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THE FRESH-WATER TRICLADS (TURBELLARIA) OF ALASKA

By Roman Kenk

Introduction

In 1948, during an investigation of biting insects in Alaska conducted by the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture, Dr. Reese I. Sailer collected and transmitted to me several samples of fresh-water triclads (planarians). An examination of the material revealed that the worms belonged to the genus *Polycelis*, a genus fairly common in Asia and Europe but only twice reported from North America. The finding suggested a closer relationship of the Alaskan fresh-water fauna with that of East Asia. A more thorough study of the triclads of Alaska promised to yield a more definite understanding of these zoogeographical relations.

My field trip [1] to Alaska was made in the summer of 1950. Since the available time was rather limited, the collecting was done mainly along the highways of the territory and in the vicinities of Point Barrow and Umiat.

The following roads and fresh-water localities were visited on the trip: Steese Highway in the section between Fairbanks and Birch Creek (milepost 103); Elliot Highway, from Fairbanks to Livengood; tundra lakes and pools in the vicinity of Point Barrow; Colville River, several streams, and a lake near Umiat; Mount McKinley Park Road, a section of about 15 miles adjoining the railroad station; Glenn Highway, from Anchorage to Glenallen; road from Palmer to

[1] This study was supported by the Arctic Institute of North America under contractual arrangement with the Office of Naval Research.

Willow; road from Anchorage to Potter; and Richardson Highway, section between Valdez and Glenallen.

No fresh-water triclads were found by me either at Point Barrow or at Umiat. I received, however, from the U. S. National Museum, a sample of triclads collected by P. F. Scholander in a lake near Umiat. The relative scarcity of planarians in tundra lakes and pools may be due to the high acidity of the waters or to the extremely severe conditions prevailing in them during the long winter season.

Grateful acknowledgment is made of the very helpful cooperation which was extended to me by several agencies in Alaska: The Arctic Research Laboratory, Point Barrow; the U. S. Public Health Service, Anchorage; the Alaska Road Commission, Fairbanks, Anchorage, and Glenallen; and the Division of Forestry, Bureau of Land Management, Fairbanks and Anchorage. I also wish to express my indebtedness to Prof. Edward G. Reinhard of the Catholic University of America and to Dr. Fenner A. Chace, Jr., and Dr. Doris M. Cochran of the U. S. National Museum who kindly permitted me to use their laboratory and office facilities in Washington, D. C.

Four species of fresh-water triclads were collected in Alaska. Two are inhabitants of the White Mountains, a mountain range extending in an east-west direction north of Fairbanks. The other two are widely distributed in waters of the Alaska Range and of the southern section of Alaska and one of them reaches as far north as Umiat.

Family Planariidae

Genus *Phagocata* Leidy

Phagocata nivea, new species

Figure 21; Plate 6, Figure 1

Description.—This is a slender, rather delicate species. Mature specimens measure up to 8 mm. in length and about 1.5 mm. in width. In the quietly gliding animal the anterior end is truncated,with a very slightly bulging frontal outline and with rounded lateral corners (auricles). There is no distinct narrowing or neck behind the auricles and the lateral margins of the head are approximately parallel. Behind the head, the body widens and soon reaches its greatest width. From there on, the lateral margins of the body run parallel up to the level of the mouth, to converge again in the postpharyngeal region and to meet in a bluntly pointed posterior end.

The species lacks pigment and usually appears white and somewhat transparent. The intestinal contents may shine through the body wall and give the animal a certain amount of color; the margins of the body, the head region, and the areas occupied by the pharynx and the copulatory apparatus, however, are always white.

There are two rather small eyes, situated close together (about one-fourth the body width apart at the level of the eyes) and far removed from the frontal end. This character, easily recognized in life, distinguishes the species from another white triclad with which it shares its habitat, *Dendrocoelopsis alaskensis*, described as new on p. 178.

The pharynx is inserted, in sexually mature specimens, somewhat behind the middle of the body and measures about one-sixth of the body length. The copulatory organs occupy the anterior half of the postpharyngeal region.

The animal moves by gliding only; crawling movements, such as are seen in other triclads, particularly in those equipped with anterior adhesive organs, have not been observed in this species.

From the description it may be seen that the species in life shows a close resemblance to other species of the same genus, particularly to the American *Phagocata morgani*, the European *P. albissima*, *P. vitta*, and related forms. A separation of these species can be made only on the basis of anatomical characters.

Only those characters of the digestive system that have a taxonomic significance are discussed here. The pharynx has a structure typical of the family Planariidae; i. e., the fibers of the internal muscle zone are arranged in two distinct layers, a thick inner circular layer and a narrower outer longitudinal one. The anterior intestinal trunk bears 10 or 11 branches on each side. Each posterior trunk has 21 to 27 lateral branches and numerous short medial branches in both the pharyngeal and postpharyngeal regions.

The testes are numerous and are arranged, on each side of the midline, in a longitudinal zone extending from a short distance behind the ovary almost to the posterior end of the body. Their position is predominantly ventral, below the intestinal branches. Only a few testes extend into the mesenchymatic "septa" between the branches toward the dorsal side.

The two ovaries are typical, each situated approximately below the second intestinal branch. An undifferentiated mass of cells, the parovarium, is attached to the dorsolateral side of each ovary.

The genital pore (*pg*), situated about halfway between the mouth and the posterior end of the body, leads into a small cavity (*ac*) which continues to the left and dorsally into the duct of the copulatory bursa (*bd*) and to the right and anteriorly into the male atrium (*am*). This cavity may be considered to represent a common genital atrium. In some specimens, however, there appears to be no differentiation of the atrium into male and common parts, and the bursa duct and an undivided atrium meet at or near the genital pore. These variations are obviously due to the different states of muscular contraction in which the animals were killed. The atrium, narrow at the genital aperture, widens as it extends forward, to the right side of the midline.

It is lined with a tall, glandular epithelium, the cells of which project into the cavity in a villuslike fashion. Below the epithelium there are two layers of muscle fibers, one circular and the other longitudinal.

The penis consists of a spherical, muscular bulb embedded in the mesenchyme, and a moderately large papilla projecting into the male atrium. The bulb is pierced by numerous gland ducts which open into the lumen of both the bulb and the papilla. The shape of the papilla is subject to great variation, due apparently to the state of contraction of the organ. It may be twisted to one side and even partly inverted into the lumen of the penis (similar to the pseudoflagellum of various dendrocoelids). The shape shown in figure 21 appears to be that of the organ at rest. The outer wall of the papilla is covered with a tall to cubical epithelium similar to that lining the atrium. Below the epithelium there is a layer of circular muscle fibers followed by another of longitudinal fibers. The shape of the penis lumen (*lp*) is as changeable as that of the papilla. Typically, it appears to be wider in the bulb than it is in the papilla, though there is no distinct ejaculatory duct differentiated. The lumen opens ventrally to the tip of the papilla. The two vasa deferentia (*vd*) penetrate the penis bulb from both sides and empty into the penis lumen separately, but not far apart.

The two oviducts converge at the level of the copulatory apparatus, the left one passing between the bursa duct and the male atrium, and unite at a point dorsally to the atrium. The rather long common oviduct (*odc*) curves ventrally and opens into the posterior part of the male atrium. The terminal sections of the paired oviducts and the greater part of the common oviduct receive the outlets of numerous eosinophilic glands, the cell bodies of which are scattered in the surrounding mesenchyme, particularly dorsally to the atrium.

The copulatory bursa (*b*) is of moderate to large size and is irregularly lobed. The bursa duct or stalk (*bd*) is wide, runs posteriorly to the left of the midline, and curves ventrally to reach the genital aperture. It is lined with a tall, glandular epithelium and surrounded with a strong muscular coat consisting of intermingled circular and longitudinal fibers.

Taxonomic position.—The genus *Phagocata* Leidy (*Fonticola* Komárek) in its present extent (cf. Hyman, 1937, pp. 300–302) has representatives in Europe, Asia, and North America. The genus is not quite homogeneous and will probably, in due time, be subdivided into several genera (cf. Beauchamp, 1939). For the purpose of comparison, we may consider here only those species of the genus that lack pigment. Though the presence, or the lack, of pigment is a character of subordinate taxonomic value, it may nevertheless serve well as a character of specific rank. The Alaskan form differs from

European species such as *P. vitta* (Dugès) and *P. albissima* (Vejdovský) and from the American white *P. morgani* (Stevens and Boring) mainly in the structure of the male copulatory organ. Asia has several species of *Phagocata*, the majority of them pigmented forms. Of the three unpigmented Asiatic species that may belong to the genus, two

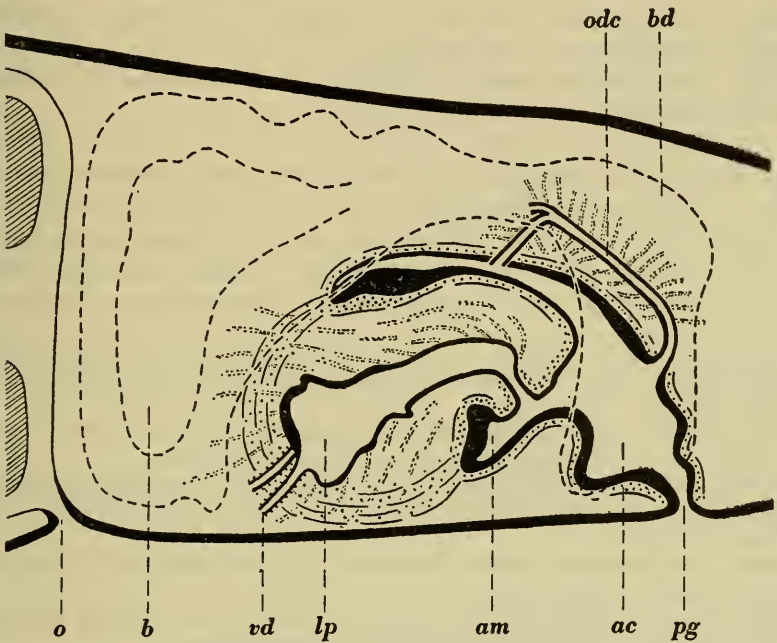


FIGURE 21.—*Phagocata nivea*, diagram of the copulatory organs in longitudinal section, × 92. *ac*, common atrium; *am*, male atrium; *b*, copulatory bursa; *bd*, bursa stalk; *lp*, penis lumen; *o*, mouth; *odc*, common oviduct; *pg*, genital pore; *vd*, vas deferens.

have been described from immature specimens and the anatomy of their reproductive systems is not known: *Planaria pellucida* Ijima and Kaburaki (1916) from Sakhalin and a species from the Baikal region assigned tentatively to *Fonticola* by Bazikalova (1947). A third species, *Phagocata coarctata* (Arndt, 1922), from the vicinity of Vladivostok, is sufficiently well known, although no fully mature individuals of this species have been studied. *P. coarctata* differs from *P. nivea* externally in being smaller and broader, and in having a different contour of the anterior end, which bears protruding lateral lobes, and a greater distance between the two eyes. Anatomically, the two species are, undoubtedly, closely related.[2]

[2] Livanov and Zabusova (1940, p. 146) state that a reexamination of Arndt's slides of *Planaria coarctata* showed that the arrangement of the muscle fibers of the pharynx conformed with the dendrocoelid type (circular and longitudinal fibers of the internal muscle zone intermingled). Arndt (1922, p. 108) described the anatomy of the pharynx in minute detail and indicated, both in a figure (pl. 4, fig. 7) and in the text, a typical planariid pattern. I must assume that some confusion occurred somewhere, probably in the identification of the slides sent to Livanov.

In *Phagocata nivea* the penis lumen opens usually below the tip of the penis papilla. This character has been used by Livanov and Zabusova (1940, p. 96) to segregate a group of Asiatic species from *Phagocata* and to place them in a new genus, *Penecurva*. The same character is found, however, in a common North American species, *Phagocata morgani*, which shows no other close relations with the Asiatic group. This character is apparently inadequate as a basis for the establishment of a new genus.

Holotype.—On one slide, USNM 22332, creek crossing Elliot Highway at milepost [3] 31.0, July 24, 1950.

Distribution and ecology.—*Phagocata nivea* was collected in cool, fast mountain streams on the slopes of the White Mountains, a range north of Fairbanks. The temperature of the water ranged from 3.2 to 7.2° C. (July). The animals are cold-stenothermic and do not tolerate sudden increases in temperature. They were often found in the company of another white triclad, *Dendrocoelopsis alaskensis*.

Stream on Steese Highway (pl. 8), at milepost 84.0, altitude 2,700 feet, July 19 and 21, 1950, water temperature 6.9° C.; one immature and one mature specimen, from under stones.

Willow Creek, on Steese Highway, at milepost 96.6, altitude 2,100 feet, July 19, 1950, 7.2° C.; two immature specimens, from under stones.

Spring and stream on Steese Highway, milepost 82.5, near Alaska Road Commission camp, July 21, 1950; two mature and six immature specimens, on the undersides of stones.

Fox Gulch, on Elliot Highway, milepost 1.2, July 24, 1950, 5.0° C., one small specimen near bait (beef liver).

Creek crossing Elliot Highway at milepost 31.0, July 24, 1950; 39 specimens, about half of them mature, collected under stones (holotype).

Genus *Polycelis* Ehrenberg

Polycelis borealis, new species

FIGURE 22; PLATE 6, FIGURE 2

Description.—Mature animals are usually 12 to 15 mm. long and 1.5 to 2 mm. wide (larger specimens, measuring up to 20 mm. in length, have been seen). The frontal margin is slightly convex. At the lateral corners of the head there is a pair of elongated, bluntly pointed auricles which are held raised when the animal is gliding quietly. Behind the auricles, the body first narrows slightly, then gradually widens, reaching its greatest width at the level of the pharynx. Behind the pharynx the body tapers to a moderately pointed posterior end.

The color of the dorsal side is usually a uniform light or dark brown, that of the ventral side a light grayish brown. In animals

[3] The large highways of Alaska are marked with wooden mileposts indicating only full miles. Many posts were missing at the time when the collections were made. Fractional milages were usually estimated from the nearest milepost or from the speedometer readings of the car used.

from some localities, an indistinct lighter median line occurred dorsally in the prepharyngeal region, with lighter areas above the pharynx and the copulatory organs.

The species has many small eyes (a generic character) arranged in a band along the frontal margin of the head, the base of the auricles, and the lateral margins of the body a short distance behind the head. Anteriorly the eyes are placed in more than one row, somewhat irregularly scattered; behind the head they are in a single row reaching backward about one-third to one-half the length of the prepharyngeal region. There is no narrowing of the band of eyes at the base of the auricles.

The pharynx is inserted at about the middle of the body and measures in length almost one-fourth the length of the body. The copulatory organs occupy more than half the post-pharyngeal region.

The animal moves by gliding only.

The pharynx of *Polycelis borealis* is structurally typical of the genus *Polycelis* and of the family Planariidae, the muscle zone being formed by two distinct layers, a thick circular layer adjoining the epithelium of the pharyngeal lumen and a thinner layer of longitudinal fibers. The anterior trunk of the intestine bears 5 to 6 lateral branches.

The numerous, fairly large testes are arranged in two zones, to the right and left of the anterior intestinal trunk, extending from the level of the ovaries posteriorly to the base of the pharynx. The testes are essentially ventral, though individual vesticles may extend dorsally in the mesenchymatic spaces between the intestinal branches and occupy almost the entire dorsoventral diameter of the body. Where intestinal branches are present, however, the testes develop only below them. Each zone of testes reaches laterally only little beyond the ventral nerve cord.

The ovaries are situated behind the first pair of lateral branches of the anterior trunk of the intestine.

The genital pore (*pg*), situated in the midline behind the middle of the postpharyngeal region, connects with a narrow posterior extension of the genital atrium (*a*). This extension leads dorsally and somewhat to the left into the duct of the copulatory bursa and anteriorly into the widened portion of the atrium containing the penis. There is no marked division of the atrium into a posterior common atrium and an anterior male atrium. The wall of the atrium is lined with a cubical epithelium and equipped with two muscle layers, one circular and the other longitudinal.

The penis consists of a bulb embedded in the mesenchyme and a papilla projecting into the atrium. Neither of the two parts is very muscular. The shape of the penis, particularly of the papilla, is very

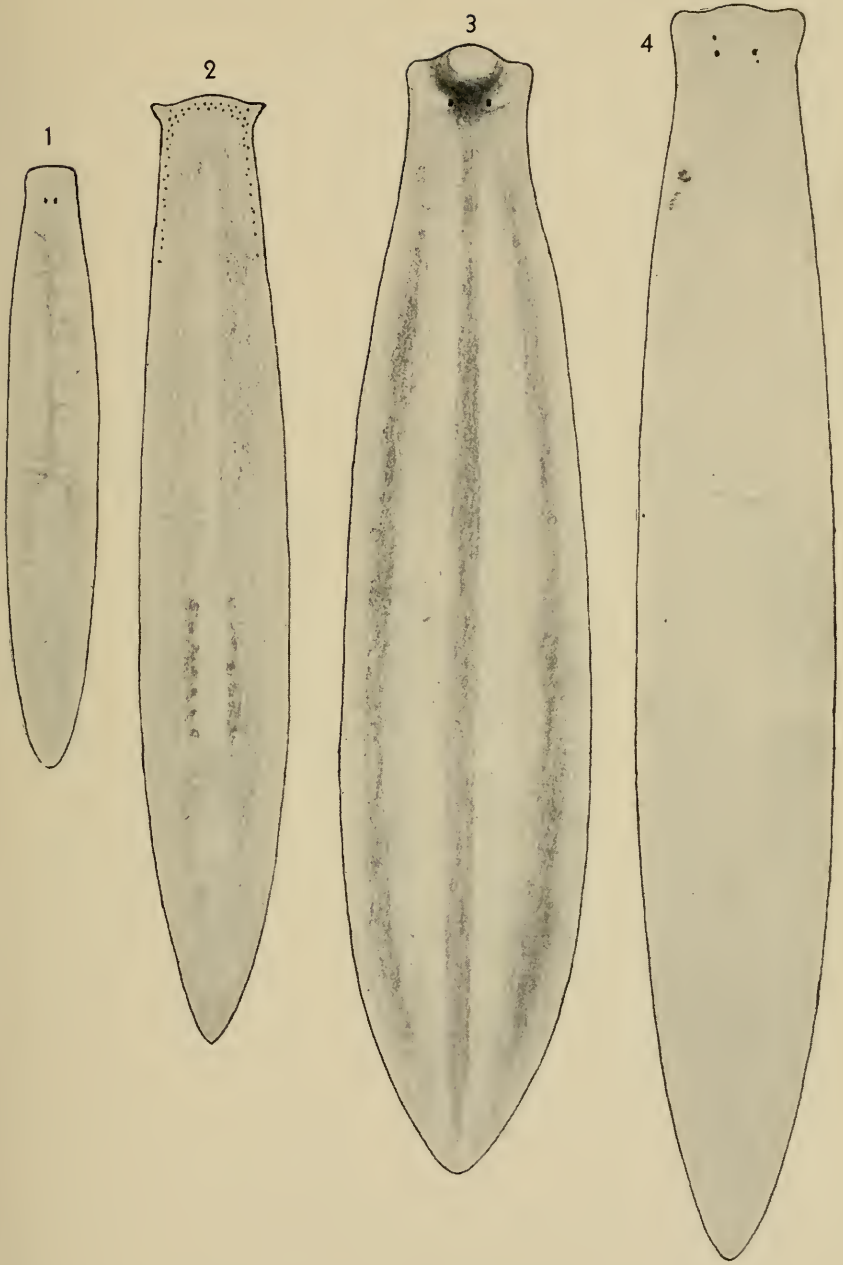
changeable. In specimens that were fixed in a well-extended condition, the bulb appears spherical and the papilla has a conical shape. The bulb contains a spacious, irregularly lobed cavity, the seminal vesicle (*vs*). Numerous gland ducts empty into the lumen of the bulb after entering the bulb, particularly from its anterior surface, and penetrating between its muscle fibers. The ducts are filled with a granular, slightly eosinophilic secretion. The two vasa deferentia (*vd*) open into the seminal vesicle separately from the anterolateral sides.

The penis papilla is conical or finger-shaped when well extended. It is covered with a cubical epithelium below which there are two rather feebly developed muscle layers, tapering in thickness toward the tip of the papilla: a layer of circular fibers adjoining the epithelium and a thinner layer of longitudinal fibers. The absence of a strong muscular wall probably accounts for the great variation in the shape of the penis papilla observed in the material. The lumen of the seminal vesicle continues into the papilla as a wide canal (*de*), opening at or near (ventrally to) the tip of the papilla. The canal is lined with an epithelium of cubical cells and lacks the gland openings characteristic of the seminal vesicle. It corresponds to an ejaculatory duct but it apparently has no distinct muscle coat.

The two oviducts, running posteriorly along the ventral nerve cords, bend dorsally and medially at the level of the copulatory organs. The left one passes through the space between the atrium and the bursa duct and unites with the oviduct of the right side dorsally to the atrium. The common oviduct (*odc*) runs ventrally and opens into the posterior part of the atrial cavity. The terminal sections of the paired oviducts and a section of the common oviduct are equipped with strongly eosinophilic shell glands.

The copulatory bursa (*b*) is a large sac with a lobed outline. It connects posteriorly with a duct of almost uniformly wide diameter, the bursa stalk (*bd*). The duct runs first posteriorly, to the left of the penis bulb, then curves ventrally and opens, from the dorsal side, into the narrow terminal portion of the atrium, close to the genital pore. The bursa stalk has a strong coat of intermingled circular and longitudinal muscle fibers. There is no histological differentiation into anterior and posterior sections of the bursa stalk.

Taxonomic position.—Polycelis borealis is the second species of the genus *Polycelis* to be found on the North American continent. The other species, *P. coronata* (Girard), reported from Wyoming and South Dakota (Hyman, 1931), resembles it closely in external appearance and probably cannot be distinguished from it in life. In both species, the shape of the anterior end is very similar. The auricles of *P. borealis* are perhaps a trifle longer and more pointed than those of *P.*



Sketches of living specimens of the four Alaskan triclad species, all ×10: 1. *Phagocata nivea;* 2. *Polycelis borealis;* 3. *Dendrocoelopsis piriformis,* striped form; 4. *Dendrocoelopsis alaskensis.*

coronata. Hyman (1931, p. 126) states that in *P. coronata* the curved band of eyes narrows as it crosses the base of the auricles; no such narrowing has been seen in *P. borealis*. These differences are, however, insignificant and do not permit a clear separation of the two forms. The same may be said of other species of the genus, which likewise could be confused with the American forms in life: the Japanese species, *P. auriculata* and *P. karafto*; and *P. schmidti* occurring both in Kamchatka and in Japan. These forms differ from each other more clearly in their anatomical characters.

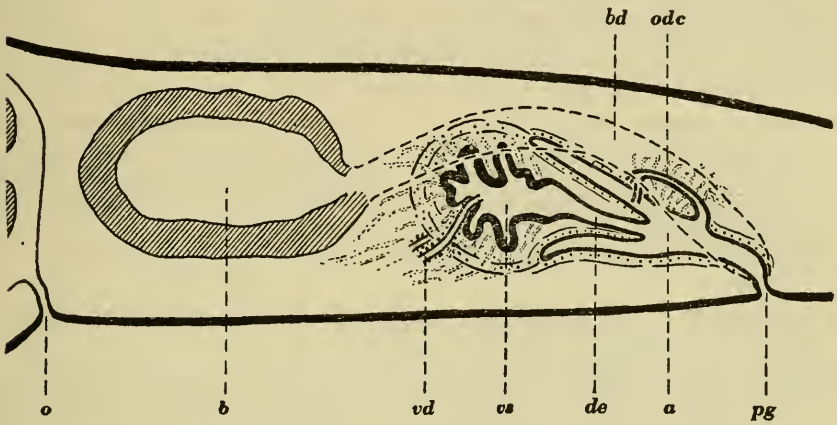


FIGURE 22.—*Polycelis borealis*, diagram of the copulatory organs in longitudinal section, × 70. *a*, atrium; *b*, bursa; *bd*, bursa stalk; *de*, ejaculatory duct; *o*, mouth; *odc*, common oviduct; *pg*, genital pore; *vd*, vas deferens; *vs*, seminal vesicle.

To gain a better insight into the systematic relations of *Polycelis borealis* to other species of the same genus, it is necessary to review the present state of the systematics of the genus. The genus *Polycelis* has a muscular pattern of the pharynx typical of the family Planariidae; the oviducts unite, without embracing the bursa stalk, to form an unpaired terminal oviduct; the testes are situated in the anterior part of the body only; the male atrium is not surrounded by radial muscle plates; and the eyes are numerous. The genus thus defined (Kenk, 1930) has today about twenty species. It may be subdivided into subgenera on the basis of structural characters of the copulatory apparatus.

Subgenus *Polycelis*, lacking adenodactyls and lacking an excessive development of the muscle coat of the male atrium. This subgenus includes *Sorocelides* Sabussowa (1929, p. 521) and *Polycelidia* Zabusova (1936, p. 152), both described as distinct genera. The subgenus comprises the following species:

Polycelis nigra (O. F. Müller), Europe
P. receptaculosa (Livanov and Zabusova, 1940), Teletskoe Lake in the Altai Mountains
P. eburnea (Muth, 1912), Aral Sea region
P. tibetica Hyman (1934), Tibet
P. koslowi (Zabusov, 1911), Tibet
P. elongata (Sabussowa, 1929), Kamchatka
P. polyopis Zabusova (1936), Kamchatka
P. karafto Ijima and Kaburaki (1916), Sakhalin
P. sapporo (Ijima and Kaburaki, 1916), Japan
P. coronata (Girard, 1894), Wyoming and South Dakota

Subgenus *Seidlia* Zabusov (1911, suppl., p. 7), distinguished by an extraordinarily thick muscle zone surrounding the male atrium. Zabusov's (1916, p. 273) genus *Rjabuschinskya* likewise belongs here. Species of the subgenus:

Polycelis sabussowi (Seidl, 1911), including Seidl's species *Sorocelis sabussowi, S. lactea, S. stummeri* (cf. Kenk, 1936), Turkestan
P. relicta (Sabussowa, 1929), Kamchatka
P. eurantron (Zabusova, 1936), Kamchatka
P. schmidti (Zabusov, 1916), including *P. ijimai* Kaburaki (1922), Kamchatka, Kurile Islands, and Japan
P. auriculata Ijima and Kaburaki (1916), Japan

The third subgenus, *Ijimia* Bergendal (1890, p. 326), is characterized by possessing solid adenodactyls:

Polycelis felina (Dalyell), including *P. cornuta* Johnson, Europe and North Africa
P. tenuis Ijima, Europe and western Asia
P. linkoi Zabusov (1901), Onega Lake in European Russia
P. oculi-marginata (Palombi, 1931), New Guinea (see Beauchamp, 1947)

Two species of the genus *Polycelis* are too incompletely known to permit their assignment to either the subgenus *Polycelis* or *Seidlia*: *P. eudendrocoeloides* (Sabussowa, 1929) from the Kamchatka Peninsula and *P. tibetica* (Zabusov, 1911, p. 349) from Tibet (*P. tibetica* Hyman, 1934, will have to be renamed if it should prove to be different from Zabusov's species).

Polycelis borealis is clearly a member of the subgenus *Polycelis*. It differs from *P. nigra* in having well-developed auricles; from *P. elongata, P. polyopis*, and *P. sapporo*, in the arrangement of the eyes; and from *P. coronata* and *P. receptaculosa* in the structure of the male copulatory organ. The reproductive system of *P. karafto* has not been described adequately and thus does not permit a comparison with that of the Alaskan species. The remaining species of the subgenus, *P. eburnea, P. koslowi*, and *P. tibetica* Hyman, two of which are known only from the study of preserved specimens, agree with *P. borealis* in being pigmented forms with prominent auricles and in having a similar anatomy of the copulatory organs. The four species are

undoubtedly very closely related; whether some of them are identical or are the same as the Alaskan form cannot be established on the basis of present knowledge. The Alaskan *Polycelis*, therefore, is described as a new species.

Holotype.—On three slides, USNM 22333, clear spring on the road from Palmer to Willow, 20.1 miles from Palmer, altitude 3,800 feet, Aug. 9, 1950.

Distribution and ecology.—Polycelis borealis is a very common species occurring in mountain streams in the southern part of Alaska (Alaska Range, Talkeetna Mountains, Chugach Range). Typically it inhabits clear, cold, fast-running waters. It has also been found, however, in several small mountain lakes which connect with streams in which the species lives. It has not been observed in silt-bearing glacier streams.

The typical temperature range of the habitats was between 3.0° and about 15° C. (August 1950). Temperatures above 15° C. (up to 22.4° C.) were encountered only rarely and only in habitats which presumably have great diurnal temperature amplitudes (shallow lakes, small exposed streams).

The great majority of the specimens collected was asexual. Sexually mature animals were seen in only 6 of the 31 localities in which the species was found. In some localities, a large percentage of the specimens exhibited freshly regenerated heads or posterior ends, indicating that vivid asexual reproduction was taking place.

Clear springs on the road from Palmer to Willow, 20.1 miles from Palmer, altitude 3,800 feet, Aug. 9, 1950, water temperature 3.0° C., numerous specimens, five mature (holotype).

Clear, fast mountain stream crossing Mount McKinley Park road, 5.5 miles from the railroad station; Aug. 5, 1950.

Streams on road from Palmer to Willow 11.9, 18.0, 19.2, 20.2, 21.6, 22.1, 22.8, and 34.0 miles from Palmer, and Ice Lake, 20.4 miles from Palmer, Aug. 9, 1950.

Streams on Glenn Highway (Anchorage to junction with Richardson Highway near Glenallen) at mileposts 33.1, 33.9, 43.5, 64.8, 89.4, 98.8, and 117.1; Aug. 11 and 13, 1950.

Streams on road from Anchorage to Potter 2.9 (Campbell Creek), 10.3, and 10.6 miles from the city limits of Anchorage, Aug. 12, 1950.

Streams on Richardson Highway (section between Valdez and Glenallen) at mileposts 20.5, 25.5 (22.4° C.), 26.3 (see pl. 7), 29.0, 37.3, 54.7, 62.6 (see pl. 7), 81.0 (Squirrel Creek), and 87.5 (Rock Creek), and lake at milepost 27.3 (22.1° C.), Aug. 15, 1950.

Polycelis borealis was also identified in samples of triclads collected by Dr. Reece I. Sailer in July and September 1948. The following localities were represented: Richardson Highway, mileposts 8.3, 187.5, 192.9, 209.7, 223.6 and 239.9, and Glenn Highway, milepost 117.1.

Family Dendrocoelidae

Genus *Dendrocoelopsis* Kenk

Dendrocoelopsis piriformis, new species

Figure 23; Plate 6, Figure 3

Description.—Sexually mature specimens of this rather broad and plump species measure up to 15 mm. in length and 3 mm. in width. In quietly gliding animals, the head is truncated, with a convex frontal margin (grasping organ). There is a visible subterminal depression corresponding to the adhesive surface of the grasping organ or sucker. The rounded lateral corners of the head are formed by the auricles, which protrude only little laterally, thus causing an insignificant narrowing (neck) to appear behind them. Behind the head, the body margins widen gradually. The greatest width is reached at the level of the mouth. Behind that level, the body tapers again to a bluntly pointed posterior end. When the animal is at rest, the body appears short and wide, about pear-shaped, the body margins often forming a wavy or irregular contour. Young specimens are more slender and their lateral margins are more nearly parallel when they are in gliding motion. At rest, however, they assume the same pyriform shape as the adults. In short, the habit of the species may be described as resembling that of European and Asiatic representatives of the genus *Bdellocephala* Man, with which it has in common the broad shape and the anterior grasping organ.

The two eyes are situated on the dorsal side of the head. Their distance from each other amounts to somewhat more than one-third the width of the head at the level of the eyes. The distance of each eye from the lateral margin is smaller than the distance from the frontal margin.

The color of the dorsal side is usually a cloudy brown or dark brownish gray. In some specimens, the pigment is arranged in definite longitudinal stripes: one sharply marked median stripe flanked on each side by a light (usually yellow) band; laterad to this band the body darkens, losing its pigment again near the lateral margin. In other specimens, lacking the two light dorsal bands, the back may be either uniformly pigmented or may show a more or less distinct darker band along the midline. Young specimens and striped adults clearly show the finer disposition of the pigment in small rounded dots, each dot apparently corresponding to an individual pigment cell.

The pigment pattern of the dorsal side of the head is quite characteristic. A very dark field between the eyes extends anteriorly to both sides of the grasping organ. The area above the organ is unpigmented and white, and so are the two elongated ocular areas antero-

laterad to the eyes. A pair of indistinct, converging streaks of lighter coloration may run posteriorly from the lateral angles of the head.

The ventral side is light gray.

The pharynx is situated, in mature animals, behind the middle of the body; the mouth, at the beginning of the last third of the body; and the genital aperture, midway between the mouth and the hind end.

The normal locomotion of the animal is quiet gliding. When disturbed, it may attach itself to the substratum (apparently with the marginal adhesive zones) or move by "crawling." Young specimens do not crawl as readily as do adult ones.

The grasping organ, or sucker, in living animals, appears as a well-marked bulge on the frontal margin of the head, showing a concave ventral depression. In preserved specimens, the frontal margin is generally curved ventrally and the site of the organ forms a thick, grooved rim. Anatomically, the organ consists of glandular and muscular elements. The subterminal adhesive surface is covered with an epithelium devoid of rhabdites and pierced by numerous gland ducts filled with a granular, eosinophilic secretion. The cell bodies of the glands are scattered through the mesenchyme of the anterior half of the prepharyngeal region, particularly above the intestine. The gland ducts run anteriorly in dense bundles and, in their terminal sections, are thickly swollen with secretion. The muscular system of the organ, which could not be analyzed in detail on account of the density of the glandular structures, has fibers attached to the adhesive surface, serving presumably as retractors.

The rather short and thick pharynx is structurally typical of the family Dendrocoelidae; its internal muscular zone consists of intermingled circular and longitudinal fibers.

Auricular sense organs are represented by two bands of sensory epithelium extending posteriorly from the sides of the frontal margin. The cells of this epithelium are less tall than are those of the surrounding body epithelum; they lack rhabdites and are approached by nerve fibers from the underlying mesenchyme. The location of these organs corresponds to the two light, longitudinal streaks on the sides of the head seen in the living animal.

The testes are of moderate size, numerous, densely packed, and occupy the dorsal half of the mesenchyme, generally above the intestinal branches. They are arranged in two wide areas on both sides of the midline, extending from the level of the ovaries close to the posterior end.

The ovaries, situated at the level of the second pair of branches of the anterior intestinal trunk, show no structural peculiarities.

The genital pore (*pg*) leads immediately into two cavities, the male atrium (*am*) and, to the right and somewhat posteriorly, the duct of

the copulatory bursa (*bd*). No common atrium is present, and both the papilla of the penis and the opening of the oviduct are situated in the "male" atrium. The atrium is a conical cavity, wide anteriorly and tapering toward the genital pore. It is lined with a cubical epithelium, below which occurs a thin layer of fine circular muscle fibers and a thicker layer of coarser longitudinal fibers.

The penis consists of a spherical, muscular bulb and an elongated papilla. The penis bulb is differentiated into a wide peripheral muscular zone and a more central parenchymatic zone which contains a cavity, the seminal vesicle (*vs*). The vesicle is lined with a glandular epithelium and its wall forms villuslike projections. The two vasa deferentia (*vd*) penetrate the penis bulb from the anterolateral sides and open into the seminal vesicle on two prominent conical papillae projecting from the anterior wall of the vesicle a short distance from each other.

The papilla of the penis is finger-shaped, tapering toward the tip, and is highly muscular. It is covered with a thin cubical epithelium. Below the epithelium there is, in the basal portion of the papilla, a thin layer of longitudinal muscles, below which lie a stronger circular layer and a second longitudinal layer. In the distal part of the papilla, the external longitudinal layer is lacking. The axis of the papilla is pierced by the ejaculatory duct (*de*) which leads from the seminal vesicle to the tip of the papilla. The duct has a cubical epithelium and a strong coat of longitudinal muscle fibers.

The two oviducts approach the midline in the region of the copulatory apparatus, the right one passing between the atrium and the bursa stalk, and unite behind and above the atrium. The common oviduct (*odc*) proceeds ventrally, then curves anteriorly, and empties into the terminal part of the atrium close to the genital pore.

The copulatory bursa (*b*) is a lobed sac lined with a tall glandular epithelium. The distal parts of the epithelial cells are filled with fine eosinophilic granules. The duct or stalk of the bursa (*bd*) is differentiated into a narrow anterior section with a weak muscular coat, which connects with the bursa, and a posterior wider section which bends ventrally and opens at the genital pore. The cells of the anterior section resemble those of the bursa in having similar granular inclusions. Those of the posterior section lack the inclusions and are ciliated. The muscle coat of the duct consists of intermingled longitudinal and circular fibers.

Taxonomic position.—I have placed the species in the genus *Dendrocoelopsis* established originally for a European species, *D. spinosipenis* (Kenk). The original definition of the genus was based on the following characters: fibers of the inner muscle zone of the

pharynx intermingled; no adenodactyl; penis papilla developed, penis bulb of simple structure; oviducts unite without embracing bursa stalk; zone of testes extending behind the level of the copulatory organs; anterior end with subterminal true sucker; eyes not numerous (Kenk, 1930). Subsequently Beauchamp (1932, p. 254) founded a new genus, *Amyadenium*, with two species, *A. vandeli* Beauchamp and *A. brementi* (Beauchamp), both from the Pyrenees. Two more species were reported by the same author in later papers, *A. chattoni* Beauchamp (1949, p. 60), again from the Pyrenees, and *A. garmieri* Beauchamp (1950, p. 65), from central France. Beauchamp recognized the close relation of the new genus to *Dendrocoelopsis*, but

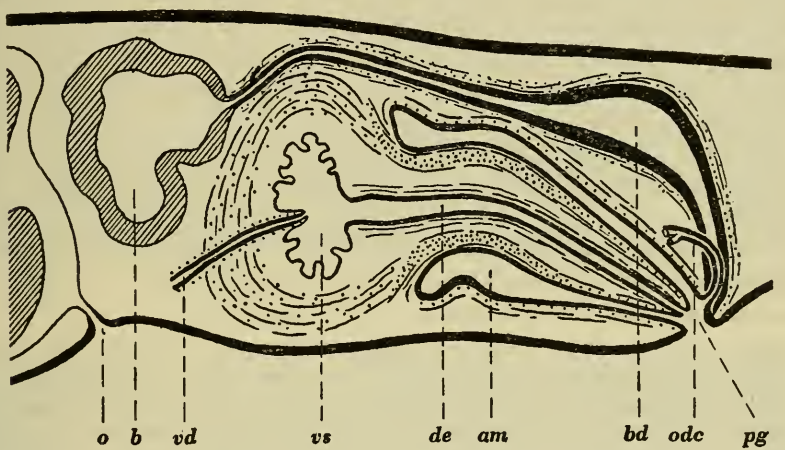


FIGURE 23.—*Dendrocoelopsis piriformis*, diagram of the copulatory organs in longitudinal section, × 60. *am*, male atrium; *b*, bursa; *bd*, bursa stalk; *de*, ejaculatory duct; *o*, mouth; *odc*, common oviduct; *pg*, genital pore; *vd*, vas deferens; *vs*, seminal vesicle.

separated it from the latter on account of the absence of a highly complex grasping organ, or true sucker (i. e., an adhesive organ separated from the surrounding mesenchyme by a muscle layer). Hyman (1935) described a dendrocoelid species from Montana under the name of *D. vaginatus*. Again the main characters of the species coincide with those of *D. spinosipenis* with the exception of the grasping organ, which is of a simpler type. The new Alaskan species, *D. piriformis*, also falls clearly in the vicinity of the species enumerated, as does another species, *D. alaskensis*, the description of which follows on p. 178. Within this group of species there is a gradual differentiation of the grasping organ, which is absent in *D. alaskensis*, present as a moderately developed adhesive organ in *D. vaginata*, *D. piriformis*, *A. brementi*, *A. vandeli*, *A. chattoni*, and *A. garmieri*, and as a more highly developed and muscular sucker in *D. spinosipenis*. A similar wide variation of the structure of the anterior grasping organ

is seen in the genus *Dendrocoelum* Örsted where, however, true suckers are not known. In general, the taxonomic value of adhesive organs in triclads appears to be subordinated to that of other anatomical structures. I therefore tentatively modify the definition of the genus *Dendrocoelopsis* by omitting the presence of a sucker as a generic character, to include the species described as *Dendrocoelopsis* and *Amyadenium*.

Dendrocoelopsis piriformis differs from the other members of the genus (in its wider extent) in several characters: It is pigmented, whereas the others lack pigment and appear white; the presence of two eyes differentiates it from the three blind species, *D. vandeli*, *D. brementi*, and *D. garmieri* and from the many-eyed *D. chattoni;* and the dorsal position of the testes separates it from *D. spinosipenis*, *D. vaginata*, *D. garmieri*, and *D. alaskensis*. Apart from these most conspicuous characters, the structure of the male copulatory organ of *D. piriformis* is distinctive.

Holotype.—On five slides, USNM 22334, Moose Creek, on Glenn Highway, milepost 186, near Alaska Road Commission camp, Aug. 14, 1950.

Distribution and Ecology.—Dendrocoelopsis piriformis is a eurythermic species and inhabits lakes and their outlets in the southern part of Alaska and also occurs in a lake near Umiat.

Long Lake, on Glenn Highway, milepost 85.9, Aug. 11, 1950, clear water, 17.8° C. (near bank); under stones, several specimens, two of them mature.

Lake on Glenn Highway, milepost 88.1, Aug. 11, 1950, water temperature varying with depth (near bank, 19° C.); under stones, several specimens, one mature.

Lake on Glenn Highway, milepost 23.5 (see pl. 8), Aug. 13, 1950, clear water, 23.6° C. (near bank); several immature specimens.

Stream crossing Glenn Highway at milepost 147.2, outlet of Snowshoe Lake, Aug. 14, 1950, moderate current, water somewhat colored, 17.0° C.; one young specimen, under a stone.

Moose Creek, on Glenn Highway, milepost 186, near Alaska Road Commission camp, Aug. 14, 1950, fast, clear stream, 16.2° C.; under stones, two mature specimens (holotype).

Pippin Lake, on Richardson Highway, milepost 84.4, Aug. 15, 1950, shallow water near bank, 20° C.; under stones, many specimens, two of them mature.

Fresh-water lake near Umiat, collected by P. F. Scholander, Aug. 15, 1948; 18 specimens, majority belonging to the plain form, 1 with distinct stripes, 5 sexually mature (USNM 23678).

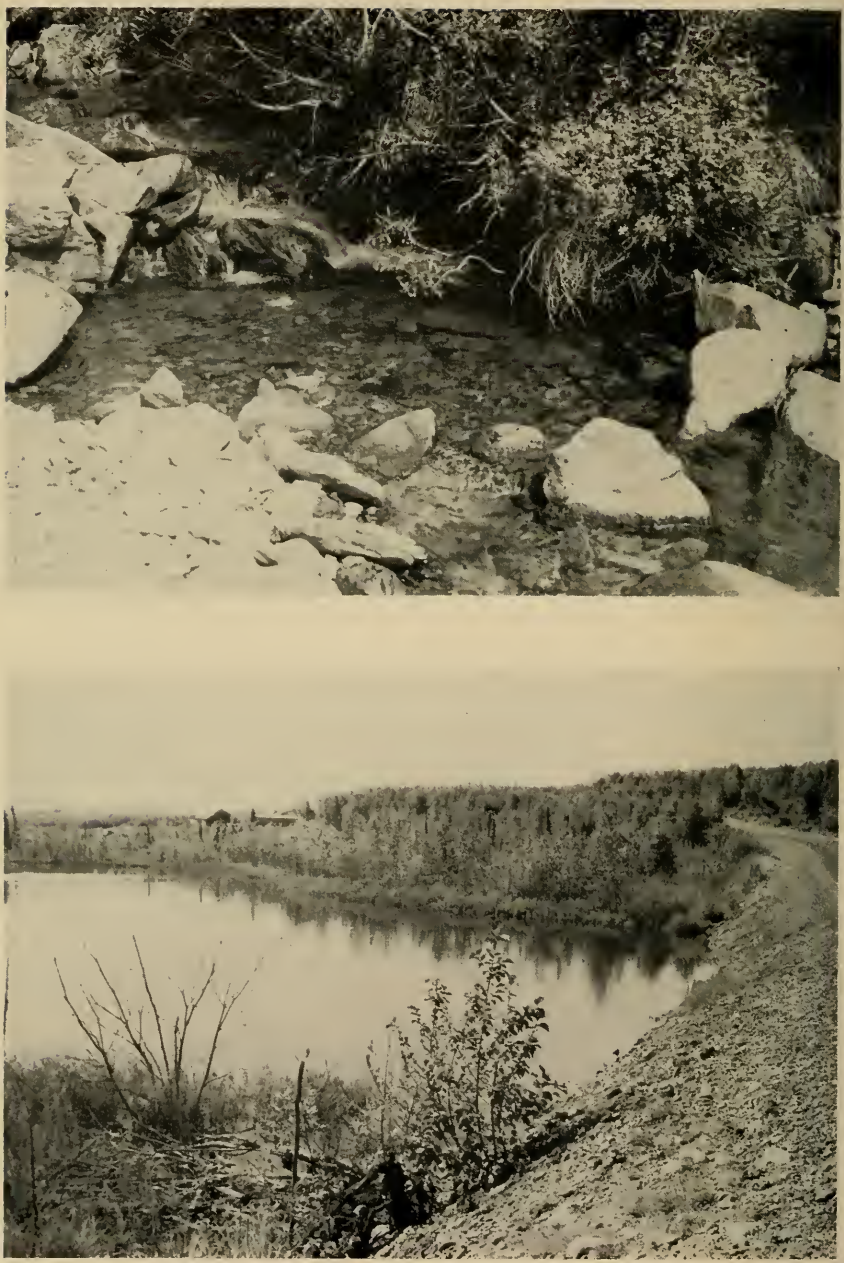
Dendrocoelopsis alaskensis, new species

FIGURE 24; PLATE 6, FIGURE 4

Description.—I had only limited material of this species and none of the animals was fully mature. The largest specimen measured 20 mm. in length and 4 mm. in width.

The anterior end is slightly lobed, with a convex frontal margin

Top: Beaver pond at milepost 62.6 of Richardson Highway, Alaska. Below the beaver dam, *Polycelis borealis* under stones. Bottom: Stream flowing along Richardson Highway, Alaska, at milepost 26.3. On the undersides of stones, *Polycelis borealis*.



Top: Stream crossing Steese Highway, Alaska, at milepost 84.0. Habitat of *Phagocata nivea* and *Dendrocoelopsis alaskensis*. Bottom: Lake at milepost 23.5 of Glenn Highway, Alaska. Under stones near bank, *Dendrocoelopsis piriformis*.

and a pair of rounded auricles protruding both anteriorly and laterally. No distinct adhesive or grasping organ is developed. There is a gentle narrowing of the head (neck) behind the auricles. Behind the head, the width of the body gradually increases until the greatest width is reached. The posterior end is bluntly pointed.

The body lacks pigment, being white except for the contents of the intestine, which may show through the body wall.

There are two principal eyes. The distance between them amounts to about one-third the width of the head at the level of the eyes. The distance of each eye from the frontal margin is equal to, or slightly larger than, the distance from the lateral margin. Additional, supernumerary, eyes were seen in a few individuals at short distances either anterior or posterior to the principal eyes.

The species bears a striking resemblance to a European species, *Dendrocoelum nausicaae* Schmidt of the Balkan Peninsula. It is generally associated with another triclad inhabiting the same streams in Alaska, *Phagocata nivea*, from which it may be distinguished by its larger size and by the position of the eyes.

A distinct adhesive organ is not seen in living animals. In histological sections, a transverse band, pierced by numerous openings of eosinophilic glands, is found below the frontal margin of the head. The nature of the glands and the local differentiation of the epithelium correspond entirely to the structure of the submarginal adhesive zone which is seen in this species, as well as in other triclads, bordering the lateral margins of the body. The frontal adhesive area may, therefore, be interpreted as an extension of the lateral adhesive zone. It is somewhat wider than the lateral one and has no muscular differentiations such as are typical of true grasping organs. The continuity of the two zones is interrupted by a short gap on each side of the head below the auricle.

The internal muscle zone of the pharynx consists of a layer of intermingled circular and longitudinal fibers. This character places the species in the family Dendrocoelidae. The anterior intestinal trunk bears a fairly large number, 21 to 24 pairs, of lateral branches, or diverticula.

Of a total of eight individuals of this species at my disposal, five were young, two showed primordia of genital structures, and only one had the principal parts of the reproductive system developed, though not fully differentiated histologically. The description of the genital organs, therefore, must be given with certain reservations.

The testes are predominantly ventral, situated mainly below the level of the intestinal diverticula, occasionally extending farther dorsally between the diverticula. No clearly recognizable testes were seen behind the level of the mouth; they may, however, appear there

when the animal matures completely. The ovaries are situated behind the third or fourth lateral branch of the anterior intestinal trunk.

The genital pore (*pg*) leads into an undivided cavity, the genital atrium (*a*), which is narrow at the pore and expands anteriorly. The narrow posterior part receives the outlet of the copulatory bursa and, anteriorly to it, the opening of the common oviduct.

The penis has a fairly large, spherical bulb and a plump and short papilla. The bulb contains a cavity with irregular outline, the seminal vesicle (*vs*), into which the two vasa deferentia (*vd*) open separately. The cavity of the bulb continues into the broad papilla and opens at its tip. The bulb has the usual coat of muscle fibers arranged in concentric layers. The papilla, which projects only little into the genital atrium, has two muscle layers underlying the outer epithelium, a circular layer and a longitudinal one. No glandular structures are differentiated in my specimen.

The two oviducts unite, without embracing the bursa duct, dorsally to the genital atrium. The common oviduct (*odc*) opens into the posterior, narrow part of the atrium from the dorsal side.

The bursa (*b*) is, in my specimen, a rather small sac with a narrow lumen. The bursa duct (*bd*) runs posteriorly, above the penis, to a level behind the genital pore. There it turns abruptly toward the ventral side. Its terminal portion is considerably wider than the anterior part of the duct and opens from the posterodorsal side into the genital atrium close to the genital aperture. In full maturity, the widened section of the bursa duct probably represents a histologically distinct vagina.

Taxonomic position.—The systematic relations of *Dendrocoelopsis alaskensis* are discussed together with those of the preceding species, *D. piriformis*. *D. alaskensis* is distinguished from all other species of the genus by the lack of a grasping organ.

Holotype. On seven slides, USNM 22335, creek crossing Elliot Highway at milepost 31.0, July 24, 1950.

Distribution and ecology.—*Dendrocoelopsis alaskensis* is an inhabitant of cool, fast streams of the White Mountains and usually shares its habitat with *Phagocata nivea*. It is a stenothermic and rheophilic species.

Clear spring and creek on Steese Highway, milepost 82.5, at the Alaska Road Commission camp, July 21, 1950; one immature specimen, under a stone.

Stream crossing Steese Highway at milepost 84.0 (see pl. 8), altitude 2,700 feet, July 21, 1950; two immature specimens, under stones, near liver bait.

Creek crossing Elliot Highway at milepost 31.0, July 24, 1950, water temperature 3.2° C.; under stones, five specimens, two of them with sexual structures (holotype).

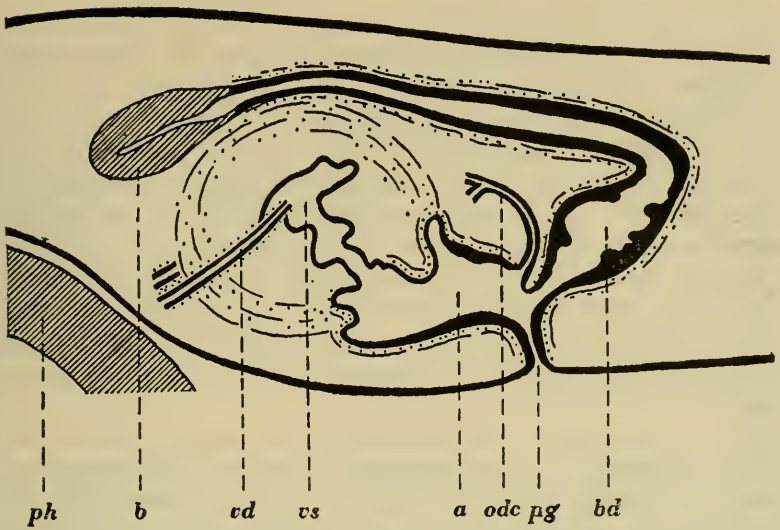


FIGURE 24.—*Dendrocoelopsis alaskensis*, diagram of the copulatory organs in longitudinal section, × 70. *a*, genital atrium; *b*, bursa; *bd*, bursa stalk; *odc*, common oviduct; *pg*, genital pore; *ph*, pharynx (extended through the mouth); *vd*, vas deferens; *vs*, seminal vesicle.

Zoogeographic conclusions

The occurrence in Alaska of four endemic species of triclads poses several interesting questions. It is known that fresh-water triclads are most abundantly represented in the northern Temperate Zone and that the number of species declines toward both the Arctic and the Tropical Zones. The paucity of the triclad fauna at high latitudes has frequently been attributed to the effects of glaciation in rather recent geologic time. During the glacial period, when huge ice masses covered great parts of the northern hemisphere, all fresh-water life over wide areas must have vanished. After the glaciers had receded, the areas were gradually repopulated by species entering them from adjacent territories. The pattern of distribution of freshwater triclads in Europe shows evidence of a definite succession of species which migrated into the previously glaciated areas in the postglacial period (cf. Thienemann's 1950 summary of the pertinent literature).

It is well known, however, that the greater part of Alaska was not covered with ice in the glacial period. Geologic evidence of glaciation has been found only in the Brooks Range, the Alaska Range (and areas south of it), and in small isolated spots in the Yukon and Kuskokwim River Valleys while the remaining surface of Alaska remained free of ice (cf. Geological Society of America,

1945). We are thus justified in assuming that the fresh-water life of Alaska was not completely destroyed even at the peaks of glaciation when practically all Canada and a considerable part of the United States were covered with ice caps.

The Alaskan fresh-water triclads show no close relationships with the present North American triclad fauna inhabiting the midwestern plains and the eastern and southern areas of the continent. A comparison with the fauna of the Rocky Mountains is not possible at present, since the West of the United States and of Canada is almost unexplored with regard to triclads and to lower aquatic invertebrates in general. In any event it appears highly improbable that Alaska was populated by species migrating to it from the south or east.

On the other hand, the relations of the Alaska triclads to the fauna of Eurasia are unmistakable. Though, according to our present knowledge, none of the Alaskan triclads is specifically identical with any Asiatic form, two species, *Phagocata nivea* and *Polycelis borealis*, are very closely related to Asiatic species of the same genera.

Figure 25 shows the geographic range of the genus *Polycelis* as it is known at present. The individual dots on the map represent either single records or groups of neighboring localities where species of the genus have been found. In interpreting the map it is to be kept in mind that not all geographical areas are equally well investigated with regard to the occurrence of lower invertebrates. Europe, Japan, and the eastern parts of the United States are comparatively well known while our knowledge of the Asiatic, Western American, and African triclads is still rather deficient. A study of the map suggests that *Polycelis* is primarily a Eurasian genus. It appears to have extended its range, in some earlier geological period, to the northern rim of Africa.[4] In a similar way it may have migrated into Alaska at the time of the cenozoic land bridges and may have penetrated south along the Rocky Mountains. It is highly probable that *Polycelis* will be found, in the future, more widely distributed in the Rockies than present collection records indicate.

The repeated emergence of a land bridge between Alaska and the eastern tip of Siberia is generally accepted by geologists and paleontologists. There is ample evidence of an exchange of faunal elements between the two continents (cf. Simpson, 1940 and 1947). The most recent corridor must have existed during the glacial stages of the Pleistocene. The volume of ice masses accumulated over vast areas of the northern hemisphere has been estimated conservatively at 34 to 42 million cubic kilometers. The corresponding depletion of

[4] The presence of *Polycelis oculi-marginata* (Palombi) in New Guinea is a zoogeographic enigma (cf. Beauchamp, 1947).

FIGURE 25.—Worldwide distribution of the genus *Polycelis*.

the ocean must have lowered the sea level 50 to 90 meters below the present level (Daly, 1934, pp. 41–50). The depth of the eastern part of the Bering Sea (within the perimeter passing through the eastern projection of Siberia, the Seward Peninsula of Alaska, and Nunivak and St. Lawrence Islands) averages less than 40 meters. Thus the ocean bottom between Alaska and Asia must have emerged with each glacial stage, forming a wide connection between the two continents. This process may have been enhanced by the uplifting of the area along the margin of the ice cap, brought about by plastic or elastic deformation of the earth crust under the weight of the ice masses.

A land bridge between Alaska and Asia must have persisted for prolonged periods of time. Simultaneously, Alaska was disconnected from other inhabitable areas of North America by broad ice fields.

In view of the geological history of Alaska we may conclude that the present Alaskan fresh-water triclads are the remnants or successors of triclads that lived in Alaska in the glacial times and perhaps even in preglacial periods, and that they are, in all probability, of Asiatic origin. It may further be assumed that some Alaskan triclads have extended their range during the postglacial period and proceeded southeast along the Rocky Mountains.[5] The occurrence of a species of *Polycelis* in Wyoming and South Dakota may have resulted from this migration. More light would be thrown on this question by a more thorough study of the triclad fauna of the Canadian and American Rockies.

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[5] I wish here to correct my assumption in a previous paper (Kenk, 1943, p. 6) that all Canadian triclads had entered Canada from the south.

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