. La température et l'humidité dans les sites de ponte, et les moeurs des larves qui demeurent dans ces sites contribuent au control des variations dans la densité des populations. Ces mêmes variables expliquent la limite nord de leur distribution géographique. L'hybridation est empêchée par des mécanismes précopulatoires; les males reconnaissent leurs propre femelles mais le mécanisme d'identification n'est pas éclairci. Nous analysons les relations phylétiques de ces espèces et des autres espèces appartenant au mêmes sous-genre en Amérique du nord. Le sous-genre Bothriopterus est redéfini et comprend en plus les espèces du sous-genre Dysidius. Finalement nous reconstruisons l'histoire passée des espèces nord américaines.

In the past three decades, important publications concerning the biology of European carabids have appeared (Larsson, 1939; Krogerus, 1948; Lindroth, 1949; Van der Drift, 1951; Thiele, 1964). Lindroth's (1961-1969) excellent monograph on Canadian carabids, enriched by ecological and biological notes, solved many taxonomic problems and thus provided the background for ecological research on North American carabids (Rivard, 1965; Johnson, Lawrence and Ellis, 1966; Carter, 1971; Harris and Whitcomb, 1971; Kirk, 1971a, 1971b).

Much of the comparative work on related species has been done with an ecologist's outlook. Gilbert (1956) worked on four species of *Calathus*; Paarman (1966) studied two related species of *Pterostichus*; and Carter (1971) studied the ecology of four species of *Patrobus*.

I approach similar work with a taxonomist's outlook. I have attempted to understand the evolutionary paths behind coexistence of species with similar requirements and prevention of hybrid formation, and to do so, I studied two species, *P. adstrictus* and *P. pensylvanicus* living in a similar habitat, and presumed to be closely related. Fortunately, both species could be recognized in the field on general habitus.

MATERIALS AND METHODS

This study was based on 5,500 adults and 500 larvae and pupae collected mostly at the George Lake Field Station, Alberta (ca. 53°57' N., 114°06' W.) from 1967 to 1970; some additional data were obtained from eastern Canada during the period 1961 to 1968. I also examined adults of *P. oblongopunctatus* Fabricius, *P. mutus* Say, *P. oregonus* LeConte, *P. tropicalis* Bates, *P. ohionis* Csiki, and *P. lustrans* LeConte.

Hand Collecting

Specimens were found under stones, logs and leaves; in logs; beneath the soil surface; and on plants. My purpose was to determine all of the habitats occupied.

Pitfall Trapping

This method was used to determine daily and seasonal locomotory activity, and population density. The main adult activity of carabids is expressed through locomotion, and hence pitfall trapping yields a good relative estimate of adult activity. I used two types of pitfall trap: cylindrical polyethylene containers, 10 cm high by 8 cm diameter; and two sizes of eave-troughs, 1.5 x 0.1 m and 0.6 x 0.08 m. The soil around the traps was tightly packed and was kept level with the rim. Over each trap a heavy wooden cover was supported on pegs about 1.5 cm above the ground to keep out rain and debris, and to shade the beetles. Various systems of traps were set out. In 1967, I put 20 groups of 10 traps each in various forest litter habitats. In each group, the polyethylene traps were 2.5 m apart over 100 m². In 1968, I added one more group of 100 polyethylene traps 5 m apart over 2500 m². In 1969, I opened a transect made of 30 long eave-troughs and put 20 short eave-troughs 2 m apart in an enclosed area (Fig. 1 and Table 1). I collected from these traps every two or three days throughout the season, and every two hours for 24 hours while studying the circadian rhythms, and recorded the number of males and females of each species per trap per unit time as well as various data on bombarding, copulation, and feeding. Pitfall trapping permitted comparison of periods of peaks of activity. Rates at which larvae were trapped were assumed to be proportional to hatching rates, as most locomotory activity occurs soon after emergence from the egg or from an earlier instar.

Table 1. Location of pitfall traps for *P. adstrictus* and *P. pensylvanicus* at George Lake, Alberta, in relation to habitat characteristics.

Cover	Habitat		Grid designation*
	Dominant plant	Moisture conditions	
Forest litter	<i>Populus tremuloides</i>	Mesic	26, 24, 34, 97-S, 24
	<i>Populus balsamifera</i>	Mesic to hygic	11, 10, 33, 39, 29, 99, 17-S 98-S, 84-W
	<i>Picea glauca</i>	Mesic to hygic	75-W, 76-W, 17-S

Table 1.(concluded). Location of pitfall traps for *P. adstrictus* and *P. pensylvanicus* at George Lake, Alberta, in relation to habitat characteristics.

Cover	Habitat		Grid designation*
	Dominant plant	Moisture conditions	
Open	Graminae	Mesic	78-W, 83-W
	<i>Carex rostrata</i>	Hygic	22, 83-W, 27-SE
	<i>Ledum groenlandicum</i>	Xeric	87-W

* see Fig. 1.

Pitfall trapping yielded imprecise information about differences in relative activity of the new and old adults of each generation. See Table 2 for numbers of marked and released adults of each category. Simultaneously I obtained rough data about density and mortality of unmarked adults in the spring from an area of 98 m² enclosed by a polyethylene wall 30 cm high (the plastic was translucent and about 0.5 mm thick). The base of the wall was 10 to 15 cm under the soil surface. The upper part of the polyethylene sheet was folded inward to keep adults from climbing out on wet dirty walls. In the enclosed area, 20 short eavestroughs were uniformly distributed. The released specimens were marked with small cuts at the apex of either or both elytra or by cauterizing a small area on one interval. Each released group was marked differently (Table 2). These marked adults were obtained from outside the enclosed plot; I assumed that little interaction resulted between these and the unmarked population. The mortality rate was probably low in the field during spring and fall, as none of 70 adults kept in the laboratory died during these two periods. I found no evidence of either mice or grouse (the main predators) in the enclosed area. Density of adults was calculated on the assumption that the marked, released adults had the same age structure as the unmarked population, and that the ratio of the number of marked individuals recaptured (A) to the total number of unmarked recaptured (C) is the same as the ratio of the number of marked (B) individuals released to the original population (D), i.e. $\frac{A}{C} = \frac{B}{D}$ or $AD = BC$. Thus D, the total original population is $\frac{BC}{A}$, and the density $\frac{BC}{98A}$ per m² (modified from Southwood, 1966).

Table 2. Numbers of marked males and females of *P. adstrictus* and *P. pensylvanicus* released.

Category of adults	<i>P. adstrictus</i>		<i>P. pensylvanicus</i>	
	♂	♀	♂	♀
Fall				
Old generation marked	18	33	10	19
New generation marked	50	50	31	23
Spring				
Mixed generation marked	25	25	25	25

Dissection of Females

As mature eggs are laid within a few hours when the conditions are right, the number of

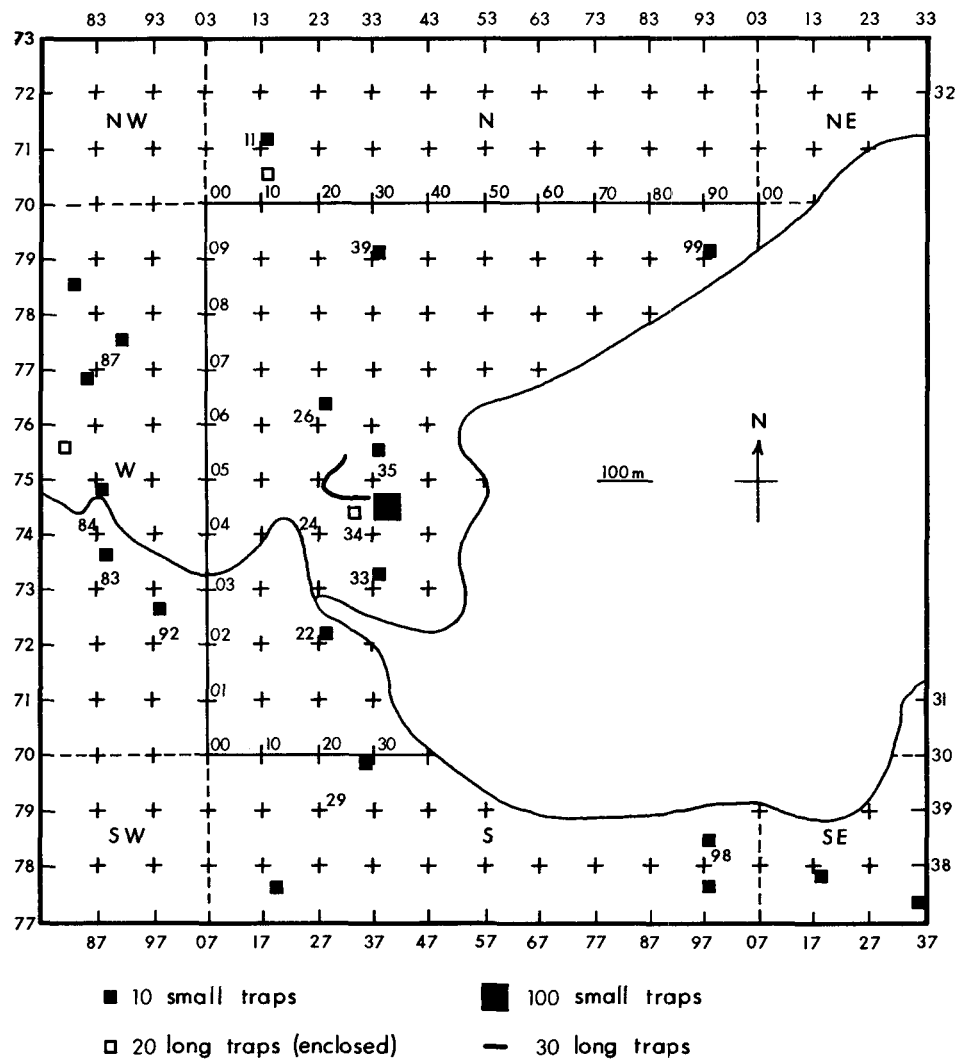


Fig. 1. George Lake Field Station, Alberta, showing the location of groups of traps for *P. adstrictus* and *P. pensylvanicus*.

females with mature eggs and the average number of eggs per female help to define the period during which females are gravid and the period of oviposition (Rivard, 1964). The presence of the *corpora lutea* permit recognition of the females of the old generation in early spring and after mid-July. In 1968, females of *P. adstrictus* (127) and *P. pensylvanicus* (43) were stored in 70% alcohol for later examination. In 1970, females of *P. adstrictus* (28) and *P. pensylvanicus* (35) were collected and dissected immediately. For each female, I recorded date of collection, larger parasites, development of the *corpora lutea* (for freshly killed specimens only), and the number of eggs at least 0.75 times as large as mature eggs.

Morphology

For a phyletic analysis I studied external and internal structures of 10 males of each species and 127 females of *P. adstrictus* and 43 females of *P. pensylvanicus*. To determine the relationships of these two species, adult specimens of *P. mutus*, *P. lustrans*, *P. ohioensis*, *P. tropicalis*, *P. oregonus*, and *P. oblongopunctatus* were similarly studied. Dry adults were dissected according to Becker's (1958) method. I followed Schuler's (1965) nomenclature of female genitalia. The elytral length (from apex of scutellum to apex of longer elytron) and the pronotal length (along midline between apex and base) were measured on 25 specimens of each sex of each species with a calibrated ocular micrometer.

The structural characteristics of numerous larvae of each instar of each species were studied.

Volatile Sex Attractants

Because pheromones can serve as isolating mechanisms, I tested females indirectly for secretion of volatile chemicals which attract males of their own species. Virgins were used because females may mate only once. An apparatus (20 cm by 20 cm) consisting of two plexiglass floors separated by a nylon screen was used to prevent physical contact between males and females. Each floor had four compartments which corresponded in position with compartments in the other floor. Those of the upper floor were interconnected (Fig. 2). In each hole of the lower floor were placed moist paper and five specimens of one sex of one species (each hole had a different sex and species). On the upper floor I liberated 10 males of the species to be studied. I recorded the position of the males on the upper floor relative to the distribution of sex and species on the lower floor every hour for 24 hours. The experiments were done at 20 °C in an incubator within normal daylight hours under diffused artificial light from the incubator ceiling.

Mating Experiments

The ability of the males to distinguish females of their own species was investigated by offering males homospecific and heterospecific females, and by observing the approach to the female by the male. I paired 50 males of each species with females of the same species, 25 males with females of the other species, and made trios of 25 males with females of both species. Each pair or trio was placed in a plastic vial 35 mm in diameter and 70 mm high containing moist paper and food. Every two or four hours I checked for mating pairs. Direct observation of copulation was made by placing two to four males and five or six well-fed females in plastic boxes 15 cm by 7.5 cm by 4 cm with 1.0 cm of moist peat moss. I observed how the males approached the females and the reaction of a mating pair to being separated.

Preferendum Experiments about Oviposition

Soil moisture. — Because eggs can be desiccated easily, the female oviposition response to soil moisture may play an important role in the survival of the eggs. To investigate this, the following experiment was carried out in a plexiglass cage (interior measurements: 37 cm by

37 cm by 1 cm high) the floor of which was 7 mm thick with 25 compartments (55 mm in diameter) evenly distributed each about 1 cm distant from the adjacent ones. The ceiling of the cage was 3 mm thick with one small entrance hole, which was blocked during experiments. Each compartment contained a 54 mm dish (6 mm deep) with moistened peat moss as follows: A, 0%; B, 26%; C, 53%; D, 79%; and E, 106%. Each moisture concentration was replicated five times, and the dishes were distributed Latin Square fashion (modified from Doane, 1967). Because no noticeable change in the weight of each dish before and after the experiment was found, I conclude that the amount of water in the peat moss did not change. I noticed no difference between data collected along the edges, at the center and at the corners due to thigmotaxis. For each experiment I used 25 well-fed females of one species. These were kept at 20 C for five to six days. During this period the beetles were fed twice. At the end of the experiment, eggs were counted and the number recorded with the date for each moisture.

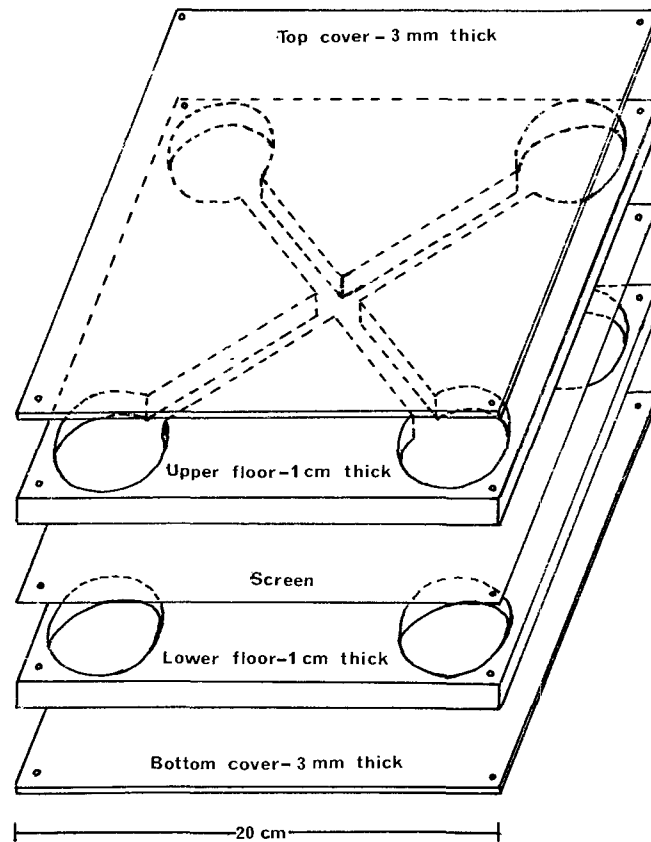


Fig. 2. Apparatus used to test for the presence of a volatile attractant in females of *P. adstrictus* and *P. pensylvanicus*.

Soil Density. — To penetrate a log, beetles must dig through rather compact decayed material to find suitable sites for oviposition. This experiment was designed to test the ability of each species to dig in material offering a range of difficulties of penetration. This experiment was set up as for the preceding experiment except that I used five different peat moss densities all at a moisture of 79%. Pressure was applied using a dish containing a weight above one filled with peat moss for ten seconds to achieve the following densities: A, 0 g/cm²; B, 25 g/cm²; C, 50 g/cm²; D, 75 g/cm²; E, 100 g/cm².

Soil Texture. — The structure of the oviposition site is important relative to evaporation rate. Eggs are easily desiccated, and thus sites with lower evaporation rates should have been selected for. Under laboratory conditions (15 to 23 C), moistened sifted forest soil, peat moss, sand and paper were placed in plastic boxes (7.5 cm by 15 cm by 3 cm) with 10 well-fed females. Eggs were counted each day for six days on each substrate.

Oviposition. — To study oviposition behaviour, females were kept under various conditions of moisture, temperature, substrate and soil density (Table 3). For oviposition rate per day over the season, I used groups of ten females in plastic boxes (7.5 cm by 15 cm by 3 cm) with a moist substrate. I also placed single females in small boxes (5 cm by 5 cm). Each female received every other day 0.20 of a *Tenebrio* sp. larva. The eggs were collected and counted daily or every four hours, and the soil in which they were laying was replaced with fresh soil after the counts were made. The count of eggs by searching was not exact as up to 10% may have escaped observation. When a precise count was needed, the eggs were floated in a saturated sugar solution (Southwood, 1966).

Table 3. Numbers of females kept for specified experiments under described conditions of temperature, substrate, and period of captivity for *P. adstrictus* (a) and *P. pensylvanicus* (p).

Conditions		Oviposition experiments							
		Kept in groups of 10		Kept singly		Kept as groups of 25 for soil moisture preference		Kept as groups of 25 for soil density preference	
		a	p	a	p	a	p	a	p
Temperature	Laboratory (15-25C)	50	50	2	6	0	0	0	0
	Incubator (20C)	30	30	0	0	25	25	25	25
	Cooler (15-20C)	40	40	11	10	0	0	0	0
Substrate	Sifted forest soil	30	30	13	16	0	0	0	0
	Sifted peat moss	70	70	0	0	25	25	25	25
	Sifted sand	10	10	0	0	0	0	0	0
	Absorbent paper	10	10	0	0	0	0	0	0
Period of Captivity	48 hours	40	40	2	6	25	25	25	25
	< 48 hours	80	80	11	10	0	0	0	0

Eggs. — Effects of moisture and temperature on developmental rate and survival of eggs were examined as follows. Some of the eggs were incubated in a box (5 cm by 5 cm) on a piece of moist paper over a very dilute detergent solution 2 mm in depth (two to four drops of detergent per 100 ml of water). Other eggs were kept in a saturated atmosphere but on a dry substrate. Some experiments were conducted at field temperatures (5 to 15 C), others at laboratory temperatures (10 to 25 C), and others at incubator temperature (20 C) (Table 4). For precise data, eggs were collected 24 hours after the females were introduced (damaged eggs were discarded). During incubation, eggs covered with fungi were removed to avoid contamination of other eggs. The original number of eggs collected and the number which hatched were recorded.

Table 4. Numbers of eggs of *P. adstrictus* (a) and *P. pensylvanicus* (p) used in experiments to determine water absorption and incubation period at various temperatures.

Conditions of temperature	Absorption of water by the eggs		Incubation period	
	a	p	a	p
Laboratory (15-25 C)	0	0	3300+	1200+
Incubator (20 C)	8	8	83	19
Cooler (15-20 C)	0	0	20	15

Larvae and Pupae. — Because larval and pupal development rates determine if adults emerge before winter, the effect of temperature on the development rate was studied by rearing 10 larvae of each species in an incubator at 20 C with day length similar to that in natural conditions. The larvae were reared individually in plastic containers 20 mm by 35 mm in diameter on a substrate of moist peat moss. The larvae were fed 0.20 of a *Tenebrio* sp. larva every other day, and the old food was removed during the feeding; moldy moss was replaced (method modified from Thiele, 1968a).

DISTRIBUTION, ECOLOGY, AND MORPHOLOGY OF *P. PENNSYLVANICUS*

Geographical Distribution and Habitat

This strictly American species ranges in the east from the southern limit of the boreal forest in Newfoundland south at least to Pennsylvania, through central North America north of the prairies, to central and southern British Columbia in the west (Lindroth, 1966).

Adults of this species may be obtained only under leaf litter (Lindroth, 1955, 1966), not under bark or in rotten logs. In southern Quebec, adults occur in most forest litter habitats. In central Alberta, they are restricted to deciduous forest litter on moist soil. The immatures are collected under similar conditions. Eggs are probably laid in the soil in moist areas, larvae occur below the leaves as well as in the soil, and pupae are probably in the soil as they were not found in logs.

Ecological Characteristics

Cycle. — Overwintering adults become active in the spring, (both young adults which emerged the previous fall, and those more than a year old). This period of searching for food and mates continues from the end of April or early May to the end of May or early June. Then activity of the adults decreases until the end of June when they enter a summer quiescent period.

During the spring, females oviposit usually from mid-May to the last week of June and then enter a quiescent period. The eggs hatch between mid-June and the last week of July. The larval stage is completed by September. At the end of the third instar, each larva builds a pupating cell about 2 cm by 1 cm and becomes quiescent until pupation. The pupal stage generally lasts from early August until late September. Finally new adults emerge, but remain in the pupal cell for a few days until the cuticle tans. Then both young and old adults become active again in the forest litter. Young adults often mate at this time, although females do not oviposit. This renewed activity continues usually until the end of October or early November in central Alberta. As the soil freezes, adults dig under rocks, in the soil or in logs. Often diapausing adults form aggregates of 20 or more, although solitary specimens were observed frequently in southern Quebec.

Adults. — Table 5 gives data on the relative activity of each sex and age-group. During the fall, marked adults of the old generation were slightly more active than those of the new generation. The old generation for the unmarked population (the density of which cannot be estimated) represent 33% of the captures among 14 females. Females of the old generation were apparently less active than the males; but females of the new generation were probably as active as the males. In the spring of 1970, males were probably as active as females. 80% of captured unmarked adults were female, suggesting a high male mortality, as the previous fall, hand collecting had yielded as many males as females. Population density in the spring was estimated at 0.6 specimen per square meter. Despite mortality, many adults survived two and even three winters as shown by the recapture of marked specimens. The development of the *corpora lutea* shows that 11 of 23 females survived at least two winters.

Table 5. Number of captured adults, percentage of released adults recaptured, of females in marked released populations and in catch, and relative activity of the sexes of *P. adstrictus* and *P. pensylvanicus*.

Category of adults	Number Captured	% females in released population	% released adults recaptured	% females in catch	female activity relative to male
<i>P. adstrictus</i>					
Fall					
Old generation marked	11	35	22	64	♀ > ♂
New generation marked	12	50	12	63	♀ ≥ ♂
Unmarked -	5	—	—	80	—
Spring					
Old generation marked	26	35	—	77	♀ > ♂
New generation marked	13	50	—	85	♀ > ♂
Mixed generations marked	21	50	42	48	♀ = ♂
Unmarked	20	—	—	25	—
<i>P. pensylvanicus</i>					
Fall					
Old generation marked	18	66	62	39	♀ < ♂
New generation marked	26	43	48	42	♀ = ♂
Unmarked	35	—	—	40	—

Table 5. (concluded). Number of captured adults, percentage of released adults recaptured, of females in marked released populations and in catch, and relative activity of the sexes of *P. adstrictus* and *P. pensylvanicus*.

Category of adults	Number captured	% females in released population	% released adults recaptured	% females in catch	female activity relative to male
<i>P. pensylvanicus</i>					
Spring					
Old generation marked	19	66	—	100	♀ > ♂
New generation marked	7	43	—	100	♀ > ♂
Mixed generations marked	19	50	38	58	♀ = ♂
Unmarked	24	—	—	80	—

The activity cycle (Fig. 3) was similar from year to year. In early spring there was an outburst of activity which increased and remained high until the end of May or early June. Then the activity decreased very quickly until late June when very few specimens were trapped. This probably signalled a period of quiescence which lasted at least until mid-August. Another increase in activity was followed by a peak between the end of September and mid-October. This peak was caused partly by an increase in activity of the old generation, but mostly by the newly emerged adults. This peak may decrease by itself or be interrupted abruptly by the beginning of the winter. Trapping rate showed differences in the activity between the sexes. More males were trapped in early spring following which there was an increase in female activity. Female activity was greatest just after overall activity of the population began to decrease. In early fall when adults were emerging, females were trapped at a rate similar to that of the males.

Greatest activity occurred around midnight (Fig. 4). Increases and decreases were gradual. However, in late fall when the night temperature was below 0 C, most specimens were trapped during daylight hours (Chymko, 1969).

Table 6. Results of tests of females for volatile sex attractants. Average distribution of 10 males of the tested species among the four chambers of the upper floor, in relation to the sex and species on the lower floor (25 readings).

Species on the lower floor		Average number of males of tested species on the upper floor	
		Species	
Males	<i>P. adstrictus</i>	<i>P. adstrictus</i>	<i>P. pensylvanicus</i>
	<i>P. pensylvanicus</i>	1.92 ± 0.54*	1.28 ± 0.54
Females	<i>P. adstrictus</i>	1.96 ± 0.67	1.40 ± 0.10
	<i>P. pensylvanicus</i>	1.72 ± 0.50	1.44 ± 0.63
		1.88 ± 0.74	1.16 ± 0.64

* 95% confidence limit

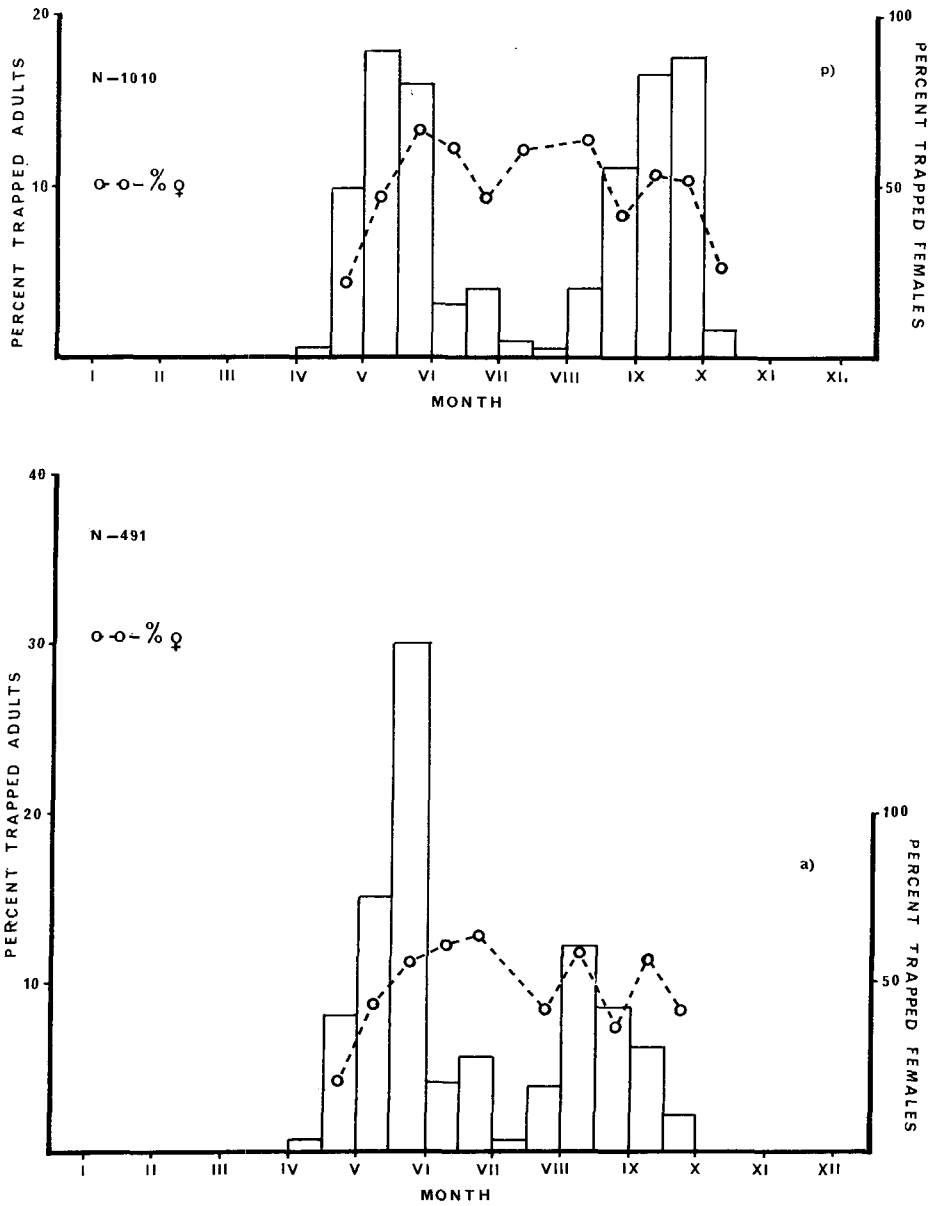


Fig. 3. Frequency distribution, in 15-day intervals, of captured adults and of females in 1969 of a) *P. adstrictus* and p) *P. pensylvanicus*. N is the total number of trapped adults.

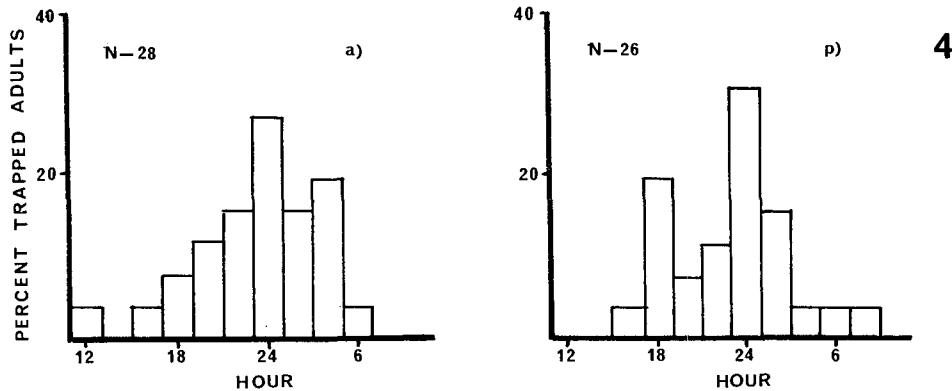


Fig. 4. Distribution of adults captured at two-hour intervals at George Lake in early June, 1969 of a) *P. adstrictus* and p) *P. pensylvanicus*. N is the total number of trapped adults.

Mating occurred in late fall (Chymko, 1969) during emergence of new adults, and in early spring until early June (16 copulations were observed in pitfall traps). Couples were observed both at night and during the day. Mating lasted about 12 hours under laboratory conditions. In the laboratory, I observed 15 matings in 75 trials, and males mated only with females of their own species even if offered females of both species. Table 6 indicates that males are not especially attracted to virgin females in the absence of physical contact.

Oviposition extended from mid-May until mid-July (Fig. 5). In 1970, the maximum oviposition rate by specimens freshly collected and kept at 20 C was reached on May 10. Dissected females had a low average number of eggs before mid-May in 1967 (Fig. 6). Generally, 99% of the eggs were laid by June 22. This suggests a day-length control of the end of the oviposition period. The average number of eggs per dissected female over the oviposition period was 9.9. This average does not represent the egg production of each female over the reproductive period as each laid an average of 22 at temperatures approximating those in the field. In early spring, there were no eggs; during May the average increased; after mid-June it decreased rapidly and by the end of June most females were spent. Females brought into the laboratory laid a large number of eggs within two or three days; thereafter they laid only a few eggs (Tables 7 and 8). The average number of eggs laid by another 10 females kept singly at approximately field temperatures was 9.0 over three days. This average is close to the average number (9.9) found in dissected females. The average production per female was 0.6 egg daily for the oviposition period. This does not agree with the average of 9.0 eggs in three days as mentioned before. As the average peak production corresponded closely to the average number per female, I think that eggs are laid in batches after being accumulated for some time, and that a batch is as large as the total mature egg content of each female. Assuming that no eggs are laid between batches, it probably takes two weeks for another batch to develop. For oviposition, females used mostly the wettest soil conditions (Fig. 7). Eggs were laid in various granular materials such as sifted forest soil, peat moss, and sand (more than 1.1 eggs per female per day), but were not laid on non-granular substrates such as paper. The loosest soil conditions were most used for oviposition (Fig. 8).

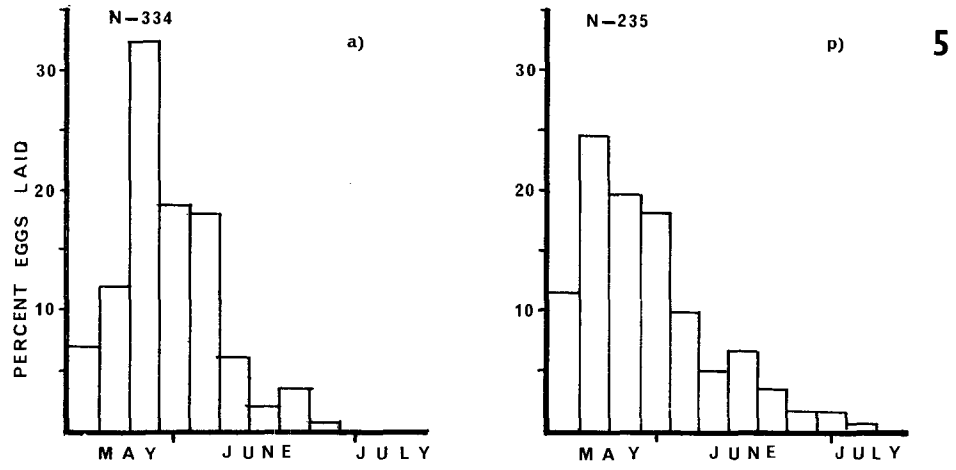


Fig. 5. Frequency distribution of eggs laid per five-day interval in 1969 under temperature conditions approximating field conditions and natural light and day length conditions of a) *P. adstrictus* and p) *P. pensylvanicus*. N is the total number of eggs.

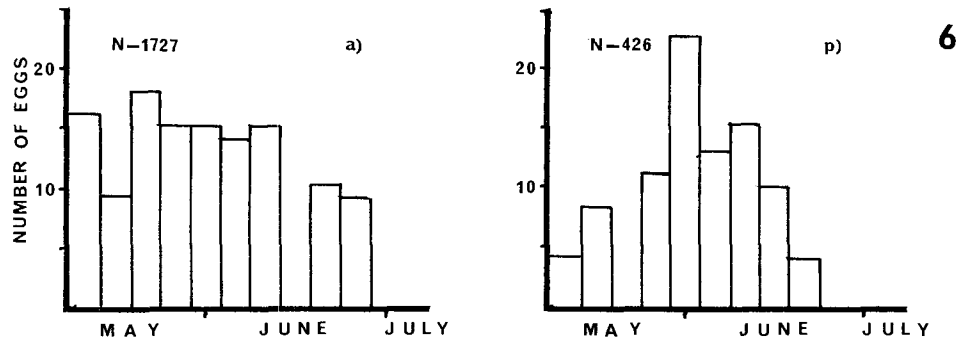


Fig. 6. Frequency distribution of average number of eggs per dissected female at five-day intervals of a) *P. adstrictus* and p) *P. pensylvanicus*. N is the total number of eggs.

Table 7. Number of eggs laid per day by single females of *P. adstrictus* and *P. pensylvanicus*.

Species	Specimen designation	Number of days after capture										Mean egg production per day
		1	2	3	4	5	6	7	8	9	10	
		Number of eggs per day										
<i>P. adstrictus</i>	1	22	1	7	3	5	2	4	2	5	1	4.0
	2	0	23	0	0	8	0	9	4	1	5	4.6
<i>P. pensylvanicus</i>	1	1	7	8	2	1	5	2	5	0	0	3.1
	2	0	0	3	2	1	0	0	0	0	0	0.6
	3	1	2	3	1	0	1	0	0	0	0	0.8
	4	2	5	1	0	1	1	0	0	0	0	1.0
	5	1	0	1	1	0	0	0	0	0	0	0.3

Table 8. Number of eggs laid by each of 10 females of *P. adstrictus* and *P. pensylvanicus* in 24 hours over two days after capture at approximately field temperatures.

Species	Day	Specimen Designation									
		1	2	3	4	5	6	7	8	9	10
		Number of Eggs per Specimen									
<i>P. adstrictus</i>	1	12	11	11	7	7	1	10	10	11	22
	2	0	2	0	1	8	1	4	2	0	4
<i>P. pensylvanicus</i>	1	0	0	0	2	5	7	3	7	5	0
	2	2	6	5	3	1	3	0	2	7	1

Egg Stage. — In 1968, 90 to 100% of several hundred eggs hatched. At 20 C, 11 eggs required 10.6 ± 0.8 days to hatch; under field temperatures (ca 7 C) 15 eggs required 39.5 ± 1 days to hatch. At temperatures higher than 25 C, more than 50% of the eggs died, but eight exposed accidentally to -5 C for 24 hours hatched. Eggs absorb water from the soil; just after oviposition the maximum length x maximum width was 1.44 ± 0.05 mm² while just before hatching, it was 1.57 ± 0.06 mm². Excess moisture or lack of it killed the eggs (15 eggs tested). Within the range 26 to 100% moisture, 90 to 100% of eggs hatched.

Larvae. — Pitfall trapping data for 1968 showed that the average emergence dates of the first, second, and third instar larvae were on June 13, June 23, and July 5 respectively. The duration of the first instar was 11.5 days, and the second was 14.1 days. In the laboratory at 20 C the first instar lasted seven to eight days and the second eight to nine days. The total larval development took 28.3 days. As no temperature higher than 19 C was recorded in the litter (average high around 15 C) it is probable that larval development took place at temperatures less than 20 C.

Pupae. — From pitfall data of 1969, the peak of emergence of third instar larvae was on July 23, and of the teneral adults on September 30. Thus there was an interval of 70 days. Ten specimens reared at 20 C passed as pupae 45% of the inactive period from quiescent third instar larvae to partly tanned adults, suggesting a pupal period of 31 days.

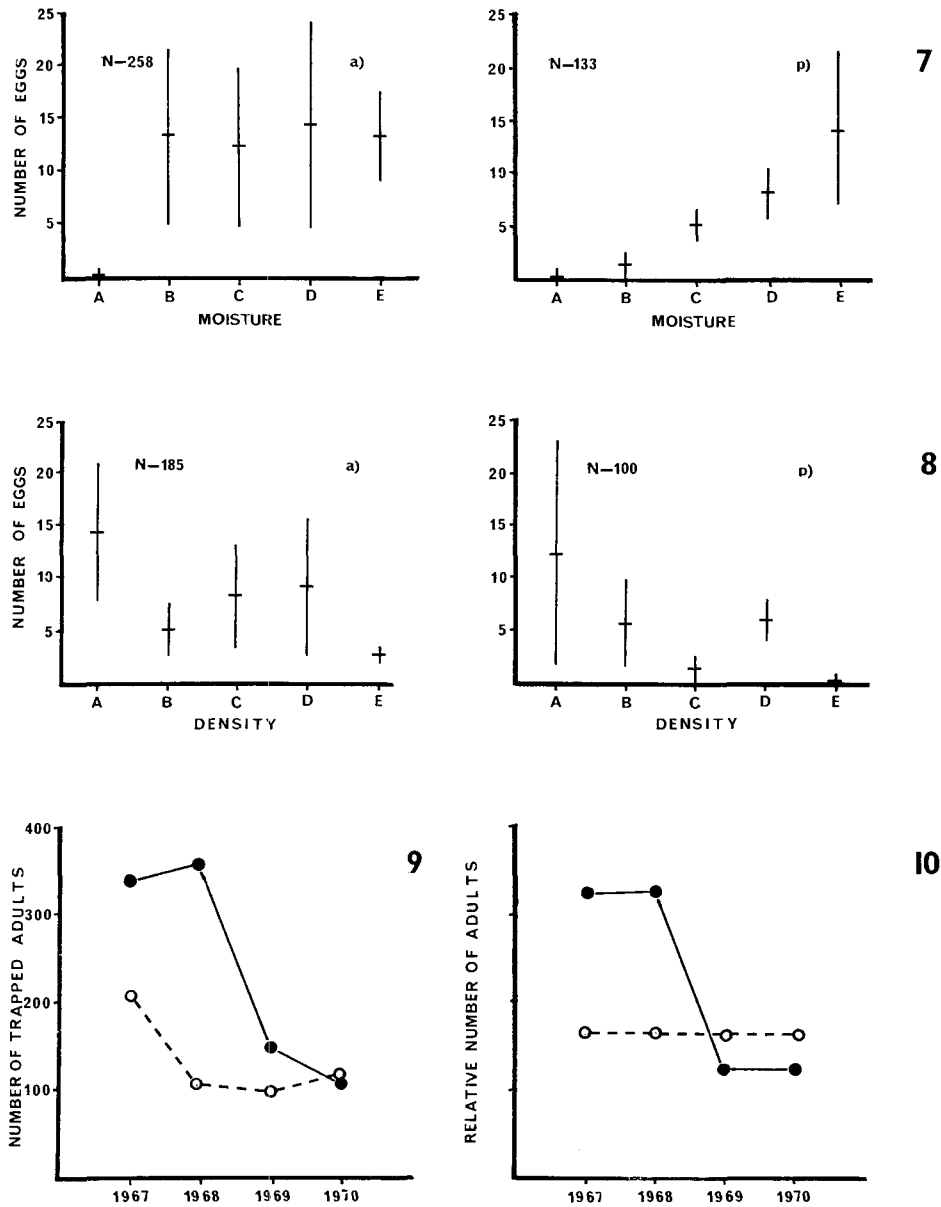


Fig. 7. Average number of eggs laid by 25 females of a) *P. adstrictus* and p) *P. pensylvanicus* over six days in soil of various moisture content. The mean is represented by a horizontal line. 95% confidence limits are represented by a vertical line. N is the total number of eggs. Fig. 8. Average number of eggs laid by 25 females of a) *P. adstrictus* and p) *P. pensylvanicus* in soil of a given density in six days. The mean is represented by a horizontal line, vertical line represents 95% confidence limits. N is the total number of eggs. Fig. 9. Number of adults of *P. adstrictus* and *P. pensylvanicus* collected per 200 pitfall traps during June at George Lake for the period 1967 to 1970. ——— *P. adstrictus*; - - - - - *P. pensylvanicus*. Fig. 10. Diagram illustrating hypothesized changes in relative abundance of adults of *P. pensylvanicus* and *P. adstrictus* at George Lake for the period 1967 to 1970. ——— *P. adstrictus*; - - - - - *P. pensylvanicus*.

Population Fluctuations from 1967 to 1970.

The population of *P. pensylvanicus* probably changed little during this period (Fig. 9).

Morphology of *P. pensylvanicus*

Adults. – Lindroth (1966) described the external structures of adults including the male genitalia. However, the female internal reproductive tract also has interesting characteristics (Fig. 11). On the dorsum of the *bursa copulatrix* is the apparent opening to the short, wide spermathecal duct. The apical reservoir is small, and its inner diameter is about three times larger than the inner diameter of the spermathecal duct. The long duct of the spermathecal gland originates on the side of the spermathecal duct about 0.20 of its length from the bursal opening. The inner diameter of this convoluted tube is 0.5 of the inner diameter of the spermathecal duct. This duct ends in a small vesicle which is followed immediately by a very large securiform spermathecal gland.

Barlow *et al* (1969) attempted to find other characteristics for distinguishing *P. adstrictus* from *P. pensylvanicus* by comparing the relative position of the widest point of the pronotum. I felt that the position of this point was difficult to determine and that it had little discriminating value. However, compared to *P. adstrictus*, the elytra of *P. pensylvanicus* are shorter relative to the pronotum length (pronotum length/elytra length more than 0.43).

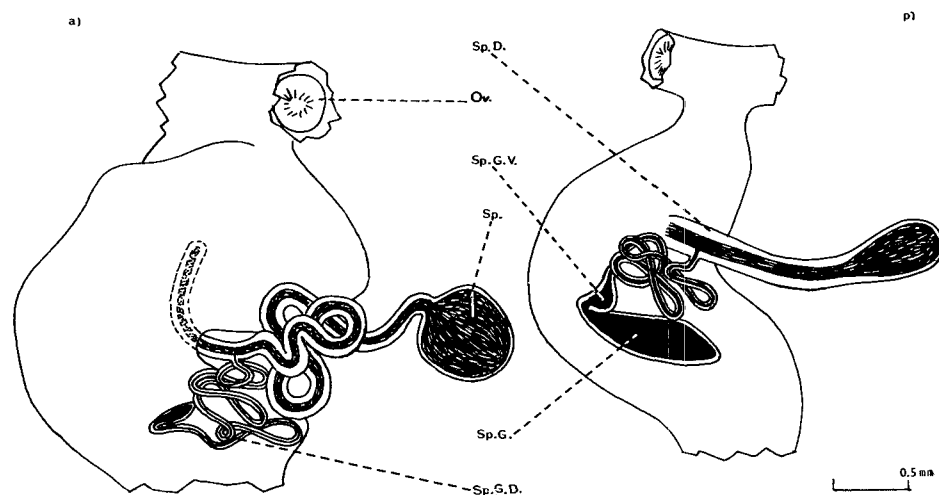


Fig. 11. Dorsal view of the female internal reproductive system (ovaries, part of vagina, and ovipositor omitted). a) *P. adstrictus*; p) *P. pensylvanicus*; Sp. - spermatheca; Sp. D. - spermathecal duct; Sp. G. D. - spermathecal gland duct; Sp. G. V. - spermathecal gland vesicle; Sp. G. - spermathecal gland; Ov. - oviduct.

Description of the Larvae of P. pensylvanicus. – The generic characteristics are as described by van Emden (1942).

The larvae of this species are paler than are those of *P. adstrictus*. The innermost basal setae of the mesonotum are absent or little developed depending on the instar.

Third Instar Larva

Head Width. 1.4 to 1.7 mm.

Colour. Following rufo-testaceous: head, mandibles, mentum, and head appendages. Terga of thorax, prosternum, and legs testaceous.

Chaetotaxy. Tergites and sternites with numerous irregular small setae. Innermost basal setae of mesonotum about 0.2 to 0.4 times as long as external basal setae. Nine setae on urogomphi. Five setae on abdominal epipleurites.

Thorax. Pronotum about 1.5 times as wide as long; meso- and metanota each twice as wide as long.

Abdomen. Terga at base twice as wide as long, and at apex 1.5 times as wide as long. Urogomphi moderately long and slightly curved inward at apex.

Microsculpture. Cells on frons convex, thus head dull.

Second Instar Larva

Differing from the third instar in the following.

Head Width. 1.0 to 1.2 mm.

Chaetotaxy. Fewer irregular setae. Innermost basal setae of mesonotum about 0.1 to 0.2 times as long as external setae.

First Instar Larva

Differs from the two preceding instars in the following.

Head Width. 0.6 to 0.7 mm. Egg bursters present on frons. Cervical grooves on genae not curved ventro-laterally to eye level. No membranous area near middle of maxillary palp along outer margins.

Chaetotaxy. No irregular small setae. Innermost basal setae of mesonotum absent or barely suggested. Five setae on urogomphi, two setae on abdominal ventrites and postventrites; no setae on hypopleurites. Abdominal epipleurites each with one long seta, in some specimens, a suggested second one.

DISTRIBUTION, ECOLOGY, AND MORPHOLOGY OF *P. ADSTRICTUS*

Geographical Distribution and Habitat

P. adstrictus, one of the most widely distributed species of Carabids, has been reported from Iceland, northern British Isles, Ireland, Faeroes, Denmark, westward through northern Russia, Siberia, northern Mongolia to Kamchatka (Lindroth, 1945). In America, it has been found from Newfoundland to Attu in Alaska, and to southern Canada (London, Ontario); at high altitudes it occurs south to California and to southern New England (Locust Spring Recreation Area, Virginia).

Adults are in woodland as well as in open land, including cultivated fields (Frank, 1971). Specimens are found on the coastal tundra of southern Labrador, Kodiak and Aleutian Islands, but not on the more northern tundra (Lindroth, 1966). These beetles are found in moist to dry soil, and often in rotten logs. The preferred habitat varies with the region. In the coastal regions specimens are relatively independent of forest cover, while in the interior, as in Alberta, they are found mostly in tall grassland and in forests (Frank, 1971). In Norway, Lindroth (1945) observed that they were most abundant in moderately moist areas. In this region, these beetles seemed synanthropic. In Alberta they are found in forest habitats even in their darkest parts (white spruce forest), or in wet conditions as at the edge of marshes. At sea level

in eastern Canada near Montreal, individuals are restricted to forest litter on north-facing slopes in dark cool conditions. Adults may be found in most litter habitats. In the spring, individuals are often under bark where they oviposit; two eggs were found in moist decayed wood. First and second instar larvae were found mostly in rotten logs while the third instar occurred commonly in leaf litter as well as in the old logs. The pupae were commonly collected in rotten logs in moist cool situations.

Ecological Characteristics

Cycle. — In early spring the adults become active, and seek food and mates. Activity starts to decrease at the end of May or early June, and the beetles enter a summer quiescent period. Oviposition occurs during the period of high activity from early May until the last week of June. Eggs start to hatch by mid-June. The young larvae develop rapidly and by mid-August and September the new adults emerge from the pupal cells after their cuticles are almost tanned. During the emergence period, both new and old adults are active in the litter. Adults become inactive from September to November and overwinter either singly or in aggregations in logs or under stones.

Adults. — Seasonal activity was similar from year to year. Most adults were quiescent during the fall. However, in spring, as males were about as active as females, it is probable that unmarked females were rare relative to unmarked males. Recaptures as well as dissection of ovaries showed that females especially can survive more than one winter. In spring, the density of unmarked adults was estimated at 0.5 beetle per square meter. Frank (1971) observed 1.8 beetles per square meter in cropland. During May, activity remained very high but decreased from the end of May until the end of June. Frank (1971) observed high activity until July in cropland. By August, as new adults emerged, both old and new generation adults became active again. Activity decreased again in October. Females were generally as active as males except in very early spring when a higher proportion of males was trapped. By the end of May or early June, a greater proportion of females was caught (Fig. 3). Adults show a greater rate of activity at night (Fig. 4).

Mating was observed three times in the field during May and early June of 1969. The time required for copulation was 12 hours for most pairs observed in the laboratory. I observed 6 copulations in 75 trials of males placed with females of the same species. No copulations were observed with females of *P. pensylvanicus*. Data in Table 6 show that no males were attracted to virgin females of their own species in absence of direct contact.

Females oviposited from early May until the last week of June (Fig. 5). However, Frank (1971) observed oviposition until mid-July. The average egg content per female was 13.6. In very early spring no eggs were present in dissected females. During May the average was high until June when it decreased. By the end of June most dissected females were spent. Freshly caught females tend to lay most of their eggs within two days with an average of 12.4 at field temperatures (Tables 7 and 8). As females lay an average of 1.15 eggs per day over the season, they probably lay eggs in batches of sizes approximating the number of mature eggs in their abdomens. The average number of eggs laid by a female at field temperatures was 32.

Eggs are laid in moist to wet soil, but not in dry soil (Fig. 7). They were laid in various granular materials such as sifted forest soil, peat moss, and sand, but not on non-granular substrates such as absorbent paper. Females do not avoid digging in better packed soils to oviposit suggesting that penetration of rotten logs may not present a problem for them.

Egg Stage. — Under suitable conditions of temperature (less than 20 C) and moisture, 90 to 100% of eggs hatched. Rate of egg development is similar among individuals as 75 eggs at 20 C hatched in 9.6 ± 0.7 days. Under field temperature conditions, 20 eggs completed their development in 36 ± 1.1 days. At temperatures over 25 C more than 50% of the eggs were lost,

but at -5 C for 24 hours no eggs were damaged. During their development, eggs absorb water from the substrate, as the maximum length x maximum width at oviposition was $1.48 \pm 0.03 \text{ mm}^2$, while at hatching time it was $1.64 \pm 0.05 \text{ mm}^2$. Under moist conditions, eggs developed well, but in dry conditions, despite a saturated atmosphere, eggs were killed rapidly through desiccation. Wet conditions also killed the eggs.

Larvae. – Average emergence dates of the first, second and third instar larvae as estimated from 1968 pitfall trapping were June 10, June 18, and June 27. The average emergence date varied yearly. Time between instars was 8.0 days from the first to the second, and 9.0 days from the second to the third. At 20 C, individuals of the first instar reached the second in eight days, and the second instar larvae reached the third in eight to nine days. Thus as field data are similar to laboratory data, I think average conditions in logs are warmer than in the litter, and are close to 20 C. In 1972 a few readings suggested that logs are warmer than 20 C when ambient temperatures are around 25 C. Total larval development at 20 C required 27.7 days. This is similar to Frank's (1971) observations.

Pupae. – From pitfall data of 1969, the inactivity period for larvae began on July 23, and the adult emergence peak was on August 23. Thus there is an interval of 31 days. Probably 45% of this period was spent in the pupal stage as judged from laboratory data. Thus, it is probable that the pupal stage was 14 days. In the laboratory, the pupal stage was completed in eight days, so the average field temperature was probably less than 20 C.

Population Fluctuations from 1967 to 1970

The *P. adstrictus* population probably decreased in 1969 and remained at a low level in 1970 (Fig. 9).

Morphology of *P. adstrictus*

Adults. – Lindroth (1966) described the external morphology as well as that of the male genitalia. American specimens except those of the west coast show longer elytra than those of *P. pensylvanicus* (pronotum length/elytra length less than 0.43). The female reproductive tract is characteristic (Fig. 11). The spermathecal duct is long, wide, and convoluted, and opens into the ventral side of the *bursa copulatrix*. The duct ends in an apical oviform reservoir eight to nine times wider than the inner diameter of the spermathecal duct. On the side of the spermathecal duct near its opening, at 0.20 of its length, is the spermathecal duct origin. The inner diameter of this duct is about one-third of the inner diameter of the spermathecal duct. This duct ends in very small vesicle which is followed immediately by a very small securiform spermathecal gland.

Description of the larvae of P. adstrictus. – The larvae of this species are darker than those of *P. pensylvanicus*. The innermost basal setae of the mesonotum are present and well developed.

Third Instar Larva

Head Width. 1.6 to 1.9 mm.

Colour. Following rufous: head, mandibles, mentum, disc of pronotum, and prosternum; head appendages slightly paler. Meso- and metaterga, and disc of abdominal terga rufo-testaceous or testaceous. Legs testaceous. Lateral and ventral sclerites, uropod, and urogomphi pale testaceous. Remaining membranous areas white.

Chaetotaxy. Tergites and sternites with numerous irregular small setae. Innermost basal setae of mesonotum about 0.75 times as long as the lateral ones. Nine setae on urogomphi. Five to seven setae on abdominal epipleurites.

Thorax. Pronotum about 1.5 times as wide as long; meso- and metanota each twice as wide as long.

Abdomen. Terga at base twice as wide as long, and at apex 1.5 times as wide as long. Urogomphi

moderate in length and slightly curved inward apically.

Microsculpture. Patchy and slightly convex cells on the frons.

Second Instar Larva

Differing from the third in the following.

Head Width. 1.0 to 1.3 mm.

Chaetotaxy. Irregular small setae less abundant. Innermost basal setae of mesonotum about 0.5 times as long as external basal setae.

First Instar Larva

Differs from the two preceding instars in the following.

Head. 0.6 to 0.8 mm in width. Egg bursters present on the frons. Cervical grooves not curved ventro-laterally to the eye level. No membranous area near middle of maxillary palp along outer margins.

Chaetotaxy. No irregular small setae. Innermost basal setae of mesonotum about 0.3 to 0.5 as long as external basal setae. Five setae on urogomphi; two setae on abdominal ventrites and post-ventrites; no setae on hypopleurites. Abdominal epipleurites with two setae; smaller one about 0.5 times as long as other.

GENERAL DISCUSSION

In the following sections I attempt to explain for these species factors involved in the observed population fluctuations, differences in their present distributions, principles involved in reproductive isolation; adaptive significance of various characteristics; and the past history and the relationships between the species.

Differences in Population Fluctuations

From 1967 to 1970 the population of each species changed as suggested by trapping data (Fig. 9). The *P. pennsylvanicus* population remained relatively stable while the *P. adstrictus* population decreased. Despite the few environmental variables studied, I think it is possible to explain these observed changes.

Biotic Factors. — Competition for food seems of secondary importance. Thiele (1968) found, with related species of *Pterostichus*, some competition effect under overcrowded conditions when food quantity was minimal. But in the field, excess food was the rule. The amount of food required by a larva is very small as in the laboratory at 20 C a single larva for each of the species completed development having fed on 2.5 *Tenebrio* larvae. Moreover, in the enclosed area where adult density was doubled, the percentage of trapped specimens with fat abdomens was similar to the percentage outside the enclosure. Cannibalism cannot explain these observations as adults do not attack tanned adults successfully even if starved for three months.

Interaction with other species of insect or with specimens of the same species is probably secondary. In the laboratory there was no evidence that specimens were attracted or repelled by other specimens. Pitfall trapping suggested this, as it was rare to get two or more specimens per small trap per day for both adults and larvae. The most susceptible stage is the larva, but encounter may be reduced as they move in a three dimensional habitat. However, hand collecting in the field suggests that the first instars are rather crowded.

Predators of importance were *Clethrionomys grapperi* Vigors, *Microtus pennsylvanicus* Ord., *Bonasa umbellus* L., *Microsorex hoyi* Baird. But I think they play little role in controlling these Carabids, as shrews and grouse are rare per unit area, and as mice, from stomach analysis, feed rarely on these beetles. Possibly spiders eat these beetles (Exiline and Hatch, 1934; Leech, 1971), but pitfall observations showed the opposite except when adults are not fully tanned;

but larvae could be regularly eaten by spiders as observed in the laboratory.

Parasites and diseases during the study period played a minor role as suggested by dissection and by the numerous live specimens kept in the laboratory for long periods. Less than 5% of adults were attacked by gordian worms, and less than 5% of pupae were attacked by fungi.

Table 9. Summary for each development stage of behavioural and physiological characteristics for *P. adstrictus* and *P. pensylvanicus*.

Stage	Species	
	<i>P. pensylvanicus</i>	<i>P. adstrictus</i>
Females	<ul style="list-style-type: none"> – oviposit under litter – oviposit on wettest substrates – start oviposition by mid-May – lay 0.7 times as many eggs as <i>P. adstrictus</i> 	<ul style="list-style-type: none"> – oviposit in logs – oviposit in various moist substrates – start ovipositing earlier – lay 1.5 times more eggs than <i>P. pensylvanicus</i>
Eggs	<ul style="list-style-type: none"> – laid on granular substrates – must absorb water from substrate – low temperature for short period has no effect – high temperature increases mortality – hatch later than <i>P. adstrictus</i> under similar conditions 	<ul style="list-style-type: none"> – hatch earlier than <i>P. pensylvanicus</i> under similar conditions
Larvae	<ul style="list-style-type: none"> – Move easily in gradients of moisture, R.H., and temperature (Paarman, 1967) – develop in 28 days at 20 C – develop slower in the field than <i>P. adstrictus</i> – very cannibalistic 	<ul style="list-style-type: none"> – develop faster in the field than <i>P. pensylvanicus</i>
Pupae	<ul style="list-style-type: none"> – killed by low R.H. – not killed by low substrate moisture – develop in 8 days at 20 C – often develop slower in the field than <i>P. adstrictus</i> – cannot overwinter 	<ul style="list-style-type: none"> – often develop faster in the field than <i>P. pensylvanicus</i>
Teneral	<ul style="list-style-type: none"> – can overwinter – mate, but do not oviposit before winter 	

Abiotic Factors. – These factors can be summarized under weather conditions affecting the micro-habitat of each stage. Various data related to behavioural and physiological characteristics are summarized in Table 9. Each of these characteristics is affected by the different physical qualities of the micro-environment of the stage. Logs can be warmer than the soil below the litter, thus accelerating larval and pupal development; but they could dry out rapidly and increase the mortality rate of immobile stages. If climatic effect of one period is added to the next, these interacting factors could favour or suppress one or both species in similar or

different ways. The final result is the number of adults surviving for reproduction in the following season. The probable climatic effects on the populations of both species are summarized in Table 10. Considering the climatic changes over these years it seems that the observed and expected results are in agreement (Fig. 9 and 10).

Table 10. The probable effect of weather on each developmental stage of *P. adstrictus* and *P. pensylvanicus* during spring, early summer, and late summer.

Period	Condition	Species	
		<i>P. pensylvanicus</i>	<i>P. adstrictus</i>
		Effects	
Spring	Dry	– low egg mortality – fast development	– high egg mortality – faster development than <i>P. pensylvanicus</i>
	Wet	– low egg mortality – slow development	– as for <i>P. pensylvanicus</i> – slow development, but faster than <i>P. pensylvanicus</i>
Early Summer	Dry	– larval mortality rate low – development fast	– as for <i>P. pensylvanicus</i> – development faster than for <i>P. pensylvanicus</i>
	Wet	– larval mortality rate low – development much slower than <i>P. adstrictus</i>	– as for <i>P. pensylvanicus</i> – development slow
Late Summer	Dry	– pupal mortality low – development fast	– as for <i>P. pensylvanicus</i> – development faster than for <i>P. pensylvanicus</i>
	Wet	– pupal mortality low – development very slow	– as for <i>P. pensylvanicus</i> – development slow, but faster than for <i>P. pensylvanicus</i>

I believe there are two main principles behind the population changes of both species. Firstly, the changes are related to difference in oviposition behaviour and sites, to egg sensitivity, and to moisture conditions of these sites during development. Thus in the spring of 1967 soil and logs were very moist, but later during summer and fall they dried. The moisture in the soil was still adequate. Thus, in 1968, the population size of both species remained almost the same as in the previous year. The spring of 1968, until mid-June, was drier, so most of the logs were dried by June (estimated by touch), while under the litter the moisture was still adequate (estimated by touch). During this period, eggs in the log habitat were probably mostly killed, while in the soil they were little affected. Thus fewer adults of *P. adstrictus* were produced in the fall of 1968, and in the spring of 1969 fewer adults were trapped. Because moisture conditions in the spring of 1969 and 1970 were good in the logs, egg mortality due to drying of the habitat was probably low, so changes in these years may have been due to other factors.

Secondly, changes are related to average temperature in the chosen habitat, as it affects the

development rate. Thus the size of the future population depends on the proportion of immatures reaching adult stage before winter. Ecdysis of *P. adstrictus* from the pupae was usually completed in September, but in 1970, probably because of the wetter and cooler summer, the peak of emergence occurred only three weeks before winter. *P. pensylvanicus* adults emerged later than those of *P. adstrictus* on average. In 1968, 1969 and 1970, their emergence was incomplete when winter set in.

Difference in the Distributions of the Species

P. adstrictus is spread across the boreal forest northward to the tundra, while *P. pensylvanicus* is found across the southern boreal forest and mixed forest. Only *P. adstrictus* reaches the west coast. My data permit a discussion only of the northern limits of both distributions, and of the western limit of *P. pensylvanicus* distribution. Development rate is the primary subject of this discussion. Both species require the same time to develop from egg to adult under similar conditions. Between the northern limits of distribution, one main difference exists: the duration of the warm season. Thus *P. adstrictus*, whose range extends further north, must be able to complete its development faster in order to survive the shorter summer. *P. pensylvanicus* populations reach their northern limit about 300 miles north of Edmonton at Fort MacMurray (Lindroth, 1966). Even near Edmonton, pupal emergence is partially curtailed by arrival of winter. I assume that the average temperature of the chosen environment is the key to faster development. So each species is under selection pressure to choose an environment which submits immature stages to warmer conditions. *P. adstrictus* females oviposit in warmer habitats, while *P. pensylvanicus* restricted their oviposition sites to open forest in central Alberta. This last adaptation is an improvement over other *P. pensylvanicus* populations, but the restriction to forest and litter is a less efficient way to find warmer conditions for immatures. Thus, the female and larval behaviour explains why immatures of *P. adstrictus* complete their development faster than those of *P. pensylvanicus*, and hence why the range of *P. adstrictus* extends further north.

P. pensylvanicus populations extend only as far west as central British Columbia. Specimens may have crossed to that province north of the prairies in a deciduous forest as they seem to avoid spruce and fir forests. Most of the Rocky Mountains present a coniferous barrier except around the Peace River area where widespread aspen forest still extends across to central British Columbia. Farther west, *P. pensylvanicus* is met by semi desert conditions and by the coastal coniferous forest.

Reproductive Isolating Mechanisms

Reproductive isolation of these two species is indicated by concordant distribution of several character states with no individuals showing intermediate combinations of these states. In the experiments discussed, males attempted to mate only with females of the same species. Thus, the mechanism probably is precopulatory and involves the sense of touch, smell, taste, hearing or vision. One experiment suggests that there is no olfactory attractant. There is no evidence for sound receiving or transmitting organs so hearing is probably not used. Copulation occurs in the dark so vision is not used. The remaining likely senses are those of touch and taste. In the laboratory, beetles move apparently at random in the rearing boxes. At short distances, perhaps when the palpi touch, there may be some interaction. Most of this interaction is of no consequence as the beetles just change their paths. Sometimes copulation may occur, but only if the female is approached by the male from behind. However, this approach does not always result in mating. Even during mating season, few females are receptive and those only for a short time. I have not seen females mating a second time. If sense of touch is involved, there should be some morphological difference in the surface near the apex of the

female abdomen, but none is evident. Because of the rapidity and the briefness of the transmitted information, I suspect that the mechanism is a chemical message that can be sensed by palpi.

Adaptative Significance of Behavioural and Morphological Characteristics.

In general, adults and larvae live in the same habitat although larvae are more restricted. Because oviposition is linked to the spring activity of the adults, it is an important adaptation that adults remain in the habitat that is suited to the immature stages. This prevents oviposition in unfavourable habitats. In the fall activity period, there is no oviposition, and the adults may occupy a much wider range of habitats. Adults spend the quiescent period and the winter diapause in habitats similar to those occupied in the spring, and the soils of these habitats are not subject to soaking. This is an important adaptation, as it encourages a higher adult survival rate by decreasing mortality due to drowning or to freezing to death in ice. The microhabitats chosen by the females for oviposition involve a conflict between higher development rate and higher survival rate, and this conflict has been solved differently by the two species. Behaviour of females in choosing the environmental conditions for oviposition is an important adaptation for insuring the success of the species from year to year. From available evidence, I believe that the egg stage is critical as it depends on stable moisture conditions for survival. In this respect, *P. pensylvanicus* is better adapted because the females usually choose very moist conditions. *P. adstrictus* females counteract the higher egg mortality rate by laying eggs in batches. The simultaneous existence of features of the preferred habitat, including soil structure, texture, and moisture, may serve as a triggering mechanism for oviposition. The 'preferred' sites are rare, so when such a site is found it is important that the female is adapted to lay many eggs. Thus females accumulate their eggs until suitable habitats are encountered. Thiele (1968b) pointed out that most carabids reproduce in summer which suggests that spring reproduction is not characteristic of forest litter species, although a spring cycle may help in reducing competition among forest litter carabids by separating spring carabids from summer carabids.

Adults of both species are most active in spring. Most of this activity is linked with the search for food, as most trapped adults had full crops; a greater consumption of food is important in providing energy for egg production. Also, this activity is important in increasing the probability of finding suitable oviposition sites. Hence, the spring activity cycle is linked with the success of oviposition. After the spring activity, adults enter a summer quiescent period which reduces competition with other carabid adults and especially with their own larvae, and so may be of adaptive significance. There is another lesser activity peak in the fall, due primarily to emergence of new adults which search for food, mates, and winter quarters. Adults which spend the summer in aestivation enter the winter diapause with or without fall activity. So the fall activity peak is probably important for the development of fat reserves in the new adults and for increasing the number of fertilized females, and consequently is significant in the survival of the species.

Mating adaptations are similar in both species. Apparently, most of the mating behaviour is linked to the absence of attractants as females and males probably encounter each other at random. In both species there are as many males as females, females are receptive in the fall (at least in *P. pensylvanicus*), and again in spring until early June, and females have spermathecae (preserving sperm for at least three months, and probably nine). All these characteristics help to insure that there is a high proportion of mated females.

Relationship between *P. adstrictus* and *P. pensylvanicus* and their Past History.

After studies of related species of the subgenera *Bothriopterus* and *Dysidius*, I feel that *P. adstrictus* and *P. pensylvanicus* are not as closely related as first anticipated, in spite of

their many similarities. I will attempt here to show the relationships between *P. adstrictus* and *P. pensylvanicus* with reference to other known American species of *Bothriopterus* and *Dysidius*; to explain the past history of each species with reference to known relationships and distributions; and, on the basis of the preceding postulates, to outline the history of the behavioural characteristics with species reference to *P. adstrictus* and *P. pensylvanicus*.

Phylogenetic Relationships Derived from Adult Structure

In the Nearctic Region, five species are related to *P. adstrictus* and *P. pensylvanicus*. This relationship has been pointed out by Lindroth (1966) with reference to the shape of the median lobe in the male and the absence of sclerites from the internal sac. This group of seven species is included in two subgenera: *Bothriopterus* (four species including *P. adstrictus* and *P. pensylvanicus*), and *Dysidius* (three species). *Dysidius* was defined by the presence of three unexpanded foveae on the disc of each elytron, and similar male and female microsculpture. These differences are partly diagnostic as *P. pensylvanicus* specimens have poorly expanded elytral discal foveae and nearly similar male and female microsculpture, and as *P. tropicalis* specimens and the European *P. angustatus* specimens have only three discal foveae. To determine relationships, an analysis of characteristics of Nearctic species was made (Table 11). The most difficult task was to determine if a character was plesiotypic or apotypic. To comply with Dollo's Law, three discal foveae and unexpanded umbilical foveae were considered primitive among the species studied. The sharp apex of the median lobe in dorsal view, the small size of the spermatheca, and the presence of a brush on the hind tibia, were considered as apotypic for single species in well-defined subgroups. The incomplete pronotal bead, and the expanded dorsal discal foveae were considered plesiotypic to comply with Dollo's Law. A phylogeny showing the relationships among the species is suggested (Fig. 12) in which the most primitive form is *P. tropicalis*, and the most derived one is *P. adstrictus*. With Tschischérine (1900) I see no important reason for separating *P. tropicalis* from *Bothriopterus*, and as the *Dysidius* are considered derived from the *P. tropicalis* ancestor, I have considered all the species studied here as members of one subgenus, *Bothriopterus*.

Table 11. Analysis of characteristics of Nearctic species of the subgenus *Bothriopterus*.

Character	Character designation	Evolutionary state of the character	
		Plesiotypic	Apotypic
Pronotal basal bead	1	incomplete	complete
Number of elytral discal foveae	2	three	five
Diameter of elytral discal foveae	3	expanded	not expanded
Diameter of foveae of the umbilicate series	4	not expanded	expanded
Brush on interior hind tibia of males	5	absent	present
Apex of median lobe in dorsal view	6	wide	narrow
Shape of spermatheca	7	globular	elongate
Size of spermatheca	8	large	small

Past History of Nearctic *Bothriopterus*

From evidence of present distributions, past land bridges, past changes in flora, and probable

relations among the Nearctic *Bothriopterus*, the following past history may be postulated. First, *Bothriopterus* today forms two groups: a boreal one with *P. adstrictus*, and a temperate one with the remaining species. Second, only *P. adstrictus*, which is still very widespread in Eurasia, is closely related to Eurasian species. Third, the most diversified branches of *Bothriopterus* are found in Eurasia (Tschitschérine, 1900; Lindroth, 1945; Jedlička, 1962). These three points suggest that the area of origin of the Nearctic *Bothriopterus* is Eurasia, and that there were at least two widely separated periods of introduction of *Bothriopterus* into the Nearctic Region, one rather recent, and one or two very old. Eurasia and the Nearctic Region were united in three main periods: in the Miocene until 12 million years ago, in the late Miocene from 10 million to 3.5 million years ago, and repeatedly in the Pleistocene with the advance and retreat of the ice sheet (MacGinitie, 1958; Hopkins, 1967; Repenning, 1967).

Because *P. adstrictus* did not speciate in the Nearctic Region, I believe that it arrived during the Pleistocene (probably invading more than once, as Lindroth (1966) shows evidence of subspeciation in the Aleutians and California). Because the other Nearctic species are very different from Eurasian species, I believe they evolved here a long time ago, and may have invaded the Nearctic Region at one of the two periods of land connections during the Miocene. Because *P. oregonus* and *P. pensylvanicus* are adapted to more northerly climates (though mostly south of the boreal forest), I believe they came less than 10 million years ago when mixed and boreal forests were developing over Beringia (Wolfe and Leopold, 1967; Coope, 1968a and 1968b; Hopkins *et al.*, 1971). Thus *P. oregonus* whose ancestors were more restricted to drier and coniferous habitats, remains in the west (east of the coastal range), while the ancestors of *P. pensylvanicus* spread in the deciduous and moister forest habitats. The ancestors of *P. oregonus* are probably shared with *P. adstrictus* rather than *P. pensylvanicus* (as suggested by Lindroth *in litt.*). Also, because the remaining species are restricted to warmer climates (usually the deciduous forest biome), I believe that their ancestors came more than 12 million years ago (summarized in Fig. 13).

Probably prolonged geographical isolation was provided by natural barriers (Mayr, 1969). The barriers of greatest interest here are shifts in average temperature, and development of the ice sheets and of the prairie. I believe that the first Nearctic invader, the *P. tropicalis* and *P. mutus* group ancestor, spread widely over North America and northern Middle America. Later the originally continuous range was separated into northern and southern populations by the development of grasslands in the southern U. S. A. The southern population became what we know today as *P. tropicalis* which is restricted to high altitudes in southern Mexico. The northern population was separated into eastern and western populations with the northward development of the southern grassland. In time the western population became *P. lustrans* and the eastern one became *P. mutus* and *P. ohionis* (a more southern species than *P. mutus*). These last three species probably evolved in the Nearctic Region as no close relatives are known in Asia (Jedlička, 1962). This pattern of distribution and speciation of this first Nearctic invader is very similar to conclusions reached by Ball (1970) and Ball and Nègre (1972) about the *melanocephalus* group of the genus *Calathus*. The members of this group as those of the *tropicalis* group share similar habitat requirements and often occur together in the cool temperate regions of North America.

Past History and Behavioural Characteristics Studied in *P. adstrictus* and *P. pensylvanicus*.

The many ecological character states shared by *P. pensylvanicus* and *P. adstrictus* lead to a question about each similarity: is it plesiotypic or apotypic? If apotypic, the similarity must be the result of convergent evolution because the two taxa are not sister species. For differing character states, one may ask which of the two is plesiotypic and which is apotypic, or are both apotypic? To answer the question, data must be available on the distribution of

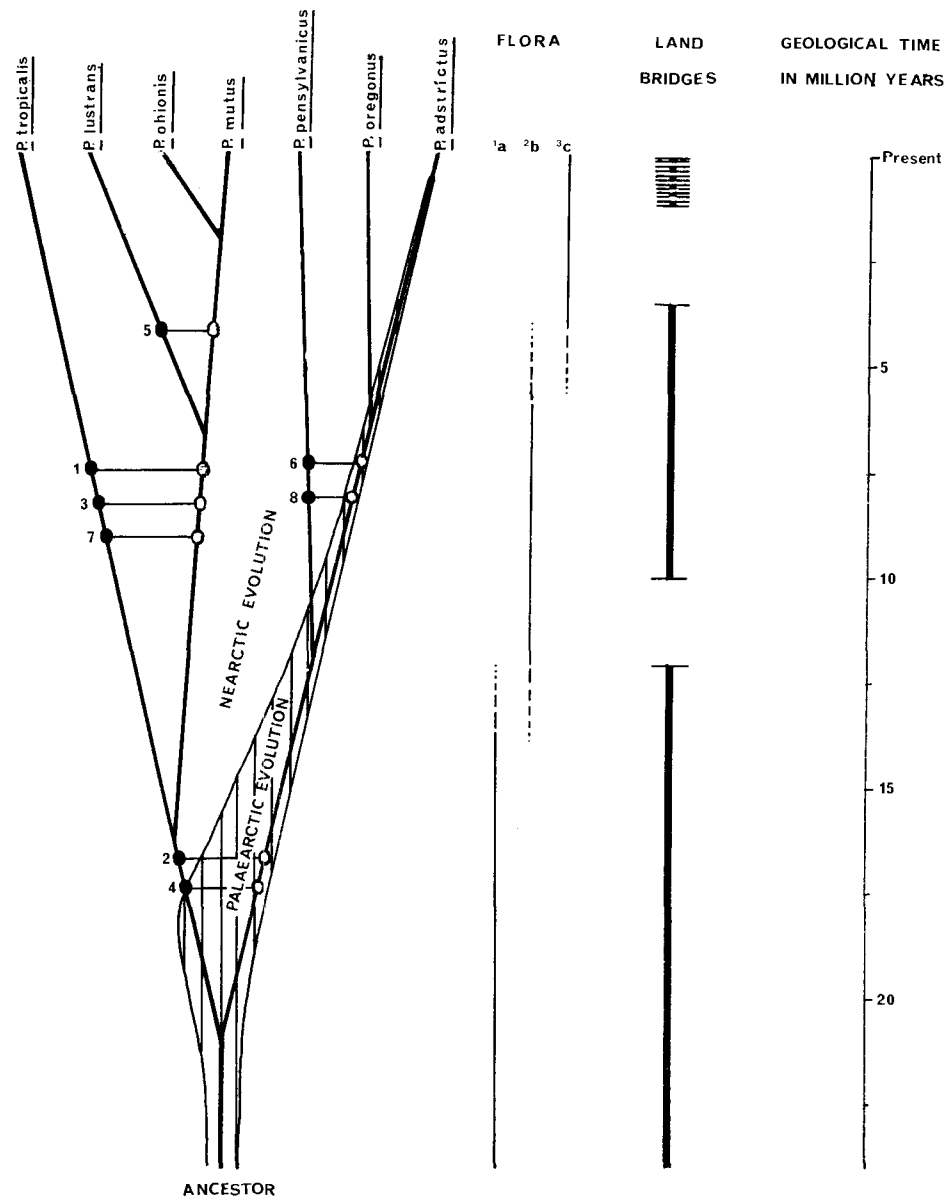


Fig. 12. Diagram of the phylogeny of the Nearctic species of *Bothriopterus* in relation to geological time, land bridges in the Beringia area, forest cover in Beringia, and time of arrival in the New World. land bridges I forest cover | plesiotypic characters ● apotypic characters ◻ 1 arcto-tertiary forest 2 coniferous forest 3 taiga.

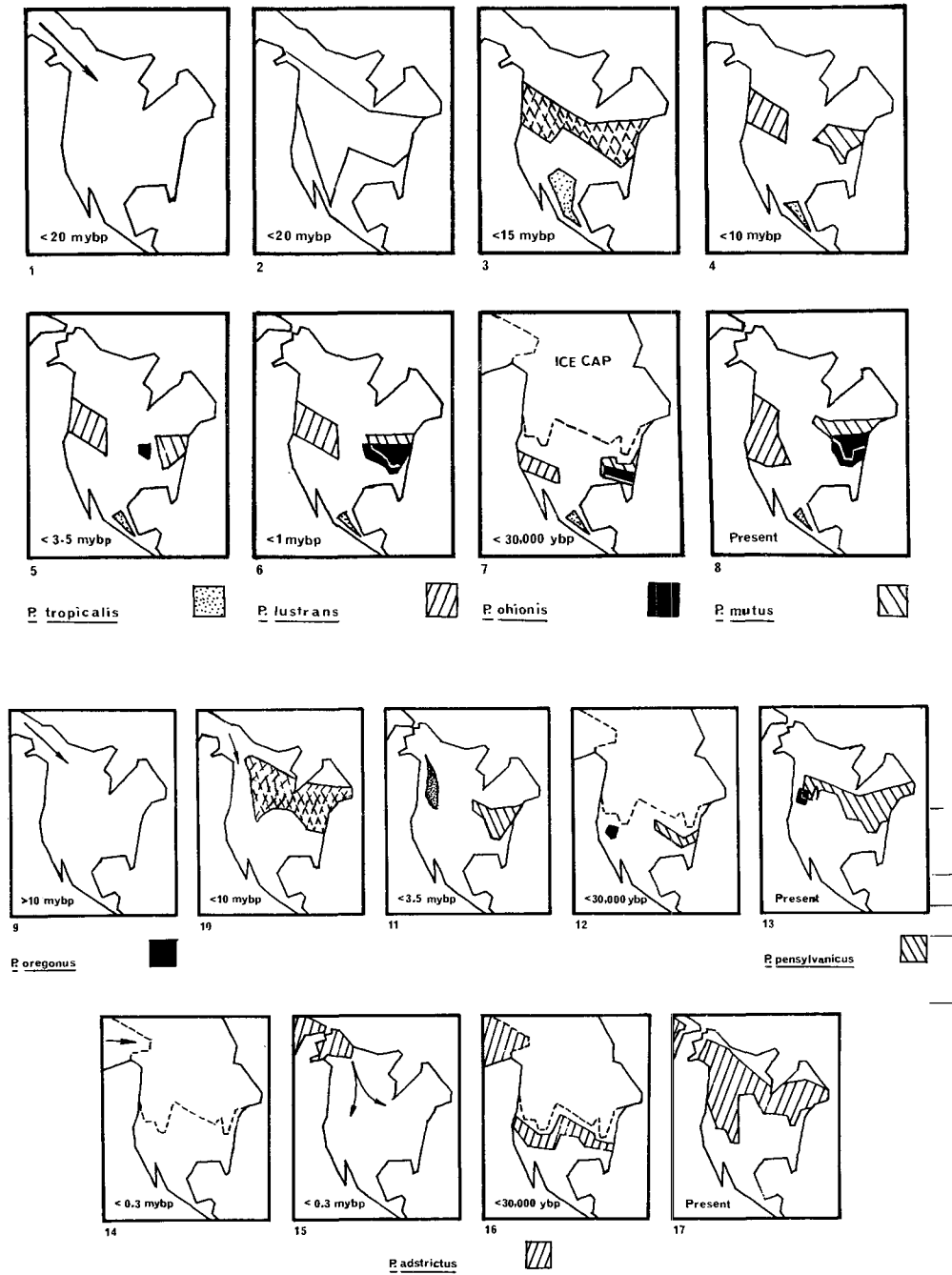


Fig. 13. Diagrammatic sequence of *Bothriopterus* evolution in the New World. Diagrams 1 to 8 represent the first invasion giving *P. tropicalis*, *P. lustrans*, *P. mutus*, and *P. ohionis*. Diagrams 9 to 13 represent the second and third invasions giving *P. oregonus* and *P. pensylvanicus*. Diagrams 14 to 17 represent the fourth invasion by *P. adstrictus*.

the character states among other species of *Bothriopterus*. At present, such data are available for geographical distribution, habitat and overwintering. The history of these characteristics only is considered further.

From the present distributions, three main groups may be seen; a boreal group, a temperate group, and a subtropical group. As the subgenus probably originated in Eurasia, a species with a southern distribution is probably older than a northern one. As climatic conditions cooled, first the warm-adapted, then the cool-adapted, and finally the cold-adapted species arrived. There was probably little or no displacement of already existing species as the invaders established themselves in the climatic zone for which they were already adapted. Thus, a northern distribution is considered apotypic with respect to a southern one. So, the distribution of *P. pensylvanicus* is considered plesiotypic relative to that of *P. adstrictus*. From knowledge of habitats of extant species (Lindroth, 1966; Ball, personal communication) the three ancestors must have been unable to withstand very dry conditions, and probably lived in open habitats quite independent of litter habitats. Thus, the litter specialization in *P. pensylvanicus* is considered apotypic, while the adaptation of *P. adstrictus* to both litter and open habitats is considered plesiotypic. As far as is known, all *Bothriopterus* in temperate regions winter mainly as adults (exceptions in *P. adstrictus* reported by Lindroth (1955) and probably the Belleville, Ontario *P. pensylvanicus* population reported by Rivard (1965)). Adult overwintering probably evolved from the ancestral habit of living in open habitats. Thus, adult overwintering in *P. adstrictus* and in the Alberta population of *P. pensylvanicus* is considered plesiotypic.

Local Adaptation Problems

Many interesting local features have been observed in *P. pensylvanicus*. Such features point out many problems that need further investigation. In eastern Canada (around Montreal) this species is found in various forest litter habitats including coniferous litter; in central Canada (Thunder Bay, Ontario), Freitag (personal communication) found that *P. pensylvanicus* is apparently restricted to coniferous litter habitats; and at George Lake it is restricted entirely to deciduous litter habitats. In Belleville, Ontario, Rivard (1965) discovered that females of *P. pensylvanicus* oviposit only in mid- and late summer, while in Montreal I suspect a spring oviposition because I have collected teneral adults only in late summer. These local observations bring a few questions. Is *P. pensylvanicus* one or more species? If it is one species, does it form isolated populations? If not, what are the patterns of the local evolutionary trends? What are the evolutionary pressures?

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