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A REVISION OF THE NEARCTIC WATER BEETLES RELATED TO *POTAMONECTES DEPRESSUS* (FABRICIUS) (COLEOPTERA: DYTISCIDAE)

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ABSTRACT

The Nearctic Dytiscidae resembling *Potamonectes depressus* (Fabricius) are revised. Types are designated as follows: a lectotype for *P. depressus* (F.), a neotype for *P. elegans* (Panzer), and a lectotype for *P. rotundatus* (LeConte). One new species, *P. macronychus,* is described.

The presence of *P. depressus* in Canada was confirmed by morphological analysis of Nearctic material, and North American specimens previously determined as *P. elegans* were shown to comprise two species, *P. rotundatus* in the east and *P. macronychus* in the west.

Based on iso-electrofocusing of whole beetle proteins, *P. rotundatus* closely resembles *P. depressus* and *P. elegans,* but has one band, focused at about pH 6.42, not found in British *P. depressus* and *P. elegans.* Experimental hybridization yielded F_1 hybrids between *P. rotundatus* and *P. elegans* and between *P. rotundatus* and *P. depressus.* In both cases the hybrids were sterile and exhibited a high level of embryonic mortality. Cross-insemination in all cases resulted in an immune response leading to discolouration of the female reproductive tract, followed by cessation of egg laying. The specific distinction between *P. rotundatus* and each of the other two species, *P. depressus* and *P. elegans,* was thus confirmed.

Two Palaearctic dytiscids, *Potamonectes depressus* (Fabricius) and *P. elegans* (Panzer), present peculiar taxonomic and evolutionary problems. As is now well known, the two forms are very distinct, and readily separable on a number of characters. Notably the aedeagus of *P. depressus* is broad and blunt-ended compared with the narrower tapering one of *P. elegans,* and the protarsal claws are longer and more hooked in *P. depressus,* while short and more evenly curved in *P. elegans.* General accounts of these beetles are given by F. Balfour-Browne (1940), Guignot (1931–1933), Zaitzev (1953) and Franciscolo (1979). Franciscolo (1979) clarified the use of the generic name *Potamonectes* Zimmermann 1921 [type species: *Dytiscus elegans* Panzer (designated by Guignot 1941)] for these species.

While both *P. depressus* and *P. elegans* have extensive ranges in which their morphological separation presents no difficulty, there are areas where the ranges of the two forms overlap and where populations morphologically intermediate

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between the two forms occur. F. Balfour-Browne (1919) gave an account of such a situation in southern Scotland, while Franck (1935) described a similar situation in northern Germany. This morphological intergradation between *P. depressus* and *P. elegans* suggests that they should not be regarded as separate species, and F. Balfour-Browne (1940) referred to them as the "*depressus-elegans* complex." As will be shown in this paper, the complex between *P. depressus* and *P. elegans* is a Palaearctic phenomenon, and is therefore not considered further here.

It has long been realised that beetles resembling *P. depressus-elegans* occur in the Nearctic. In 1863 LeConte described *Hydroporus rotundatus,* giving Toronto as the type locality. Crotch (1873) noted that *H. rotundatus* was "allied to *depressus*" (which at that time included *elegans*); Fall (1923) placed *H. rotundatus* as a synonym of *H. depressus* and described it as rare and "exclusively northern," occurring from Nova Scotia to Lake Superior.

Zimmermann (1920) used the generic name *Deronectes* and, unaware of the aedeagal differences, equated *D. rotundatus* with *D. depressus,* though he treated *D. depressus* and *D. elegans* as separate species. In a footnote on Canadian specimens in a later paper (Zimmermann 1933:168) he suggested that these specimens may be intermediate between *P. depressus* and *P. elegans* because, although the male protarsal claws are elongate and unequal, the aedeagus is of the *elegans* type. The situation was apparently clarified by J. Balfour-Browne (1948), who examined the aedeagi of 50 males and reported that all specimens from Canada and the United States were indeed *P. elegans.* He also commented on the curiously disjunct distribution of *P. elegans*—in the Palaearctic only in western Europe, but also in the Nearctic, with *P. depressus* in eastern Europe and Siberia. Zaitzev (1953) stated that *P. depressus* occurs in Canada, though he did not say the same for *P. elegans,* and he did not give the source of his information.

Larson (1975), in his review of the Dytiscidae of Alberta, established for the first time that true *P. depressus,* with the broad aedeagus, occurs in Canada, giving five localities in northern Alberta and the Mackenzie District of the Northwest Territories. He found a dividing line between the ranges of *P. depressus* and "*elegans*" (with a narrow aedeagus) at about 55–56°N, though "*elegans*" occurred at one site north of this line. Larson further commented on the much greater difference in length between the protarsal claws on *P. elegans* and those of *P. depressus,* and suggested that Zaitzev may have reversed this character. This was the first indication that Nearctic "*elegans*" was not the same as the Palaearctic form. Larson found no evidence of introgression between his two forms.

The Nearctic species of *Deronectes, sensu lato* (including *Potamonectes*) were reviewed by Zimmerman and Smith (1975), but they did not separate the true *P. depressus* from the species with narrow, tapering aedeagi.

There have been no careful comparisons of Nearctic material of *P. depressus* and "*elegans*" with Palaearctic material. It is clear that there are some anomalies, such as the male protarsal claw character, which require investigation. Such comparisons are therefore attempted here.

A starting point for the investigations has to be description and comparison of the relevant types, with lectotype and neotype designations where appropriate. It is not necessary to consider here types relating to Palaearctic forms which are considered to be junior synonyms of either *P. depressus* or *P. elegans,* but clearly these two names must be fixed by reference to type material, and the types of *H. rotundatus* must also be considered.

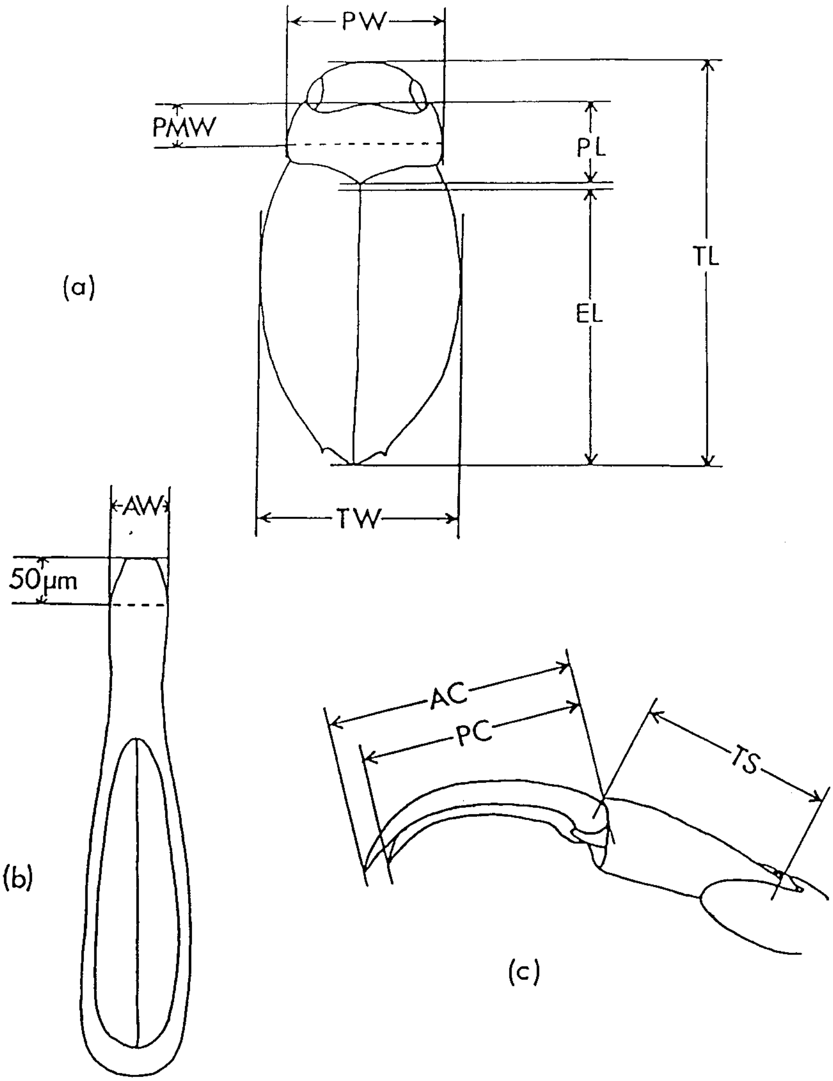

Fig. 1. Microscopic measurements. a, whole beetle measurements: EL = elytral length; PL = pronotal length; PMW = position of maximum pronotal width; PW = pronotal width; TL = total length; TW = total width. b, Aedeagus: AW = aedeagal width. c, Protarsus: AC = length of anterior claw; PC = length of posterior claw; TS = length of fifth tarsal segment.

Before these types are discussed it is necessary to give an account of the taxonomic characters used and the measurements taken. The types may then be seen in perspective. The next stage is to consider the pattern of variation shown by Nearctic material, which reveals a further species, here described as *P. macronychus,* sp. n.

Finally, experimental evidence of the taxonomic separation of *P. rotundatus* from *P. depressus* and *P. elegans* is presented. This consists of whole protein analysis by isoelectrofocusing and experimental hybridization between *P. rotundatus* from Newfoundland and English *P. elegans* and Scottish *P. depressus.*

Taxonomic Characters and Measurements

The taxonomic characters and measurements (taken using a Wild M-5 Stereomicroscope with eyepiece graticule) used in the morphological analysis are as follows:

1. Shape of Aedeagus (Figs. 4, 5, 9–18). This is the most useful single character for distinguishing *P. depressus* from other species. As a shape character it is best appreciated from the figures, but it may be expressed conveniently as the aedeagal width (AW) at a standard distance (50 μm) from the apex (Fig. 1b). It was necessary to estimate width to 0.1 of a graticule division, and in an attempt to minimize errors, adjacent graticule squares were grouped in pairs to give 21 3.58 μm width classes. The range of AW was 20 μm for the narrowest *P. elegans* to 95 μm for the widest *P. depressus.* A sample of 94 aedeagal widths, which had been measured, were checked using scanning electron microscopy, and 85% of these were placed within one width class of the measured values. After correction of a few clear experimental errors the measurements obtained by light microscopy were used throughout the study.

2. Shape of Parameres (Figs. 6, 23–34). The parameres of *P. depressus* (Figs. 23–25) are more robust than those of *P. elegans* (Fig. 26), with a larger discoid membrane. No convenient way of measuring the difference in paramere shape was found, but examination of material and reference to the illustrations permits their form to be assessed.

3. Protarsal Claws of Male. The claws of *P. depressus* are longer than those of *P. elegans,* on average 21.4% longer than the fifth tarsomere (TS) as against 15.6% longer—with the tarsomere not showing interspecific size differences. Further, the longer (anterior) claw is more hooked in *P. depressus* (Fig. 7), and more evenly curved in *P. elegans* (Fig. 8). The protarsal claws of *P. macronychus* are the longest of all (Figs. 41–44), but are not hooked as in *P. depressus.* The differences in the relative lengths of the anterior and posterior claws (AC and PC) showed no significant difference between *P. depressus* and *P. elegans.* The tarsal claws were placed perpendicular to the line of sight for measurement (Fig. 1c).

4. Body Shape. Measurements were taken (Fig. 1) with the beetle placed so that the anterior edge of the clypeus and the apex of the elytra were in the same focal plane, as were the lateral margins of the elytra at their widest point. The following body shape parameters were determined and analyzed: total length (TL), total width (TW), TW/TL, elytral length (EL), EL/TL, pronotal length (PL), pronotal width (PW) PL/PW, PW/TW, position of pronotal maximum width (PMW), and PMW/PL.

5. Elytral Colour. It is traditional (*e.g.,* F. Balfour-Browne 1940) to regard *P. depressus* as darker than *P. elegans,* but both forms are too variable for the colour to be useful. This is particularly true of the extent to which the black markings are developed. Both *P. depressus* and *P. elegans* have the elytra varying from almost entirely black to pale yellow with the black marks very reduced. This variation occurs in populations geographically far removed from the zones of sympatry of the two forms. There is thus no basis for using colour in analyzing the Nearctic species.

Type Material and Species Description

1. *Potamonectes depressus* (Fabricius)
(Figs. 4, 6, 7)

Dytiscus depressus Fabricius 1775, Systema Entomologiae, p. 233, no. 20. Type locality: Sweden.

Type Material. The Fabrician collection, in the Zoological Museum, Copenhagen, contains two syntypes of *D. depressus*, both agreeing with Fabricius's description, with the label "*depressus*" in Fabricius's handwriting. Both specimens (1 ♂, 1 ♀) have been remounted on cards. The male is here designated lectotype. The aedeagophore has been dissected out and is mounted on the card with the specimen.

Lectotype ♂: *Dytiscus depressus* Fabricius. *Measurements:* TL: 5.21 mm, TW: 2.58 mm. Oblong-oval, convex, TW/TL = 0.49; PMW behind middle of pronotum; ground colour mainly ferruginous, with piceous to black markings; venter ferruginous; all surfaces densely punctate, with coarse punctures; dorsum weakly shining.

Head: Posterior margin of frons narrowly black; antennae ferruginous; terminal segment of each maxillary palpus strongly infuscate apically.

Pronotum: Broadly rounded laterally, with obtusely rounded hind angles; lateral margins with narrow bead, partly visible on hind margin; PL/PW = 0.44; PW/TW = 0.87; PMW = 0.57 (behind middle of pronotum); disc coarsely granulate, with coarse and fine punctures; anterior margin broadly black; posterior margin narrowly black and contiguous with a pair of large black spots on posterior half of disc on either side of midline.

Elytra: EL/TL = 0.71; slightly rounded laterally; apical angles slightly drawn out; lateral margin with small, acute, subapical tooth; disc with at least 2 weak linear rows of larger punctures; basal and sutural margins and 7 or 8 longitudinal vittae broad, black or piceous, extensively coalescing, and with interruptions forming 5 small pale areas; lateral margin pale, narrow and contiguous with 3 of these pale areas.

Legs: Ferruginous; segments 1–3 of protarsus dilated, setose ventrally; anterior protarsal claw elongate and broadened, 0.33 mm long, parallel-sided for basal two-thirds and strongly curved in apical third, 12.5% longer than posterior claw and 18% longer than apical protarsal segment (Fig. 7); posterior claw narrower and more evenly curved.

Genitalia: Apex of aedeagus in dorsal view expanded and spatulate, with greatest width 90 μm (Fig. 4); maximum width of middle portion 18% of length; in side view tapered and decreasingly curved till apical fifth, then sinuate; parameres strongly sclerotized and rectangular, with discoid membrane large and nearly circular (Fig. 6), and with its basal margin transverse.

Remarks. The form of the aedeagus, parameres and protarsal claws are all distinctive, and confirm the validity of the current concept of *P. depressus.*

2. *Potamonectes elegans* (Panzer)
(Figs. 5, 8)

Dytiscus elegans Panzer 1794, Fauna Insectorum Germaniae initia, vol. 1 (24), p. 5. Type locality: Germany.

Type Material. Panzer gave "Germania" as the type locality for *D. elegans,* and said that the material described and figured by him came from the collection of D. H. Schneider of Stralsund. Stralsund is on the Baltic coast, within the known range of *P. depressus,* and at least 150 km NE of the nearest localities with *P. elegans* as currently understood. However, Panzer's figure of *D. elegans* is clearly unlike specimens of *P. depressus* from Vilm, near Stralsund, so that

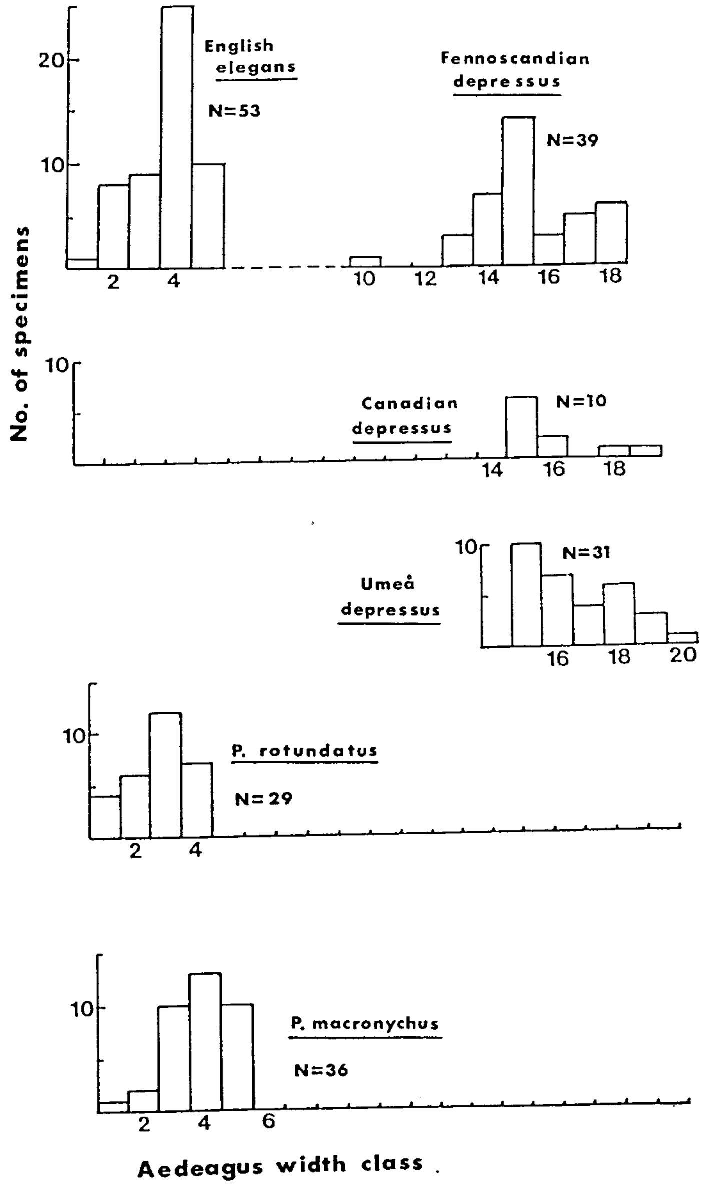

Fig. 2. Histograms of aedeagus width classes in *Potamonectes elegans, P. depressus, P. rotundatus* and *P. macronychus*. For explanation of the aedeagus width classes, see text.

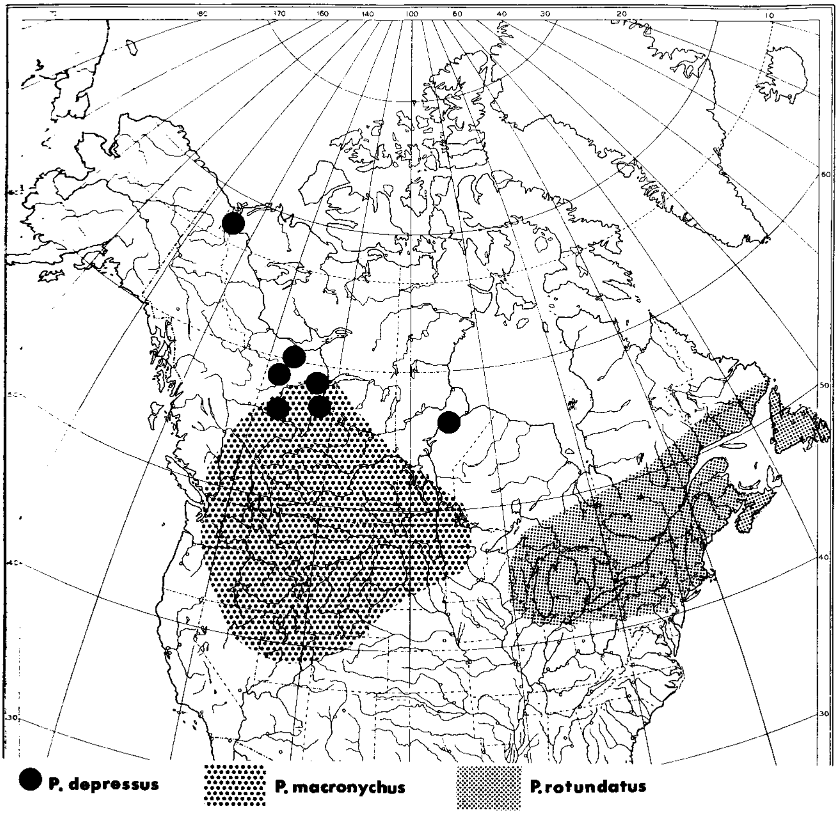

Fig. 3. Map showing the distributions of *Potamonectes depressus* (Nearctic range only), *P. rotundatus* and *P. macronychus.*

it is unlikely that Schneider's material came from Stralsund. There is no record of Schneider's collection since it was auctioned in Stralsund in 1828 (Horn and Kahle 1935–1937).

Most of Panzer's types are in the Natural History Museum, Humboldt University, Berlin. They are included in the museum's "Historical Series," but are not labelled specifically as Panzer's material. The *P. elegans* in the Historical Series are listed in the museum's old catalogues under the number 10111 as "Europa, 10 specimens" (M. Uhlig, curator, in litt.). A "type series" of 10 specimens was sent by Dr Uhlig. All had been remounted on cards and bear Franck's determination labels. The six males in the series have the aedeagi mounted separately, but lack the parameres. The specimens are as follows:

a. Two males and two females bearing the number 10111. The first specimen of this series (a female) has a label in Illiger's handwriting "*Depressus* St., *Dyt, depressus* Pk. Fab. *D. elegans* Pz. Pr.*", outlined in black and with the "St." a later addition in a different hand. It also bears the label "*elegans* Sturm". The other three specimens are labelled "Europa".

b. Two males from Munich, one bearing the label "*brevis* Sturm. Monach." in Sturm's handwriting.

Table 1. Measurements of typical *Potamonectes depressus* (Sweden, Finland, European USSR) and *P. elegans* (S. England). For measurements and ratios the data are: mean ± standard error, sample size, and observed range; for *t*-tests: *t*-value, degrees of freedom, and probability. For explanation of measurements and abbreviations, see text and Figure 1.

Character	Males		
	P. depressus	*P. elegans*	Student's *t*-test
AW (μm)	74.0 ± 1.1 (37) (53.2–82.6)	31.0 ± 0.6 (53) (22.0–36.7)	40.92 (88) $P < 0.0001$
TL (mm)	4.89 ± 0.03 (38) (4.44–5.16)	4.62 ± 0.02 (63) (4.14–4.89)	8.230 (99) $P < 0.001$
TW (mm)	2.38 ± 0.02 (38) (2.11–2.63)	2.38 ± 0.02 (64) (2.10–2.58)	0.0133 (100) N.S.
TW/TL	0.485 ± 0.002 (36) (0.461–0.513)	0.514–0.001 (63) (0.494–0.535)	12.35 (97) $P < 0.001$
EL/TL	0.691 ± 0.002 (38) (0.671–0.718)	0.671 ± 0.001 (63) (0.648–0.700)	8.761 (99) $P < 0.001$
PL/PW	0.464 ± 0.003 (42) (0.415–0.504)	0.476 ± 0.002 (66) (0.452–0.511)	4.380 (106) $P < 0.001$
PMW/PL	0.585 ± 0.006 (42) (0.504–0.714)	0.511 ± 0.005 (66) (0.423–0.607)	9.408 (106) $P < 0.001$
PW/TW	0.850 ± 0.004 (38) (0.801–0.899)	0.829 ± 0.002 (64) (0.786–0.864)	5.525 (100) $P < 0.001$
AC (μm)	301 ± 2 (38) (264–330)	261 ± 2 (63) (235–284)	15.63 (99) $P < 0.001$
AC/PC	1.064 ± 0.003 (37) (1.024–1.113)	1.074 ± 0.003 (63) (1.029–1.128)	2.306 (98) $P < 0.05$
AC/TS	1.214 ± 0.011 (35) (1.111–1.370)	1.156 ± 0.008 (62) (1.062–1.333)	4.260 (95) $P < 0.001$

c. Two males from the Harz mountains, one with the label "*elegans* Ill. Harz".

d. Two males bearing the label "Gallia bor.".

The specimens of greatest relevance are the four bearing the number 10111, though as none can be attributed with any certainty to Panzer, there is insufficient evidence to regard them as syntypes. However, they are almost certainly from Germany (the "Pr" on Illiger's label means Prussia), and they have the characteristic blotchy appearance illustrated by Panzer (1794). This blotchiness of the elytral pattern is a local variation within the range of pattern shown by *P. elegans* as currently interpreted. The best course of action seems to be that proposed by M. Uhlig (in litt.), *i.e.*, the designation of one of these specimens as neotype. Both males have their aedeagi (though not the parameres) available, and as the darker of the two is less damaged, it is here designated neotype.

Neotype ♂: *Dytiscus elegans* Panzer. *Measurements:* TL: 4.65 mm, TW: 2.38 mm. Oblong-oval, convex, TW/TL = 0.51; lateral margins of pronotum and elytra sharply discontinuous; PMW anterior to middle of pronotum; ground colour mainly ochraceous, with piceous to black markings; venter testaceous; all surfaces densely punctate, with medium punctures; dorsum weakly shining.

Table 1. Extended.

Females		
P. depressus	*P. elegans*	Student's *t*-test
4.74 ± 0.02 (48) (4.39–5.02)	4.56 ± 0.02 (30) (4.35–4.78)	6.192 (76) $P < 0.001$
2.46 ± 0.02 (47) (2.25–2.68)	2.44 ± 0.02 (30) (2.27–2.60)	1.154 (75) N.S.
0.509 ± 0.002 (47) (0.492–0.537)	0.534 ± 0.002 (30) (0.516–0.556)	9.399 (75) $P < 0.001$
0.700 ± 0.002 (46) (0.674–0.719)	0.690 ± 0.002 (30) (0.666–0.712)	4.057 (74) $P < 0.001$
0.470 ± 0.002 (47) (0.444–0.498)	0.479 ± 0.002 (30) (0.461–0.505)	3.394 (75) $P < 0.002$
0.492 ± 0.006 (47) (0.366–0.571)	0.394 ± 0.007 (30) (0.310–0.464)	10.89 (75) $P < 0.001$
0.792 ± 0.002 (45) (0.765–0.821)	0.781 ± 0.003 (30) (0.752–0.828)	3.113 (73) $P < 0.01$
167 ± 2 (49) (143–189)	158 ± 1 (30) (141–178)	4.048 (77) $P < 0.001$
0.801 ± 0.007 (49) (0.700–0.901)	0.795 ± 0.009 (30) (0.667–0.882)	0.5321 (77) N.S.

Head: Posterior margin of frons narrowly infuscate; antennae ochraceous; terminal segment of each maxillary palpus somewhat infuscate apically.

Pronotum: Broadly rounded laterally, hind angles obtusely rounded; lateral bead very narrow; PL/PW = 0.49; PW/TW = 0.83; PMW = 0.46 (anterior to middle of pronotum); disc granulate, with coarse and fine punctures; anterior margin narrowly infuscate; posterior margin narrowly black and contiguous with pair of small piceous spots on posterior third of disc on either side of midline.

Elytra: EL/TL = 0.67; strongly rounded laterally; lateral margin with small, acute, subapical tooth; disc with 2 weak linear rows of larger punctures; sutural margin and 7 or 8 longitudinal vittae narrow, piceous, slightly coalescing and with interruptions forming 6 pale areas including the apex; lateral margin pale, broad, and contiguous with 4 of these areas.

Legs: Ochraceous to ferruginous; terminal tarsal segments infuscate apically; segments 1–3 of protarsus dilated, setose ventrally; anterior protarsal claw somewhat elongate and broadened, 0.24 mm long, evenly and strongly arcuate from base to apex, 6% longer than posterior claw and 10% longer than fifth protarsal segment (Fig. 8); posterior protarsal claw slightly narrower.

Genitalia: Aedeagus in dorsal view evenly tapered to acute, narrowly rounded apex (Fig. 5); maximum width of middle portion 15% of length; in side view tapered and decreasingly curved to apex, except for middle third of dorsum which is flattened; (parameres not available).

REMARKS. The shapes of the aedeagus and protarsal claws and all other features of this specimen are in accordance with the current concept of *P. elegans.*

3. *Potamonectes rotundatus* (LeConte)
(Figs. 13, 38)

Hydroporus rotundatus LeConte 1863, Smithsonian Miscellaneous Collections 167, p. 21. Type locality: Toronto, Ontario, Canada.

TYPE MATERIAL. LeConte's collection, in the Museum of Comparative Zoology, Harvard University, contains three specimens (2 ♂♂, 1 ♀) standing as syntypes of *H. rotundatus.* One of the males had been dissected and mounted on a card with its genitalia. It bears the labels "Can." and "*rotundatus* 3". It is here designated lectotype.

LECTOTYPE ♂: *Hydroporus rotundatus* LeConte. *Measurements:* TL: 4.96 mm, TW: 2.55 mm. Oblong-oval, convex, TW/TL = 0.51; lateral margins of pronotum and elytra sharply discontinuous; PMW behind middle of pronotum; ground colour mainly ferruginous, with piceous to black markings; venter ferruginous; all surfaces densely punctate; head and pronotum somewhat dull, elytra more shining.

Head: Posterior margin of frons very narrowly black; antennae ochraceous, each segment slightly darkened apically; terminal segment of each maxillary palpus slightly infuscate.

Pronotum: Broadly rounded laterally, hind angles obtusely rounded; lateral margins with narrow bead; PL/PW = 0.46; PW/TW = 0.85; PMW = 0.56 (behind middle of pronotum); disc granulate, with coarse and fine punctures; anterior margin broadly piceous; posterior margin narrowly black and contiguous with a pair of piceous spots on posterior half of disc on either side of midline.

Elytra: EL/TL = 0.7; rounded laterally; lateral margins with small acute subapical tooth; disc with 2 weak linear rows of larger punctures; sutural margin and 7 or 8 longitudinal vittae black, extensively coalescing, and with interruptions forming 6 pale areas including the apex; lateral margins pale, narrow and contiguous with 4 of these areas.

Legs: Ferruginous; segments 1–3 of protarsus dilated, setose ventrally; anterior protarsal claw elongate and broadened, 0.27 mm long, evenly but not strongly arcuate from base to apex, ending in a fine point, 15% longer than posterior claw and 12% longer than fifth protarsal segment (Fig. 38); posterior protarsal claw narrower and more strongly arcuate.

Genitalia: Aedeagus in dorsal view evenly tapered to acute, narrowly rounded apex, with maximum width of middle portion 13% of length (Fig. 13); in side view tapered and decreasingly curved to apex; parameres lightly sclerotized and tapering apically, the discoid membrane small and with basal margin oblique.

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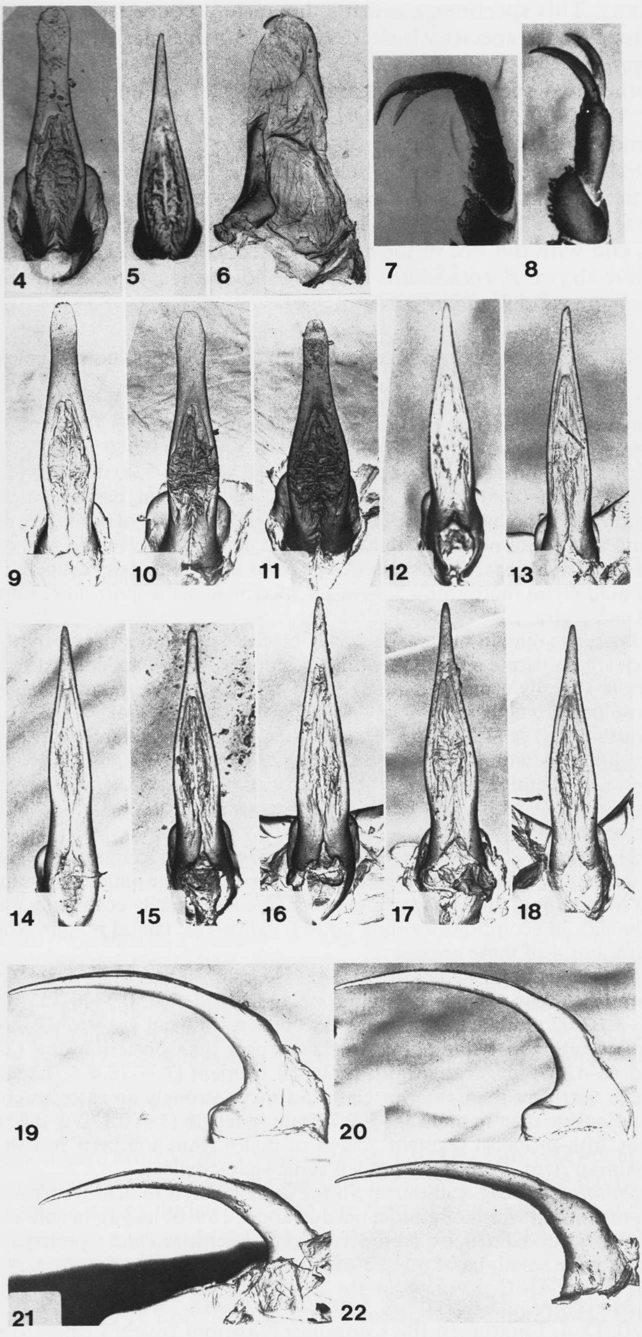
Figs. 4–22. Scanning electron micrographs of aedeagi (4, 5, 9–18 in dorsal view; 19–22 in profile), paramere (6) and protarsi (7, 8), *Potamonectes* spp. 4, *P. depressus,* lectotype. 5, *P. elegans,* neotype. 6, *P. depressus,* lectotype, inner face. 7, *P. depressus,* lectotype. 8, *P. elegans,* neotype. 9, *P. depressus,* R. Vindel, Åmsele, Sweden. 10, *P. depressus,* Gillam, Manitoba. 11, *P. depressus,* Hay R., Northwest Territories. 12, *P. elegans,* R. Wey, Tilford, Surrey, England. 13, *P. rotundatus,* lectotype. 14, *P. rotundatus,* Thunder R., Quebec. 15, *P. rotundatus,* Topsail Beach, Newfoundland. 16, *P. macronychus,* holotype. 17, *P. macronychus,* Green L., Saskatchewan. 18, *P. macronychus,* Winnipeg, Manitoba. 19, *P. rotundatus,* Montreal, Quebec. 20, *P. rotundatus,* Thunder R., Quebec. 21, *P. macronychus,* Winnipeg, Manitoba. 22, *P. macronychus,* Salmon Arm, British Columbia. Scale = 0.5 mm.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REMARKS. This specimen confirms the current concept of *P. rotundatus* in that it belongs to the species which, in eastern North America, has been referred to *P. elegans.*

The other two specimens are paralectotypes. The female bears the labels "Can.", "Type 6002" (on red) and "*H. rotundatus* LeC.". The male is labelled "Can." and "*rotundatus* 2". Both specimens are *P. rotundatus.*

Detailed morphological assessment of *P. rotundatus* is given in the analysis of Nearctic material, but the lectotype may be seen to resemble *P. elegans* in the general form of the aedeagus and protarsal claws, to be rather large and elongate, and with the PMW too far back (see Table 1). Hybridization experiments have shown *P. rotundatus* to be a good species, reproductively isolated from *P. elegans* and *P. depressus.*

4. *Potamonectes macronychus* Shirt and Angus, **new species**
(Figs. 16–18, 21, 22, 32–34, 41–44)

Measurements: Males (n = 144) TL 4.77–5.56 mm ($\bar{x}$ = 5.23 ± 0.02 mm), TW 2.38–2.88 mm ($\bar{x}$ = 2.67 ± 0.01 mm), TW/TL 0.481–0.546 ($\bar{x}$ = 0.510 ± 0.001); females (n = 164) TL 4.57–5.52 mm ($\bar{x}$ = 5.05 ± 0.02 mm), TW 2.35–3.00 mm ($\bar{x}$ = 2.69 ± 0.01 mm), TW/TL 0.504–0.556 ($\bar{x}$ = 0.531 ± 0.001). Oblong-oval, convex; lateral margins of pronotum and elytra sharply discontinuous; maximum width of pronotum near middle in male, and anterior to middle in female; ground colour testaceous to pale rufous, with piceous to black markings; all surfaces densely and finely punctate; head and pronotum somewhat dull, elytra more shining; younger specimens with short, fine, white setae on pronotum and elytra.

Head: Posterior margin of frons narrowly black or piceous; antennae with 5–7 distal segments clearly infuscate apically; terminal segment of each maxillary palpus infuscate.

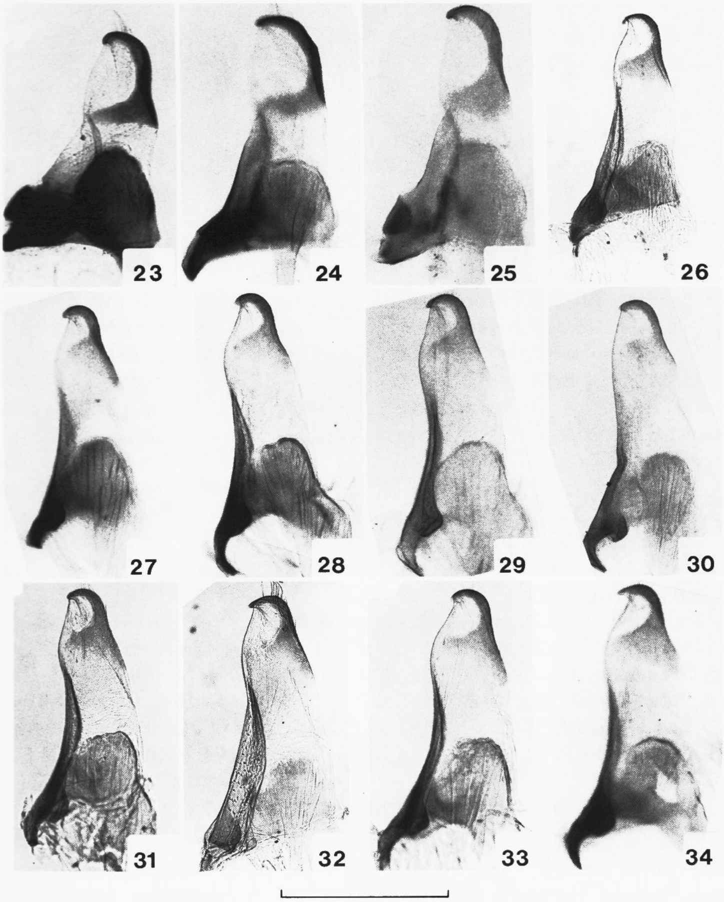
Pronotum: Broadly rounded laterally, hind angles obtusely rounded; lateral margins with narrow bead; length in mid line 44–50% of width in male, 45–57% in female; greatest width 80–87% of TW in male, 73–81% in female; greatest width 40–60% of median length from anterior margin in male, 25–50% in female; disc granulate, with coarse and fine punctures; anterior margin black or piceous; posterior margin narrowly black and contiguous with a pair of black or piceous spots on posterior third of disc on either side of midline.

Elytra: Length 62–72% of TL; convex laterally; lateral margin with small, acute, subapical tooth; disc with at least 2 weak linear rows of larger punctures; sutural margin and 7 or 8 longitudinal vittae narrow, black or piceous, usually coalescing only slightly, and usually with interruptions forming up to 6 pale areas; lateral margin pale and contiguous with 3 or 4 of these areas.

Legs: Testaceous to ferruginous; segments 1–3 of protarsus dilated, setose ventrally; anterior protarsal claw of male very elongate and broadened, 0.33–0.46 mm in length ($\bar{x}$ = 0.413 ± 0.002 mm), flattened in cross-section, evenly but not strongly arcuate from base to apex, ending in a fine point, 16–54% longer than posterior claw ($\bar{x}$ = 32.4 ± 0.7%), and 43–120% longer than fifth protarsal segment ($\bar{x}$ = 75.4 ± 1.1%); posterior claw of male narrower than anterior claw and more strongly arcuate; anterior claw of female less elongate than in male, 0.15–0.21 mm in length ($\bar{x}$ = 0.170 ± 0.001 mm) and shorter than fifth protarsal segment. Claws of males from southern British Columbia (Atbara, Salmon Arm, Vernon, Wynndel) somewhat smaller.

Male genitalia: Aedeagus in dorsal view evenly tapered to acute, narrowly rounded apex, with maximum width of middle portion about 16% of length; in side view tapered and decreasingly curved to apex; parameres lightly sclerotized and tapering apically, and discoid membrane small, basal margin oblique.

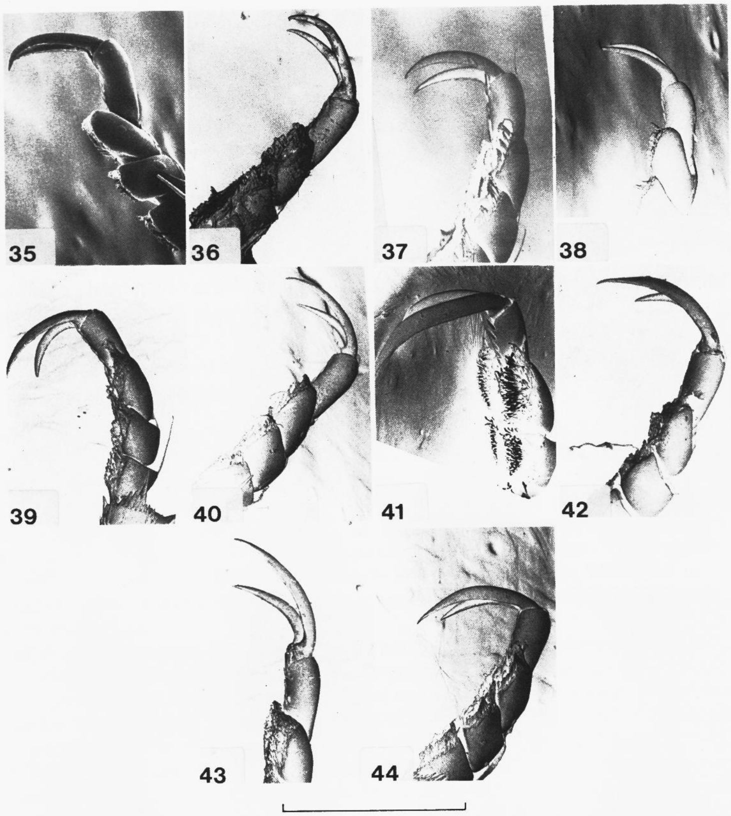
TYPE MATERIAL. Holotype ♂: Canada, Alberta, 3.5 miles N. Champion, 25.vi.1970, D. J. Larson. In the Canadian National Insect Collection, Ottawa.



Figs. 23–34. Parameres, *Potamonectes* spp. 23–25, *P. depressus* from: 23, Gulf of Bothnia, Umeå, Sweden. 24, Gillam, Manitoba. 25, Hay R., Northwest Territories. 26, *P. elegans,* R. Teme, Bucknell, Salop, England. 27–31, *P. rotundatus* from: 27, St John's, Newfoundland. 28, Natick, Massachusetts. 29, Montreal, Quebec. 30, Thunder R., Quebec. 31, Isle de Montréal, Quebec. 32–34, *P. macronychus,* paratypes from: 32, Hays, Montana. 33, Green L., Saskatchewan. 34, Crazy Woman Ck, Wyoming. Scale = 0.5 mm.

Paratypes. There are 269 paratypes (119 ♂♂, 150 ♀♀). This is fewer specimens than were mentioned above under measurements because those from southern British Columbia are excluded (because their small protarsal claws suggest that they may belong to a separate taxon) and material from near Winnipeg is also excluded as it may be transitional to *P. rotundatus.*

The collections holding the paratypes are as follows: BMNH—British Museum (Natural History), London; CNIC—Canadian National Insect Collection, Biosystematics Research Centre, Ottawa; CAS—California Academy of Sci-



Figs. 35–44. Scanning electron micrographs of protarsi, *Potamonectes* spp. 35, *P. depressus,* Gulf of Bothnia, Umeå, Sweden. 36, *P. depressus,* Indian Cabins, Alberta. 37, *P. elegans,* Stanton Harcourt, Oxford, England. 38, *P. rotundatus,* lectotype. 39, *P. rotundatus,* Isle de Montréal, Quebec. 40, *P. rotundatus,* Thunder R., Quebec. 41, *P. macronychus,* holotype. 42, 43, *P. macronychus,* paratypes; 42, Green L., Saskatchewan and 43, Hayes, Montana. 44, *P. macronychus,* Salmon Arm, British Columbia. Scale = 0.5 mm.

ences, San Francisco; DJL—Dr David Larson, Memorial University, St John's Newfoundland; and UA—University of Alberta, Edmonton.

Paratypes: CANADA. **British Columbia:** Beaver Dam L., Clinton distr; 11.x.1943; Leach & Morgan—3 ♂♂, 7 ♀♀ (CAS). Summit L., 32 miles N. Prince George; 26.vi.1944; J. Munro—1 ♂ (CAS). L. Windermere; 18.ix.1928; Owen Bryant—3 ♂♂ (CAS). **Alberta:** 20 miles W. Acme; 4.vi.1970; D. & M. Larson—1 ♂, 3 ♀♀ (UA). Jct Bulls Head Ck & Rte 1, 1.5 miles E. Medicine Hat; 21.v.1970; Larson—3 ♂♂, 7 ♀♀ (UA). Calgary; 16.x & 23.x.1927; O. Bryant—4 ♂♂, 4 ♀♀ (CAS); 1 ♂ (UA). Calgary; 20.ix.1966; R. Madge—1 ♀ (BMNH). Castor; ix.1920; F. S. Carr—1 ♂ (UA). 3.5 miles N. Champion; 25.vi.1970; D. J. Larson—4 ♂♂, 9 ♀♀ (CNIC); 1 ♂, 1 ♀ (UA). Delia; 23. & 26.viii.1926; N. Criddle—2 ♂♂, 1 ♀ (CNIC). Edmonton; 29.viii.1919, 29.vii.1922, 5.viii.1922, 30.ix.1922; F. S.

Carr—2 ♂♂, 2 ♀♀ (UA); 2 ♂♂, 2 ♀♀ (CNIC). Edmonton; 10.i.1956; D. Beckman—1 ♀ (UA). Edmonton; 30.ix.1956; A. J. Nicholson—1 ♂ (UA). Edmonton, Sturgeon R.; 13.vii.1922—2 ♀♀ (UA). Edmonton, Sturgeon R.; 30.ix.1922; F. S. Carr—1 ♀ (UA). Etzicome Ck, 3 miles E Stirling; 23.v.1971; (?) Larson—1 ♂, 2 ♀♀ (UA). Fickle L.; 9.viii.1971; D. & M. Larson—8 ♂♂, 3 ♀♀ (DJL); 8 ♂♂, 2 ♀♀ (UA). 2.5 miles N. Fox Ck; 8.vii.1970; D. & M. Larson—2 ♂♂, 6 ♀♀ (UA). Ghost Pine Ck, W. Three Hills; 24.v.1970; Larson—1 ♀ (UA). High Prairie; 22.vii.1961; A. R. Brooks—3 ♂♂, 1 ♀ (CNIC). 10 miles S. Lethbridge; 8.v.1970; D. J. Larson—1 ♀ (UA). Little Bow R., 5 miles S. Travers Dam; 24.ix.1970; D. Larson—3 ♂♂, 2 ♀♀ (UA). L. McGregor; 22.viii.1923; D. & M. Larson—4 ♂♂, 7 ♀♀ (UA). Medicine Hat; 27.iii. & 14.iv.1923; F. S. Carr—3 ♂♂, 1 ♀ (UA). 8 miles S.W. New Dayton; 13.v.1971; D. J. Larson—11 ♂♂, 15 ♀♀ (UA). Prairie R., nr. L. Claire; 6.viii.1972; D. Donald—6 ♂♂, 9 ♀♀ (UA). Hwy 2, 2 miles W. Red Deer; 3.v.1970; D. & M. Larson—1 ♀ (UA). Valleyview; 10.vii.1961; A. R. Brooks—1 ♀ (CNIC). Waterton N. P., Jct Chief Mtn Hwy & Belly R.; 7.vii.1971; D. & M. Larson—1 ♀ (UA). **Saskatchewan:** Asquith; 26.v.1940; A. R. Brooks—5 ♂♂, 10 ♀♀ (CNIC). Big River; 1.vi.1959; A. & J. Brooks—1 ♀ (CNIC). Blackstrap L.; 14.xii.1975; D. Larson—1 ♂ (DJL). Burgis; 6.vi.1959; Brooks-Wallis—1 ♀ (CNIC). Candle L.; 19.?viii.1959; A. & J. Brooks—1 ♀ (CNIC). Cookson; 4.vi.1959; A. R. Brooks—1 ♂, 5 ♀♀ (CNIC). Cut Knife; 5.vi. & 27.viii.1940; A. R. Brooks—1 ♂, 5 ♀♀ (CNIC). Elbow; 3. & 5.vi.1960; A. R. Brooks—1 ♂, 1 ♀ (CNIC). Glaslyn; 21.v.1959; A. R. Brooks—6 ♂♂, 3 ♀♀ (CNIC). Green L.; 3.vii.1959; A. R. Brooks—2 ♂♂, 1 ♀ (CNIC). Hudson Bay; 6.ix.1958; A. & J. Brooks—1 ♀ (CNIC). Lumsden; 12.vii.1958; A. & J. Brooks—4 ♂♂, 6 ♀♀ (CNIC). Prince Albert; 23.vii.1959; A. & J. Brooks—1 ♂ (CNIC). Swift Current; 14.ix.1940; A. R. Brooks—1 ♂, 1 ♀ (CNIC). **Manitoba:** Dauphin; 17.viii.1958; A. & J. Brooks—1 ♂, 3 ♀♀ (CNIC). Horton; 28.vii.1958; A. & J. Brooks—1 ♂, 1 ♀ (CNIC). Mafeking; 3.ix.1959; A. & J. Brooks—1 ♀ (CNIC). Mile 214, HBR; 6.vii.1917; J. B. Wallis—3 ♂♂, 2 ♀♀ (CNIC). Piquitenay; 28.vii.1917; Leech Coll.;—1 ♂ (CAS).

UNITED STATES. **Montana:** Blaine Co., 12 miles S. Hays, Rte 376(?); 27.ix.1971; D. R. Whitehead—1 ♂ (UA). **Wyoming:** Johnson Co., S. Fork of Crazy Woman Ck; 26.vii.1964; H. B. Leech—3 ♂♂, 7 ♀♀ (CAS). Natrona Co., Middle Casper Ck, Hwy 20, 2.5 miles S.E. Natrona; 20.viii.1965; H. B. Leech—1 ♂, 1 ♀ (CAS). Sweetwater Co., Little Sandy R., 0.5 miles S. Farson, 6567′; 22.viii.1965; H. B. Leech—5 ♂♂, 5 ♀♀ (CAS). Uinta Co., Trib. of Muddy Ck, Hwy 80, 8.3 miles W. Ft Bridger; 23.viii.1965; F. O. Leech—1 ♂ (CAS). **Utah:** Midway, Provo R. Survey; 7.vii.1947; A. R. Gantin; Chandler Coll.—1 ♂ (CAS).

Potamonectes macronychus is a western species. It is rather larger and on the whole paler than *P. rotundatus,* from which it is very clearly distinguished by the very long protarsal claws of the male.

Morphological Analysis

1. Typical *Potamonectes depressus* and *P. elegans*

Populations of *P. depressus* from Fennoscandia and European Russia are considered typical of that form, as they are geographically well away from any *P. elegans.* Populations of *P. elegans* from southern England (from Warwickshire southwards) have been chosen as typical *P. elegans*: the form is well studied in this area, which is far removed from any *P. depressus.* Table 1 gives the results obtained from these populations. They show that, apart from details

Table 2. Measurements of European and Canadian *Potamonectes depressus*. For clarification of data, see caption to Table 1.

Character	Males		
	Europe	Canada	Student's *t*-test
AW (μm)	74.0 ± 1.1 (37) (53.2–82.6)	75.4 ± 1.8 (9) (71.6–88.1)	0.6644 (44) N.S.
TL (mm)	4.89 ± 0.03 (38) (4.44–5.16)	5.14 ± 0.04 (20) (4.81–5.36)	5.177 (56) $P < 0.001$
TW (mm)	2.38 ± 0.02 (38) (2.11–2.63)	2.59 ± 0.02 (20) (2.43–2.75)	7.328 (56) $P < 0.001$
TW/TL	0.485 ± 0.002 (36) (0.461–0.513)	0.503 ± 0.003 (20) (0.484–0.519)	5.128 (54) $P < 0.001$
EL/TL	0.691 ± 0.002 (38) (0.671–0.718)	0.713 ± 0.001 (20) (0.699–0.724)	7.891 (56) $P < 0.001$
PL/PW	0.464 ± 0.003 (42) (0.415–0.504)	0.458 ± 0.003 (21) (0.430–0.487)	1.475 (61) N.S.
PMW/PL	0.585 ± 0.006 (42) (0.504–0.714)	0.555 ± 0.007 (21) (0.478–0.605)	3.057 (61) $P < 0.001$
PW/TW	0.850 ± 0.004 (38) (0.801–0.899)	0.819 ± 0.003 (20) (0.800–0.845)	5.702 (56) $P < 0.001$
AC (μm)	301 ± 2 (38) (264–330)	305 ± 4 (21) (275–341)	0.7964 (57) N.S.
AC/PC	1.064 ± 0.003 (37) (1.024–1.113)	1.101 ± 0.009 (21) (1.038–1.125)	4.509 (56) $P < 0.001$
AC/TS	1.214 ± 0.011 (35) (1.111–1.370)	1.210 ± 0.014 (21) 1.134–1.388)	0.1800 (54) N.S.

of the male genitalia and protarsal claws, only features of the pronotal shape give any separation of the two taxa. These data show the range of variation in the two taxa where they exist allopatrically. Analysis of populations from the British area of sympatry, where there is clear evidence of introgression, is given by Shirt (1983).

2. Nearctic Material

Mounted material totalling 63 *Potamonectes depressus* and 647 "*elegans*" (*P. rotundatus* and *P. macronychus*) has been examined, and full measurements taken from 48 *P. depressus,* 126 *P. rotundatus* and 314 *P. macronychus* among this material. Scanning electron micrographs were taken of selected aedeagi and protarsal claws, while selected parameres were mounted on slides and photographed. It was soon apparent that while Canadian *P. depressus* were conspecific with Palaearctic material, the Nearctic "*elegans*" were not only different from true *P. elegans,* but comprised two distinct species, *P. rotundatus* and *P. macronychus.*

A. *POTAMONECTES DEPRESSUS.* Measurements of *P. depressus* from Canada are compared with those of Fennoscandian specimens in Table 2. The two most important characters, aedeagus width and length of male anterior protarsal claw, show no significant difference. Canadian beetles are, however, significantly longer than European ones, and have proportionately greater widths,

Table 2. Extended.

Females		
Europe	Canada	Student's t-test
4.74 ± 0.02 (48) (4.39–5.02)	5.01 ± 0.02 (26) (4.68–5.29)	8.132 (72) $P < 0.001$
2.46 ± 0.02 (47) (2.25–2.68)	2.61 ± 0.02 (25) (2.36–2.77)	6.472 (70) $P < 0.001$
0.509 ± 0.002 (47) (0.492–0.537)	0.520 ± 0.002 (25) (0.496–0.536)	3.938 (70) $P < 0.001$
0.700 ± 0.002 (46) (0.674–0.719)	0.707 ± 0.002 (26) (0.690–0.729)	2.901 (70) $P < 0.01$
0.458 ± 0.002 (47) (0.444–0.498)	0.458 ± 0.002 (27) (0.438–0.475)	4.343 (72) $P < 0.001$
0.492 ± 0.006 (47) (0.366–0.571)	0.502 ± 0.007 (27) (0.404–0.600)	1.057 (72) N.S.
0.792 ± 0.002 (45) (0.765–0.821)	0.782 ± 0.002 (25) (0.761–0.806)	3.015 (68) $P < 0.01$
167 ± 2 (49) (143–189)	169 ± 2 (26) (147–195)	0.4800 (73) N.S.
0.801 ± 0.007 (49) (0.700–0.901)	0.776 ± 0.011 (26) (0.654–0.882)	1.995 (73) N.S.

longer elytra and narrower pronota. Also, the mean difference in male protarsal claw length is 10.1% in Canada, compared with 6.4% in Europe. However, these differences are slight, and fall within the range of variation of European *P. depressus*. In general appearance, Canadian *P. depressus* resemble European specimens, but tend to have less extensive dark markings. They are also somewhat larger and wider. In these respects they resemble specimens from the Swedish Gulf of Bothnia. The size distribution of aedeagus width (Fig. 2) is skewed over width classes 15–19, and in this respect Canadian material further resembles the Bothnia (Umeå) population (Fig. 2).

Aedeagi (Figs. 9–11), male protarsus (Fig. 36) and parameres (Figs. 23–25) all closely resemble those of typical *P. depressus* from northern Europe.

B. *Potamonectes rotundatas* and *P. macronychus*. From their general appearance these two species are evidently close relatives of *P. depressus* and *P. elegans*. The eastern *P. rotundatus* resembles European *P. depressus* in its size and darker colouring, while the western *P. macronychus* is the largest member of the group, resembling a large, pale *P. elegans*. *Potamonectes rotundatus* differs from *P. macronychus* in all respects except EL/TL and PW/TW, though in most specimens the difference in size is the most obvious character (Tables 3, 4). Similarly, both *P. rotundatus* and *P. macronychus* differ from *P. elegans* in all characters except PL/PW of *P. rotundatus*, and AW of *P. macronychus*.

Table 3. Measurements of S. English *Potamonectes elegans* and Nearctic *P. rotundatus* and *P. macronychus*. For clarification of data, see caption to Table 1.

Character	Males		
	P. elegans	*P. rotundatus*	*P. macronychus*
AW (μm)	31.0 ± 0.6 (52) (23.9–36.7)	27.3 ± 0.7 (29) (20.2–33.0)	31.2 ± 0.6 (36) (22.0–36.7)
TL (mm)	4.62 ± 0.02 (63) (4.14–4.89)	4.89 ± 0.02 (64) (4.48–5.31)	5.23 ± 0.02 (146) (4.77–5.56)
TW (mm)	2.38 ± 0.02 (64) (2.10–2.58)	2.48 ± 0.02 (64) (2.26–2.64)	2.67 ± 0.01 (144) (2.38–2.88)
TW/TL	0.514 ± 0.001 (63) (0.494–0.535)	0.506 ± 0.001 (64) (0.485–0.522)	0.510 ± 0.001 (144) (0.481–0.546)
EL/TL	0.671 ± 0.001 (63) (0.648–0.700)	0.695 ± 0.002 (64) (0.673–0.732)	0.695 ± 0.001 (146) (0.624–0.719)
PL/PW	0.476 ± 0.002 (66) (0.452–0.511)	0.473 ± 0.002 (61) (0.455–0.507)	0.466 ± 0.001 (147) (0.438–0.502)
PMW/PL	0.511 ± 0.005 (66) (0.423–0.607)	0.504 ± 0.005 (61) (0.417–0.588)	0.491 ± 0.003 (147) (0.401–0.604)
PL/TW	0.829 ± 0.002 (64) (0.786–0.864)	0.838 ± 0.002 (61) (0.797–0.871)	0.837 ± 0.001 (144) (0.796–0.871)
AC (μm)	261 ± 2 (63) (235–284)	292 ± 4 (62) (255–371)	402 ± 2 (145) (310–464)
AC/PC	1.074 ± 0.003 (63) (1.029–1.128)	1.150 ± 0.008 (26) (1.034–1.331)	1.311 ± 0.007 (144) (1.131–1.544)
AC/TS	1.156 ± 0.008 (62) (1.062–1.333)	1.267 ± 0.014 (62) (1.065–1.578)	1.704 ± 0.014 (145) (1.278–2.195)

Distribution of aedeagus width (Fig. 2) was similar to populations in Europe. The slightly greater width in *P. macronychus* compared with *P. rotundatus* may be related to its greater overall size. However, the aedeagus of the American forms differs from that of *P. elegans* in other aspects which are difficult to measure, appearing somewhat longer in *P. macronychus* and relatively narrower overall in *P. rotundatus* (Figs. 13–18). The flattened dorsal area of the aedeagus is generally less marked in *P. rotundatus* and *P. macronychus* than it is in *P. elegans* (Figs. 19–22).

The most distinctive character is the form of the male anterior protarsal claw in both *P. rotundatus* and *P. macronychus,* these being uniformly but not strongly arcuate, with the apex extended into a fine point, more finely tapered than in *P. elegans* (Figs. 37–44). Specimens of *P. macronychus* from part of southern British Columbia (Atbara, Salmon Arm, Vernon and Wynndel) have smaller claws than other populations of this species, although they are geographically far removed from *P. rotundatus.* It is not clear whether they represent a separate subspecies, and more work, involving more extensive collection of material and breeding experiments, is desirable. We are ascribing these specimens tentatively to *P. macronychus,* but have excluded them from the type series.

Comparison of the British Columbia specimens with typical *P. macronychus* is given by modifying the claw-based part of Table 3, as follows:

Table 3. Extended.

Females		
P. elegans	*P. rotundatus*	*P. macronychus*
4.56 ± 0.02 (30) (4.35–4.78)	4.80 ± 0.02 (62) (4.46–5.20)	5.06 ± 0.02 (166) (4.57–5.52)
2.44 ± 0.02 (30) (2.27–2.60)	2.52 ± 0.02 (62) (2.27–2.82)	2.69 ± 0.01 (165) (2.35–3.00)
0.534 ± 0.002 (30) (0.516–0.556)	0.523 ± 0.001 (62) (0.503–0.548)	0.531 ± 0.001 (164) (0.504–0.556)
0.690 ± 0.002 (30) (0.666–0.712)	0.694 ± 0.001 (62) (0.669–0.725)	0.696 ± 0.001 (164) (0.668–0.718)
0.479 ± 0.002 (30) (0.461–0.505)	0.479 ± 0.002 (62) (0.443–0.511)	0.481 ± 0.001 (166) (0.450–0.573)
0.394 ± 0.007 (30) (0.310–0.464)	0.405 ± 0.005 (62) (0.288–0.495)	0.378 ± 0.003 (167) (0.250–0.500)
0.781 ± 0.003 (30) (0.752–0.828)	0.784 ± 0.002 (62) (0.757–0.833)	0.772 ± 0.001 (164) (0.731–0.811)
158 ± 1 (30) (141–178)	153 ± 1 (59) (130–171)	170 ± 1 (165) (147–211)
0.795 ± 0.009 (30) (0.667 ± 0.882)	0.768 ± 0.007 (59) (0.640–0.880)	0.788 ± 0.005 (165) (0.641–0.964)

	P. macronychus (southern B.C.)	*P. macronychus* (typical)
n	23	121
AC (μm)	347 ± 2 (310–373)	413 ± 2 (330–464)
AC/PC	1.245 ± 0.014 (1.131–1.360)	1.326 ± 0.007 (1.157–1.544)
AC/TS	1.461 ± 0.024 (1.278–1.741)	1.754 ± 0.111 (1.429–2.195)

The claws of *P. rotundatus* are closer in length to those of European *P. depressus* than to those of *P. elegans*, but in *P. macronychus* they are much longer than either (mean length greater than 400 μm).

The greatest differences are seen when comparing the two protarsal claws with one another [mean excess of anterior over posterior = 7.4% (*P. elegans*), 15% (*P. rotundatus*) and 32.4% (*P. macronychus*)] and when comparing the anterior claw with the fifth protarsal segment [mean excess of claw over segment = 15.6% (*P. elegans*), 27.7% (*P. rotundatus*) and 75.4% (*P. macronychus*)] (Figs. 38–44).

Table 4. Statistical analysis of measurements and ratios of English *Potamonectes elegans* and Nearctic *P. rotundatus* and *P. macronychus*. For *t*-tests the data are: *t*-value, degrees of freedom and probability; for Anova (One-way Analysis of Variance) tests: *F*-value, degrees of freedom and whether the differences are significant (S.) or not (N.S.) at the 5% level (Student-Newman-Keul's Multiple Comparison Test). Asterisks (*): variances of all three samples significantly different.

	Males				
		Anova			
Character	Student's *t*-test *rotundatus*/*macronychus*	*F*	df	*elegans*/*rotundatus*	*elegans*/*macronychus*
AW	4.211 (63) $P \leq 0.001$	11.68	114	S.	N.S.
TL	13.29 (208) $P \leq 0.001$	334.1	270	S.	S.
TW	13.37 (206) $P \leq 0.001$	242.4	269	S.	S.
TW/TL	2.823 (206) $P \leq 0.01$	10.15	268	S.	S.
EL/TL	0.028 (208) N.S.	104.6	270	S.	S.
PL/PW	3.697 (206) $P \leq 0.001$	18.38	271	N.S.	S.
PMW/PL	2.512 (206) $P \leq 0.02$	8.201	271	N.S.	S.
PW/TW	0.540 (203) N.S.	6.739	266	S.	S.
AC	23.82 (205) $P \leq 0.001$	740.8*	267	S.	S.
AC/PC	14.39 (204) $P \leq 0.001$	330.1*	266	S.	S.
AC/TS	18.62 (205) $P \leq 0.001$	427.3*	266	S.	S.

Two *P. rotundatus* males from Mountain Lake, Michigan [Van Dyke Coll., 22.vi.1911 (CAS)] have somewhat mixed characters (intermediate TL and TW but PL/PW of *P. rotundatus*), and one of them has the largest claws seen in *P. rotundatus* (AC = 371 μm, AC/TS = 1.578). Conversely, two of the three *P. macronychus* males from near Winnipeg, Manitoba [J. B. Wallis, 10.ix.1911 and 2.ix.1916 (CNIC)] had TL, TW and PL/PW of *P. rotundatus*. Though one of them also had intermediate protarsal claws (AC = 330 μm), all three had the AC/TS ratio of *P. macronychus* (1.522 or greater). These two cases may be forms transitional between *P. rotundatus* and *P. macronychus* in the Michigan–Manitoba area, but we have seen hardly any material from this region.

The heavily sclerotized area in the centre of the paramere has a more oblique outline basally in most *P. rotundatus* than is usual in *P. elegans*, while the paramere of *P. macronychus* is noticeably broader than those of either *P. rotundatus* or *P. elegans* (Figs. 26–34).

As with *P. depressus* and *P. elegans*, females of *P. rotundatus* and *P. macronychus* are more difficult to separate. Although Table 4 shows a number of statistically significant differences, the data in Table 3 show that the measurements and ratios all exhibit a considerable overlap between the two species.

3. Distribution (Fig. 3)

Potamonectes depressus appears to be confined to Canada north of 55°N, though we have seen material from only seven sites. Three of these sites in northern Alberta and two in the Mackenzie District of the Northwest Territories are listed by Larson (1975). One site, Aklavik (68°25′N), is only a short distance from the Beaufort Sea [*cf.* the European limit of 69°N (Shirt 1983)]. In addition,

Table 4. Extended.

Females				
	Anova			
Student's *t*-test *rotundatus/macronychus*	*F*	df	*elegans/ rotundatus*	*elegans/ macro-nychus*
9.006 (226) $P \leq 0.001$	115.2*	255	S.	S.
10.10 (225) $P \leq 0.001$	98.31*	254	S.	S.
5.008 (224) $P \leq 0.001$	16.65	253	S.	N.S.
1.269 (224) N.S.	5.083	253	N.S.	S.
1.072 (226) N.S.	0.704	255	N.S.	N.S.
4.226 (227) $P \leq 0.001$	9.716	256	N.S.	N.S.
5.484 (224) $P \leq 0.001$	15.81	253	N.S.	S.
9.705 (222) $P \leq 0.001$	56.00*	251	S.	S.
2.323 (222) $P \leq 0.05$	3.402	251	N.S.	N.S.

there is a single male *P. depressus* among a series of *P. macronychus* taken in Prairie River, Lake Claire, Alberta [D. Donald, 6.viii.1983 (UA)], yet there appear to be no intermediate forms from this site. A lone male *P. depressus* from Gillam, Manitoba [W. J. Brown, 19.vii.1950 (CNIC)] extends the distribution of this species to Hudson's Bay, and supports Larson's (1975) suggestion that it is "perhaps . . . widely distributed in the boreal portions of the New World."

Fall (1923) gave the range of *P. rotundatus* as "Nova Scotia to Lake Superior." We have also seen specimens from southeastern Canada (southeastern Ontario, southern and eastern Quebec, Newfoundland) and northeastern United States (Massachusetts, Connecticut, New York), and Biström (1978) adds southeastern Labrador. The reference by Wallis (1973) to "Minnesota - Brandon" appears to be an error for Brandon, Manitoba, which is in *P. macronychus* territory.

Potamonectes macronychus is widespread in Canada from British Columbia to Manitoba, south of 56°N. There is a population at 56°N in the Prairie River, Lake Claire, Alberta, which is well within the range of *P. depressus* (see above). The southern limit is reached at Midway, Utah, at 40°N. We have also seen material from Montana and Wyoming. Hatch (1953) adds northeastern Washington and northern Idaho, and Larson (1975) gives North Dakota. Hatch's inclusion of western Oregon may rest on a specimen supposedly from Eugene [B. Malkin, 2.viii.1941 (CAS)]; Leech has added the note "probably England," and we concur with this as the specimen is *P. elegans.*

As already noted, specimens from southern British Columbia have smaller tarsal claws than other *P. macronychus,* and we feel that their taxonomic status requires clarification.

Some individuals in Michigan and Manitoba may show intermediate characteristics (transitional to *P. rotundatus*), but there is unfortunately very little material available from this area, and no conclusions may be reached at this time.

Experimental Analysis

A series of living *P. rotundatus* adults from near St John's, Newfoundland, was sent by Dr D. J. Larson in November 1980. This material was used in investigations of the breeding biology and immature stages, for protein analysis by iso-electrofocusing, and for experimental hybridization with *P. elegans* and *P. depressus.*

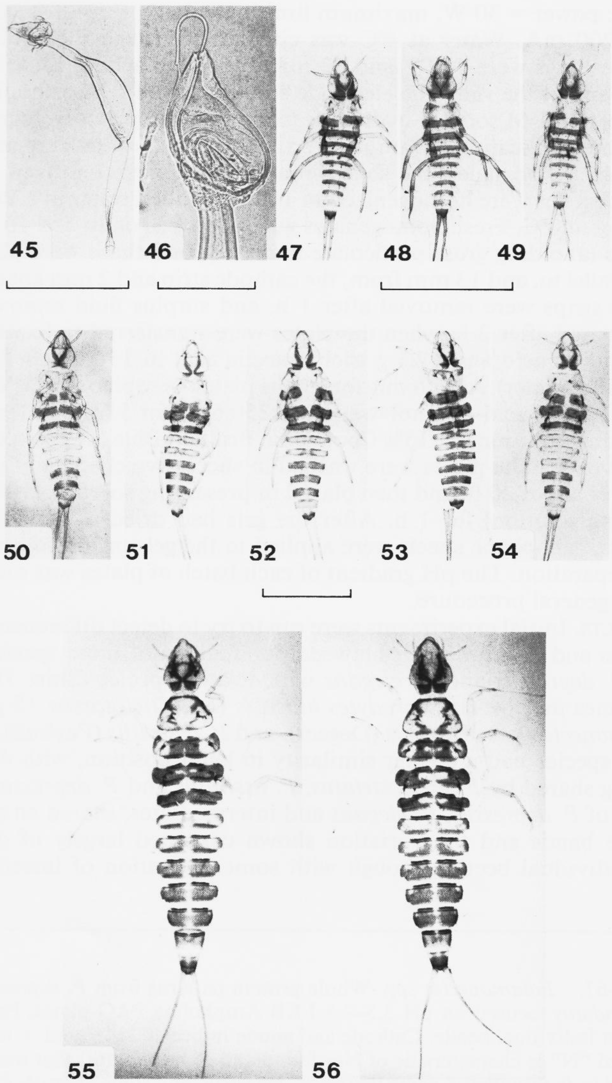
1. Breeding Biology

Burmeister (1976) showed that in the Hydroporinae there is a fertilization tract which is separate from the female genital (ovipositional) tract: there is a bursa copulatrix from which a spermathecal duct runs to the spermatheca, with the system completed by a fertilization duct running from the spermatheca to the oviduct. Angus (1985) showed that in *Potamonectes* the bursa copulatrix is small, and the spermathecal duct very long, leading to the small bilobed spermatheca. The fertilization tract and spermatheca of Swedish *P. depressus* (Angus 1985, Figs. 30, 33) are similar to those of *P. rotundatus, P. macronychus* and *P. elegans.* Mating in *P. rotundatus, P. depressus* and *P. elegans* involves a spermatophore (Figs. 45, 46), the head of which is inserted into the bursa copulatrix, and from which a thin filament is inserted into the spermathecal duct. About half the body of the spermatophore lies within the female, but the tail section and part of the wider body protrudes backwards beyond the end of the abdomen. The spermatophores of *P. rotundatus, P. depressus* and *P. elegans* appear identical. Females may carry the spermatophore for several hours, though it may be shed at once, especially in unsuccessful matings (Shirt 1983). Eggs of all the species are encased in a gelatinous envelope and attached to underwater objects such as vegetation or the sides of the aquaria. The eggs hatch in about 10 days at 20°C. There are three larval instars, and the larvae of the species are very similar to one another (Figs. 47–56). The dark elements of the colour pattern in Newfoundland *P. rotundatus* are more extensive than in some English *P. elegans,* but as the colour pattern of *P. elegans* is very variable (Shirt 1983) this may also be so in *P. rotundatus.* Our rearing experiments gave only 3 F_1 *P. rotundatus,* and, as with laboratory-reared *P. depressus* and *P. elegans,* these were slightly smaller than the norm for wild material.

2. Iso-electric Focusing of Proteins

A. Methods. Iso-electric focusing (electrofocusing) is a refinement of conventional electrophoresis in which the sample is run on a gel plate with a pH gradient. Proteins migrate until they reach a point on the plate where the pH is such that the proteins have no net electrical charge. This is the isoelectric point, and proteins in this system focus at their isoelectric points, giving a series of clearly defined bands on the plate.

Electrofocusing was carried out on an LKB 2117 Multophor apparatus (LKB-Produkter, Sweden), using an LKB 2103 Power Supply. The standard procedure recommended by Winter *et al.* (1977) was followed. LKB 1804-101 Ampholine® wide-range plates were used. The running conditions for whole



Figs. 45–56. *Potamonectes* spp. Figs. 45, 46, *P. rotundatus,* spermatophores, St John's, Newfoundland. 46, head showing filament. Figs. 47–49, first instar larvae. 47, 48, *P. rotundatus,* St John's, Newfoundland. 49, F_1 hybrid, *P. elegans* (R. Wey, Tilford, Surrey, England) × *P. rotundatus* (St John's, Newfoundland). Figs. 50–54, second instar larvae. 50, *P. elegans,* R. Wey, Tilford, Surrey, England. 51–53, *P. rotundatus* (St John's, Newfoundland). 54, F_1 hybrid, *P. elegans* (Tilford) × *P. rotundatus* (St John's). Figs. 55, 56, third instar larvae, *P. rotundatus,* St John's, Newfoundland. Scales = 1 mm except Fig. 46 = 0.2 mm.

plates were: power = 30 W, maximum limiting voltage = 1,400 V, maximum current = 200 mA. Water at 4°C was circulated through the cooling plate. Typically readings were 400 V and 83 mA initially, reaching 1,400 V and 13 mA by the end of the run. The electrode solutions were 1 M orthophosphoric acid (anode) and 1 M sodium hydroxide (cathode), and plates were pre-run for 15 min before application of samples. Active, healthy beetles were selected for electrofocusing. For males, the aedeagi and protarsi were removed and kept, then whole beetles were homogenized in 100 μl distilled water in a Potter-type homogenizer at 0°C. Fresh homogenates were adsorbed on to 5 × 10 mm filter paper strips (avoiding gross particulate material), and these were placed with the side parallel to, and 13 mm from, the cathode strip and 2 mm apart. Sample application strips were removed after 1 h, and surplus fluid removed. Runs were terminated after 2 h, when the plates were transferred to fixative (17.25 g sulphosalicylic acid and 57.5 g trichloracetic acid in 150 ml methanol and 350 ml distilled water). After fixing for 1 h the plates were placed in a "destaining solution" of acetic acid–ethanol–water (80:250:670) for 5 min, followed by 10 min in staining solution (0.115% Coomassie Brilliant Blue R-250 in destaining solution) at 60°C. The plates were washed in successive changes of destaining solution over about 20 h, and then placed in preserving solution (10% glycerol in destaining solution) for 1 h. After the gels had dried overnight at room temperature, cellophane sheets were applied to the gel surface to make a permanent preparation. The pH gradient of each batch of plates was measured as part of the general procedure.

B. Results. Initial experiments were run to try to detect differences between *P. depressus* and *P. elegans*, or between populations of these species, and to compare *P. depressus* and *P. elegans* with related species (Shirt 1983). The related species used were: *Scarodytes halensis* (F.), *Stictotarsus 12-pustulatus* (F.), *Potamonectes griseostriatus* (Degeer), and *P. assimilis* (Paykull). The *Potamonectes* species had a greater similarity in band position, with 43–51% of bands being shared by *P. griseostriatus, P. assimilis* and *P. depressus-elegans.* Specimens of *P. depressus, P. elegans* and intermediates, shared an average of 70% of the bands and the variation shown consisted largely of differences between individual beetles, though with some indication of interpopulation

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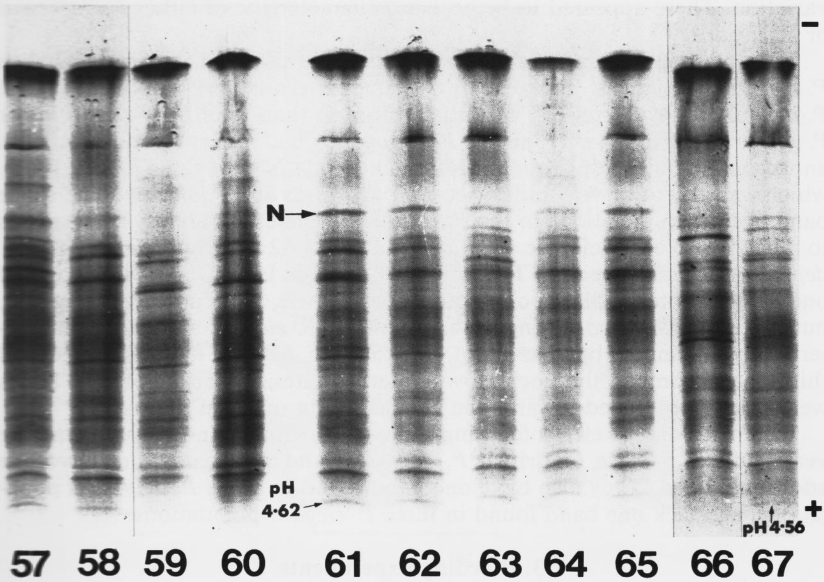
Figs. 57–67. *Potamonectes* spp. Whole protein patterns from *P. depressus-elegans* and *P. rotundatus* focused on pH 3.5–9.5 LKB Ampholine PAG-plates. Each column represents an individual beetle. Cathode and anode indicated by − and + respectively. Band marked "N" is characteristic of Newfoundland *P. rotundatus*; that marked at pH 4.62 is found in *P. rotundatus,* some British *P. depressus,* and some Scottish *P. depressus-elegans* intermediates; band at pH 4.56 has been found in some English and Scottish *P. elegans* and some Scottish *P. depressus-elegans* intermediates, but not in Newfoundland *P. rotundatus.*

Figs. 57, 58. *Potamonectes rotundatus,* Newfoundland, females. 59, 60, *P. elegans,* Stanton Harcourt, Oxford, England, females. 61–65, *P. rotundatus,* Newfoundland, males. 66, *P. depressus-elegans* intermediate, Loch Howie, Kirkcudbright, Scotland, female. 67, *P. elegans,* Stanton Harcourt, male.

Figs. 68–70. Spermatozoa, heads stained with aceto-lactic orcein, tails shown by phase contrast. 68, *P. rotundatus,* Newfoundland. 69, F_1 hybrid, *P. elegans* (R. Wey, Tilford, Surrey, England) × *P. rotundatus* (St John's, Newfoundland). 70, F_1 hybrid, *P. rotundatus* (St John's) × *P. depressus* (Loch Urr, Dumfriesshire, Scotland). Note feeble "double" tails of hybrid spermatozoa. Scale = 20 μm.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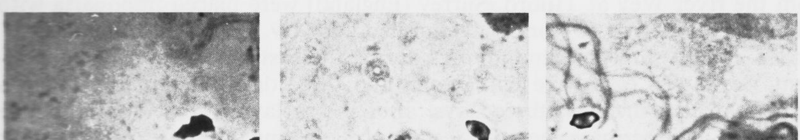
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variation. There appeared to be no band characteristic of either *P. depressus* or *P. elegans.*

Eight male and seven female *P. rotundatus* were analyzed, with some English *P. elegans* as controls. The general banding pattern is very similar to that of *P. depressus* and *P. elegans,* and much more so than to either *P. assimilis* or *P. griseostriatus.* However, all the *P. rotundatus* had a very strong band with an isoelectric point at pH about 6.41–6.43 (band "N" in Figs. 57, 58, 61–65), which was absent or very indistinct in *P. depressus* and *P. elegans.* The single band nearest to the anode in the *P. rotundatus* plates apparently corresponds to a band with an isoelectric point at about pH 4.62 found in some British *P. depressus* (Rydal Water and Talkin Tarn, Cumbria; Loch Doon, Ayrshire) and one Scottish intermediate population (Loch Howie, Kirkcudbright) (Fig. 66), but lacking in *P. elegans.* English and Scottish *P. elegans* are usually characterized by an anodal band at about pH 4.56 (Fig. 67) and there is evidence of this band in some of the Loch Howie intermediates. Unfortunately the bands were poorly developed towards the anodal end in many of the runs.

In conclusion, the electrofocusing bands of Newfoundland *P. rotundatus* are very similar to those of British *P. depressus* and *P. elegans,* but have one additional band. They also have one band found in some *P. depressus* populations, and lack one band found in three *P. elegans* populations.

3. Breeding Experiments

A. *Potamonectes elegans* × *P. rotundatus.* Two wild female *P. elegans* from the river Wey at Tilford, Surrey (England) were placed in aquaria with wild male *P. rotundatus* from Newfoundland on 9.iv.1981. Tilford female "1" carried at least three spermatophores during the first nine days of the experiment. Seventeen eggs were laid in the first three days after mating, then a further three in the next three days, after which laying ceased. The female carried the last spermatophore for the abnormally long time of three days, after which it was pulled out, but broke, leaving the apex *in situ.* The female was then killed and dissected. It was found that the filament of the spermatophore was correctly lodged in the spermatothecal duct but was surrounded by an abnormal brown stain.

Cleavage commenced in all the eggs, but stopped at an early stage in 15 of them. Seven embryos reached the hatching stage, but three were grossly tera-

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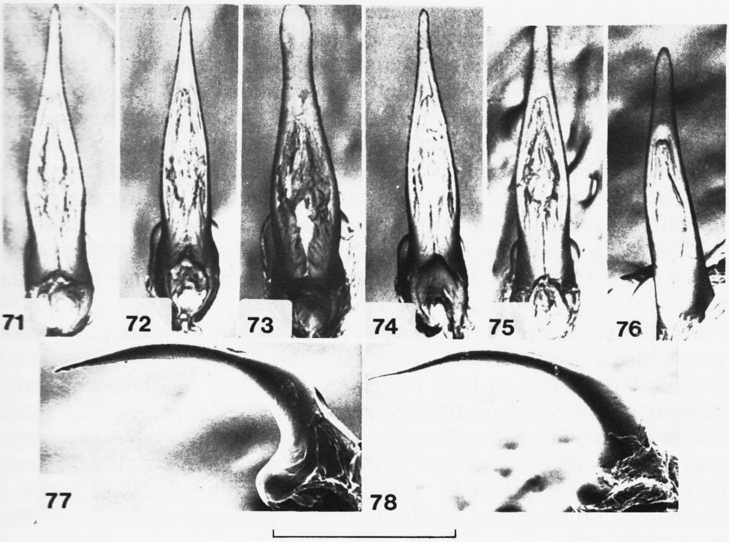
Figs. 71–76. Scanning electron micrographs of aedeagi (dorsal view), *Potamonectes* spp. and hybrids. 71, *P. rotundatus,* St John's, Newfoundland. 72, *P. elegans,* R. Wey, Tilford, Surrey, England. 73, *P. depressus,* Loch Urr, Dumfriesshire, Scotland. 74, F_1 hybrid *P. elegans* (R. Wey, female 2) × *P. rotundatus* (St John's). 75, 76, F_1 hybrids, *P. rotundatus* (St John's) × *P. depressus* (Loch Urr).

Figs. 77, 78. Scanning electron micrographs of aedeagi (lateral view) of F_1 hybrids. 77, *P. elegans* (R. Wey, female 2) × *P. rotundatus* (St John's). 78, *P. rotundatus* (St John's) × *P. depressus* (Loch Urr).

Figs. 79–82. Parameres of F_1 hybrids. 79, 80, *P. elegans* (R. Wey, female 2) × *P. rotundatus* (St John's); 81, *P. elegans* (R. Wey, female 1) × *P. rotundatus* (St John's). 82, *P. rotundatus* (St John's) × *P. depressus* (Loch Urr).

Figs. 83–86. Scanning electron micrographs of protarsi of F_1 hybrids. 83, *P. elegans* (R. Wey, female 1) × *P. rotundatus* (St John's). 84, *P. elegans* (R. Wey, female 2) × *P. rotundatus* (St John's). 85, 86, *P. rotundatus* (St John's) × *P. depressus* (Loch Urr). Scales = 0.5 mm.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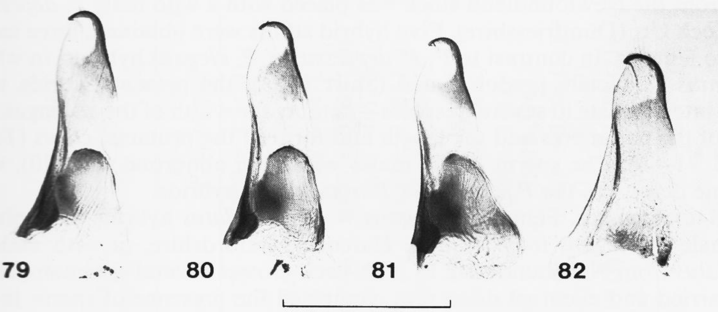
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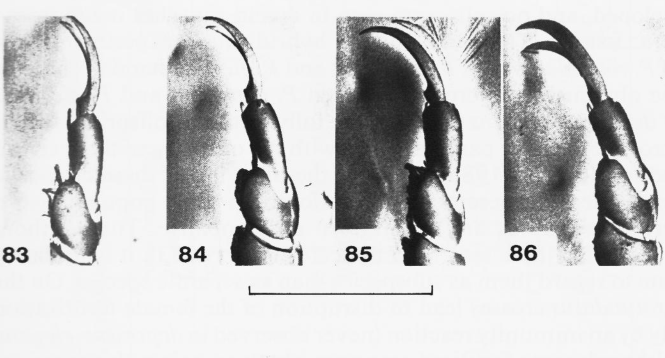
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tological and died. Four larvae hatched successfully and were reared to the adult stage, giving three males and one female.

Female "2" was not observed to mate with the first male, so that a second male, previously mated with female "1," was added on 19.v. No spermatophores were seen until 28.v., but from then until 7.vi. at least five were carried. The female was killed and dissected on 12.vi. The spermatheca and its duct were filled with a brown stain, as in female "1"; control mated females never showed this discolouration. Twenty-five eggs were laid during the first week of June, with most during the first three days, followed by a rapid fall-off and cessation of laying. Thirteen out of a first batch of 15 eggs hatched, but only two from a second batch of 10. Eleven adults were reared, five males and six females.

Larval exuviae are shown in Figures 49 and 54, and aedeagi, parameres and male protarsi in Figures 71–86. The male hybrids (Table 5) are very close to the Newfoundland facies in both replicates, including the darkened antennae characteristic of the Newfoundland *P. rotundatus* but not shown by Tilford *P. elegans*—thus confirming the parentage. Offspring of the two females were very similar to one another, except that those of female "2" have slightly narrower aedeagi. One male from female "2" had single protarsal claws. Sperm from the male hybrids proved to be highly abnormal, having double tails of "flabby" consistency (Fig. 69).

B. *Potamonectes rotundatus* × *P. depressus*. One F_1 female *P. rotundatus* from the Newfoundland stock was placed with a wild male *P. depressus* from Loch Urr (Dumfriesshire). Five hybrid adults were obtained, three males and two females. In contrast to F_1 *P. depressus* × *P. elegans* hybrids, in which *P. elegans* characters predominated (Shirt 1983), the present hybrids were clearly intermediate in several respects—notably the width of the aedeagus, the shape of the parameres and the length and form of the protarsal claws (Table 5, Figs. 71–86). The sperm of the males was again abnormal (Fig. 70), with the same defects as the *P. elegans* × *P. rotundatus* hybrids.

C. Back-crosses. Female *P. elegans* × *P. rotundatus* hybrids were placed with male *P. elegans* from Stanton Harcourt, Oxfordshire, or with male *P. rotundatus* from Newfoundland. In both back-crosses several spermatophores were carried and eventual dissection confirmed the presence of sperm in the spermathecae. The two crosses produced three and 10 eggs respectively, but none developed, and no cells were seen in orcein squashes made from them.

D. Conclusions. The results of the hybridization experiments involving crosses of *P. rotundatus* with *P. depressus* and *P. elegans* stand in sharp contrast with those obtained from crosses between *P. depressus* and *P. elegans*. *Potamonectes depressus-elegans* crosses gave fully fertile F_1 offspring, which could be back-crossed to either parental form, with the offspring of these crosses both viable and fertile (Shirt 1983). Further, the offspring of these crosses showed morphological features resembling those found in some populations from the area where *P. depressus* and *P. elegans* are sympatric. Thus, although the situation regarding these taxa is complicated (Shirt 1983), it is probably more appropriate to regard them as subspecies than as separate species. On the other hand, *P. rotundatus* crosses lead to disruption of the female fertilization tract, apparently by an immunity reaction (never observed in *depressus-elegans* crosses), and although some fertilised eggs were obtained before this reaction set in, these showed a high level of abnormality in their development. Of the few hybrids that were obtained from crosses between *P. rotundatus* and *P. depressus* and *P. elegans*, all the males had abnormal sperm, while the females, even

Table 5. Measurements of males from populations of *Potamonectes rotundatus, P. elegans* and *P. depressus* used in hybridisation experiments, and the F_1 hybrids. For clarification of data, see caption to Table 1.

	Newfoundland *P. rotundatus*	Tilford *P. elegans*	Loch Urr *P. depressus*	*P. elegans* (female 1) × *P. rotundatus*	*P. elegans* (female 2) × *P. rotundatus*	*P. rotundatus* × *P. depressus*
AW (μm)	29.9 ± 0.9 (7) (27.5–33.0)	28.3 ± 0.9 (12) (23.9–34.9)	76.7 ± 1.3 (21) (69.7–91.8)	29.4 ± 1.1 (3) (27.5–31.2)	25.3 ± 0.9 (4) (23.9–27.5)	48.3 ± 0.6 (3) (47.7–49.5)
TL (mm)	4.85 ± 0.05 (7) (4.65–5.10)	4.59 ± 0.07 (4) (4.41–4.72)	5.02 ± 0.04 (18) (4.82–5.47)	4.58 ± 0.05 (2) (4.53–4.63)	4.50 ± 0.05 (5) (4.35–4.64)	4.60 ± 0.08 (3) (4.46–4.74)
TW/TL	0.514 ± 0.008 (4) (0.495–0.531)	0.518 ± 0.003 (4) (0.509–0.524)	0.497 ± 0.003 (18) 0.474–0.527)	0.512 ± 0.008 (2) (0.504–0.519)	0.518 ± 0.007 (4) (0.503–0.531)	0.501 ± 0.007 (3) (0.492–0.514)
EL/TL	0.695 ± 0.004 (7) (0.682–0.711)	0.672 ± 0.004 (4) (0.664–0.683)	0.680 ± 0.003 (18) (0.467–0.697)	0.686 ± 0.006 (2) (0.680–0.691)	0.680 ± 0.003 (5) (0.674–0.687)	0.674 ± 0.009 (3) (0.657–0.688)
PMW/PL	0.530 ± 0.008 (7) (0.504–0.566)	0.507 ± 0.024 (4) (0.442–0.555)	0.546 ± 0.010 (19) (0.469–0.632)	0.535 ± 0.002 (3) (0.533–0.539)	0.562 ± 0.009 (5) (0.533–0.581)	0.576 ± 0.010 (3) (0.556–0.588)
AC (μm)	261 ± 4 (6) (248–272)	255 ± 3 (9) (239–266)	349 ± 3 (21) (295–376)	263 ± 6 (3) (253–270)	256 ± 2 (4) (251–261)	304 ± 6 (3) (292–310)
AC/PC	1.153 ± 0.012 (6) (1.116–1.194)	1.059 ± 0.008 (9) (1.016–1.083)	1.091 ± 0.006 (21) (1.034–1.137)	1.125 ± 0.016 (3) (1.104–1.157)	1.123 ± 0.011 (4) (1.102–1.154)	1.127 ± 0.008 (3) (1.119–1.142)
AC/TS	1.075 ± 0.013 (6) (1.047–1.134)	1.130 ± 0.019 (9) (1.032–1.220)	1.349 ± 0.015 (21) (1.247–1.508)	1.072 ± 0.013 (3) (1.053–1.098)	1.084 ± 0.013 (4) (1.045–1.101)	1.240 ± 0.016 (3) (1.223–1.271)

after successful mating with both *P. rotundatus* and *P. elegans,* laid eggs which showed no development. Thus, both male and female hybrids were sterile.

These results leave no doubt that *P. rotundatus* is a good species, separate from *P. depressus* and *P. elegans.*

Discussion

While *Potamonectes rotundatus* and *P. macronychus* are clearly allied to *P. depressus* and *P. elegans*—a closeness shown clearly by the high level of similarity in isoelectric focusing bands of extracted proteins—there are important differences, especially in the form of the protarsal claws of the male and in the form of the aedeagus (in both lateral and dorsal views).

The hybridization experiments with *P. rotundatus* × *P. depressus* and with *P. elegans* × *P. rotundatus* leave no doubt that these are separate species—a particularly valuable result as the geographical range of *P. rotundatus* does not overlap with those of these taxa. Although we have no experimental data involving *P. macronychus,* distributions of *P. macronychus* and *P. depressus* overlap in northern Alberta, where there is no evidence of morphological intergradation.

It is thus clear that, while *P. depressus* is Holarctic, *P. elegans* is not, but is confined to western Europe. North American records of *P. elegans* can be attributed to *P. rotundatus* or *P. macronychus.*

The differences between *P. rotundatus* and *P macronychus* appear sufficiently striking for them to be regarded as good species, apparently representing the eastern and western halves of a species pair. Other species pairs with distributions similar to the above are known in the Nearctic fauna, with a break between species occurring in the eastern Great Plains. The taxonomic status of the members of these pairs is not always clear-cut: *e.g.,* the staphylinids *Tachinus luridus* Er./*T. nigricornis* Mann. (two species?) and *T. basalis* Er. (two subspecies?) (Campbell 1973). Similarly, *Oxyporus occipitalis* Fauval shows a colour cline across the continent (Campbell 1969). Apart from the few specimens from the Manitoba–Michigan area already discussed, *P. rotundatus* and *P. macronychus* are relatively uniform within their own areas and there is no real evidence of a cline. However, should study of additional material from this area suggest significant introgression, then local hybridization experiments would be needed to see if there was some form of gene exchange between the two taxa, kept in check by some form of stabilizing selection—as appears to be the case with British *P. depressus* and *P. elegans* (Shirt 1983). The deviant populations of *P. macronychus* from southern British Columbia also merit further study.

What is not clear, however, is the origin of *P. rotundatus* and *P. macronychus.* Within the Nearctic fauna these species stand distinct because of their parameres with curved chitinous apices surrounding discoid membranes, elytra with subapical denticles in both sexes, and an elytral pattern of blackish vittae on a pale background, with these vittae to some extent both interrupted and also coalescing. The Palaearctic fauna is rich in species with these characters.

If the present ranges of the species are taken into consideration, then *P. depressus,* with a northern, Holarctic distribution overlapping the ranges of both *P. elegans* and *P. macronychus,* could be the evolutionary link between the various species—especially if, as seems possible, its range extended further south and east in North America during cold episodes of the Pleistocene, and it was in contact with *P. rotundatus.* It must, however, be borne in mind, that the broad aedeagus of *P. depressus* is unique within *Potamonectes,* the other species of which have aedeagi tapered like those of *P. elegans, P. rotundatus* and *P. macronychus.*

A hypothesis based on distributions would, in its simplest form, suggest that *P. depressus* originated, without complete speciation, from *P. elegans. Potamonectes depressus* then colonised the Nearctic and gave rise, with speciation, to *P. rotundatus* and/or *P. macronychus.* This hypothesis requires an initial modification of the aedeagus and parameres from that normally seen in *Potamonectes,* to that in *P. depressus,* followed by a reversal to that in *P. rotundatus* and *P. macronychus.* Although a reversal of an evolutionary change is generally considered unlikely, the degree of change involved is small and may not have presented much difficulty. One small feature of the evidence supporting the role of *P. depressus* as a connecting link, is the fact that *P. depressus* and *P. rotundatus* share a protein iso-electric band at about pH 4.62, while the *P. elegans* investigated lacked this band, but had one at about pH 4.56.

An alternative possibility is that *P. rotundatus* and *P. elegans* are parts of a "proto-*elegans*" stock which existed in both Europe and North America in the early Tertiary, before the opening of the Atlantic. *Potamonectes macronychus* would then be the sister species of *P. rotundatus.* One factor which seems to be against the idea of *P. elegans* dating from the beginning of the Tertiary is that there are numerous western European species, representing a considerable diversity of form. These species do not appear to be more recent than *P. elegans,* yet none exists in the Nearctic. It thus seems that the most likely derivation of *P. rotundatus* and *P. macronychus* is from Palaearctic *P. elegans*-like species, via *P. depressus.*

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