of the black oaks are generally acute and bristle-tipped. On this basis the black oaks now recognized in the Latah formation are: *Quercus merriami* and *Q. payettensis*. It is possible that these two should be synonymized. The status of two other species, *Q. simulata* and *Q. consimilis*, has not yet been satisfactorily determined.

Occurrence.—Latah formation (Miocene), on Poorman Creek, 22 miles east of Orofino, Idaho (Fig. 6). Collected by Boyd H. Olson. On Potlatch Creek, between Arrow Junction and Juliaetta, Idaho (Fig. 12). Collected by Roland W. Brown.

Cercidiphyllum crenatum (Unger) Brown Fig. 9

Cercidiphyllum crenatum (Unger) Brown, Jour. Paleont. **9** (7): 575–577, pl. 68, figs. 1, 6, 8–10, 1935.—U. S. Geol. Survey Prof. Paper **186**: 175, 1937.

In my 1935 paper I reported the leaves and capsules, but no seeds, of this species from the reddish shales along Bridge Creek, Oreg. The seeds are small and difficult to detect in the reddish matrix, but recently I succeeded in finding one and its counterpart. These small seeds, averaging 5 mm in length, are generally crescent-shaped, the seed portion being long and slender and about the same length as the wing which is attached laterally to the seed at almost a right angle. Small coniferous seeds (Fig. 8) from the same strata should not be confused with *Cercidiphyllum*, because their wings extend in the direction parallel to the linear axis of the seed.

Occurrence.—Oligocene (according to the usage of the U. S. Geological Survey), 9 miles north of Mitchell, Oreg.

Nymphaeites nevadensis (Knowlton) Brown, n. comb. Fig. 10

Spathyema? nevadensis Knowlton, U. S. Geol. Survey Ann. Rept. **21** (2): 211 pl. 30, figs. 17, 18, 1900.
Unknown plant. Idem, 212, pl. 30, figs. 16, 24, 25.
Nymphaea diatoma MacGinitie, Carnegie Inst. Washington Pub. **416** (2): 55, pl. 7, fig. 6; pl. 8, 1933.
Nymphaeites diatoma (MacGinitie) Arnold, Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 85, 1937.

The impressions described by Knowlton from the Esmeralda formation of Nevada as an "unknown plant" are on the same piece of rock as those he called *Spathyema? nevadensis*. An examination of the surface of a rhizome of a living water lily shows large single petiole scars flanked by aggregates of small root scars; and it is to these, respectively, that Knowlton's specimens correspond.

It is possible that some of the smaller aggregates showing a gradation in size from large to small may be the impressions of the scars on a stem of *Trapa americana*, the nuts of which are abundant in the same strata.

The seeds called *Castalia*? by Berry[6] also from the Esmeralda formation,

[6] BERRY, E. W. *The flora of the Esmeralda formation.* U. S. Nat. Mus. Proc. **72**(23): 12, pl. 1, fig. 1. 1927.

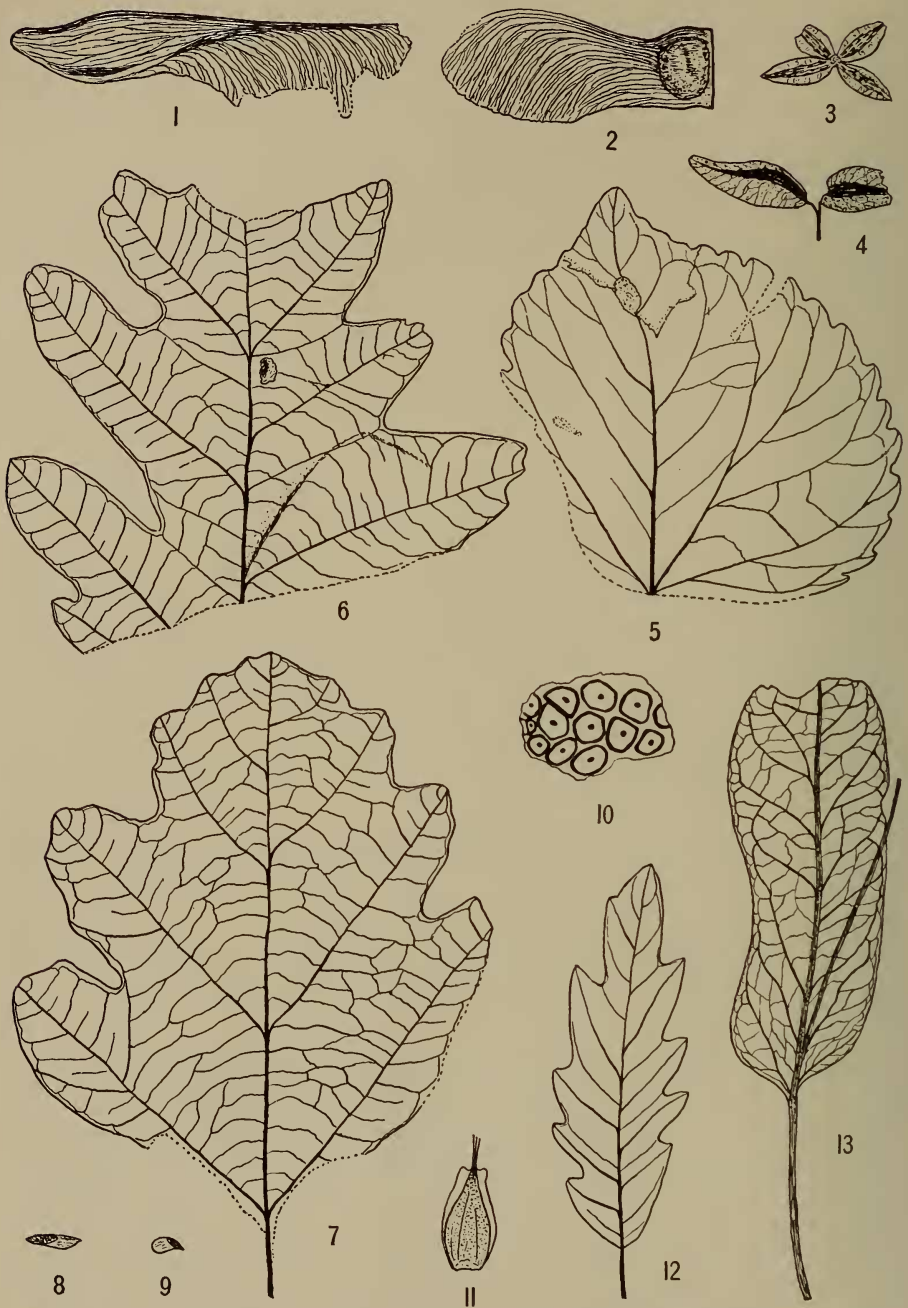

Fig. 1.—*Acer osmonti* Knowlton. Fig. 2.—*Acer scottiae* MacGinitie. Fig. 3.—*Populus jenningsi* Brown, n. sp. Figs. 4, 5.—*Populus lamottei* Chaney & Elias. Figs. 6, 12.—*Quercus columbiana* Chaney. Fig. 7.—*Quercus bretzi* Chaney. Fig. 8.—A coniferous seed. Fig. 9.—Seed of *Cercidiphyllum crenatum* (Unger) Brown. Fig. 10.—Root scars of *Nymphaeites nevadensis* (Knowlton) Brown, n. comb. Fig. 11.—Nut of *Fagus pacifica* Chaney. Fig. 13.—Fruit bract of *Tilia aspera* (Newberry) LaMotte. All figures natural size.

may have been produced by *Nymphaeites nevadensis*, but as their identity is in doubt, they are not now synonymized with the latter species. It is not possible to determine from Arnold's sketch whether his *N. rotundus*, also from Trout Creek, should be synonymized here.

The fossil figured here (Fig. 10) is an aggregate of circular to polygonal root scars showing central pits.

Occurrence.—Miocene. Esmeralda formation, Nev.; Trout Creek, Oreg.; Payette formation, on east side of Snake River, 12 miles west of Weiser, Idaho (Fig. 10). Collected by Roland W. Brown.

Amelanchier dignatus (Knowlton) Brown

Celastrus dignatus Knowlton, U. S. Geol. Survey Bull. **204**: 71, pl. 11, fig. 5, 1902.

Phyllites couleeanus Berry, U. S. Geol. Survey Prof. Paper **170**: 42, pl. 13, fig. 12, 1931.

Amelanchier scudderi Cockerell. Berry, U. S. Geol. Survey Prof. Paper **154**: 252, pl. 55, fig. 4, 1929.

Amelanchier dignatus (Knowlton) Brown, Jour. Paleont. **9**: 577, pl. 69, figs. 5, 6, 1935.—U. S. Geol. Survey Prof. Paper **186**: 176, pl. 53, fig. 11, 1937.

Amelanchier magnifolia Arnold, Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 89, pl. 4, figs. 1, 4, text figs. 2, 3, 1937.

Since my publication of the new combination, *Amelanchier dignatus* (Knowlton) Brown, in 1935, I have compared the specimens there combined with recently acquired new material and have concluded that the types of *A. peritula* Cockerell and *A. scudderi* Cockerell, from Florissant, Colo., and of *A. grayi* Chaney, from Crooked River, Oreg., on both stratigraphic and morphologic grounds, are different from *A. dignatus* and should not be synonymized with it. The three species thus removed from *A. dignatus* may represent a single species, but they at least are uniformily smaller and display sharper apexes than *A. dignatus*. Arnold's *A. magnifolia* is clearly the same as *A. dignatus* as can be seen by comparing his figures with Knowlton's *Celastrus dignatus* and Berry's *Phyllites couleeanus*. The statement that the leaves of the living *A. alnifolia* are *much* smaller than those of *A. magnifolia* is unfortunate. It is true that the average leaf of *A. alnifolia* is smaller, but in my herbarium material of *A. alnifolia* collected in Idaho in 1934 are specimens that easily match Arnold's figures of *A. magnifolia*.

Cedrela merrilli (Chaney) Brown, n. comb.

Rhus merrilli Chaney, Carnegie Inst. Washington Pub. **346** (4): 125, pl. 16, figs. 1, 2, 1927.

Cedrela pteraformis (Berry) Brown, Jour. Paleont. **9** (7): 579, 1935. Referring only to *Acer* sp.? Newberry.— U. S. Geol. Survey Prof. Paper **186**: 179, 1937. Referring only to *Pinus knowltoni* Chaney [Mason].

Although the resemblance between the fossil leaflets called *Rhus merrilli* to those of the living *Rhus sylvestris*, of China, is very striking, as pointed out

by Chaney, two considerations cast doubt on their identification as *Rhus*. First, between the secondaries of *R. sylvestris* there are usually two or more very prominent, short, intermediate secondaries, but in the fossil leaflets these intermediates are thin, few, and commonly, none. Second, the winged seeds of *Cedrela* have been found in the same strata as the leaflets. Because these leaflets can be matched easily with those from living species of *Cedrela* and because they are associated with *Cedrela* seeds it seems more probable that they represent *Cedrela* than *Rhus*.

In 1935 when I made the discovery that the winged seeds theretofore identified as *Acer* and *Gordonia* were in reality *Cedrela*, I was unaware that fossils of this genus were of widespread occurrence in the middle Cenozoic floras of the western States. Since then, remains of *Cedrela*, either leaflets, capsules, or seeds, have been identified in the collections from Florissant, Colo.; Crooked River and Bridge Creek, Oreg.; Mascall formation, John Day basin, Oreg.; Tipton, Sumpter quadrangle, Oreg.; Sucker Creek, Oreg.; 49 Camp, Nev.; Hog Creek, Idaho; and Latah formation, Spokane, Wash. These occurrences cover a large area, geographically, and a span of time from upper Oligocene to early Pliocene. It seems probable therefore, that, instead of a single species, *Cedrela pteraformis*, several species were in existence during that interval. Can these postulated species be distinguished in the fossil materials now at hand?

The earliest western species now known, *Cedrela lancifolia* (Lesquereux) Brown[7] from Florissant, has narrowly lanceolate leaflets and small seeds. It can apparently be separated readily from the other species which exhibit great variability in the size and form of their leaflets and seeds.

The leaflets from Crooked River and Bridge Creek, Oreg., are uniformly elongate elliptic. Those from the Latah formation are in general relatively short, elliptic in outline, with rather blunt apexes. Those from the John Day basin, Trout Creek, and Sucker Creek, Oreg., are lanceolate to broadly ovate-lanceolate with rather acute apexes. As regards the seeds from these several localities I have not yet detected in them such morphologic differences as would serve to distinguish them specifically, but I assume that the capsules and seeds found at any given locality belong with the leaves occurring in the same formation.

The fossil species of *Cedrela* from the western United States, on the basis of differences in foliage, therefore, now appear to be: *C. lancifolia* (Lesquereux) Brown, *C. merrilli* (Chaney) Brown, *C. oregoniana* (Lesquereux) Brown, and *C. pteraformis* (Berry) Brown.

Occurrence.—Oligocene (according to the usage of the U. S. Geological Survey), Gray ranch, Crooked River basin; and 9 miles north of Mitchell, Bridge Creek basin, Oreg.

[7] Brown, Roland W. *Additions to some fossil floras of the western United States.* U. S. Geol. Survey Prof. Paper **186**: 178, pl. 60, figs. 3, 4. 1937.

Cedrela oregoniana (Lesquereux) Brown, n. comb.

Ficus? *oregoniana* Lesquereux, U. S. Nat. Mus. Proc. **9**: 18, pl. 9, fig. 3, 1888.—Knowlton, U. S. Geol. Survey Bull. **204**: 56, pl. 10, fig. 3, 1902.

Sapindus oregonianus Knowlton. LaMotte, Carnegie Inst. Washington Pub. **455** (2): 37, pl. 1, figs. 2, 3, 5; pl. 2, figs. 1–4; pl. 3, figs. 2, 4, 5, 1935.

Sapindus affinis Newberry? MacGinitie, Carnegie Inst. Washington Pub. **416** (2): 60, 1933.

Cedrela browniana Arnold, Amer. Midland Naturalist **17** (6): 1019, fig. 11, 1936.—Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 95, pl. 7, figs. 1, 2, 1937.

Cedrela trainii Arnold, Amer. Midland Naturalist **17** (6) : 1018, figs. 1, 2, 1936.—Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 95, pl. 6, figs. 1–3, 6, 1937.

Apocynum indiana MacGinitie, Carnegie Inst. Washington Pub. **416** (2): 66, pl. 12, fig. 1, 1933.

Cedrela pteraformis (Berry) Brown, U. S. Geol. Survey Prof. Paper **186**: 179, pl. 60, fig. 9, 1937. Including also *Pinus monticolensis* Berry [LaMotte], *Pinus russelli* LaMotte, *Pseudotsuga masoni* MacGinitie [LaMotte], *Libocedrus* sp. Dorf, and *Cedrela pteraformis* (Berry) Brown in Arnold, Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 95, pl. 6, figs. 4. 7–10, 1937.

The leaflets of this species were characterized in the preceding discussion of *Cedrela merrilli*.

Occurrence.—49 Camp, Nev.; Mascall formation (Miocene), John Day basin, Oreg.; Tipton, Oreg.; Trout Creek, Oreg.; Sucker Creek, Oreg.; Hog Creek (according to Dorf, Upper Miocene or lower Pliocene), Idaho.

Cedrela pteraformis (Berry) Brown

Cedrela pteraformis (Berry) Brown, Jour. Paleont. **9** (7): 579, 1935. Referring only to *Carpolithus pteraformis* Berry and *Gordonia pteraformis* Berry. —U. S. Geol. Survey Prof. Paper **186**: 179, pl. 52, fig. 12; pl. 60, figs. 5–8, 10, 1937. Referring only to *Umbellularia dayana* (Knowlton) Berry and *Sapindus armstrongi* Berry.

Cassia spokanensis Berry, U. S. Geol. Survey Prof. Paper **156**: 253, pl. 63, fig. 8, 1929.

The specimen called *Cassia spokanensis* by Berry is the impression of a large capsule that simulates those of *Cedrela*. The seeds of *Cedrela* are abundant in the Latah formation at Spokane, Wash.

The leaflets of this species were characterized in the discussion of *Cedrela merrilli*.

Occurrence.—Latah formation (Miocene), Spokane, Wash.

Acer osmonti Knowlton Fig. 1

Acer osmonti Knowlton, U. S. Geol. Survey Bull. **204**: 72, pl. 13, fig. 3, 1902. —Brown. U. S. Geol. Survey Prof. Paper **186**: 180, pl. 58, figs. 16–18, 1937. (See synonymy and discussion.)

Rhus diluvialis Arnold, Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 93, pl. 5, fig. 4, 1937.

Both the samaras and leaves of this species are clearly of the silver maple (*Acer saccharinum*) type and may be readily identified. The fragment figured by Arnold as *Rhus diluvialis* is the lobe, probably apical, of a leaf of *A. osmonti*. The living *Rhus trilobata* to which this fragment was compared has rounded not sharp marginal teeth as displayed by the fossil. In the Sucker Creek collection of the U. S. National Museum are specimens of *Acer bendirei* Lesquereux, *A. glabroides* Brown, and *A. osmonti* Knowlton.

Occurrence.—Latah formation (Miocene) on Orofino Creek, 20 miles east of Orofino, Idaho. Collected by Boyd H. Olson.

Acer scottiae MacGinitie Fig. 2

Acer scottiae MacGinitie. Carnegie Inst. Washington Pub. **416** (2):62, pl. 11, figs. 4, 8; pl. 12, fig. 4, 1933.

Acer septilobatum Oliver. Dorf, Carnegie Inst. Washington Pub. **476** (2):122, pl. 3, fig. 5, 1936.

The samara figured here (Fig. 2) is almost identical with that figured by Dorf. Both, however, differ somewhat from the type in having the distal end of the wing less prominently upturned. All, having long, squarely truncated, proximal ends (the line of attachment to the twin), seem clearly to belong to the Platanoidea section of *Acer*.

Occurrence.—Diatomite (probably the Idaho formation of Kirkham) in road cut 11 miles south of Horseshoe Bend toward Boise, Idaho. Collected by Roland W. Brown and Don Emigh, Aug. 25, 1934.

Tilia aspera (Newberry) LaMotte Fig. 13

Tilia aspera (Newberry) LaMotte, Carnegie Inst. Washington Pub. **455** (3): 45, pl. 1, figs. 1–3; pl. 2, figs. 1, 2, 1933.

Tilia oregona LaMotte. Idem, 47, pl. 3, fig. 6. [*Platanus aspera* Newberry, U. S. Geol. Survey Mon. **35**: 102, pl. 59, fig. 3. 1898.]

Tilia sp. Arnold, Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 94, pl. 5, fig. 1, 1937.

The fragmentary bract figured here (Fig. 13) is the sole evidence of *Tilia* so far reported from Sucker Creek, Oreg. A portion of the peduncle bearing the fruit is preserved, and that is connate with the midrib of the bract for only a short distance. The peduncle of the bract, it should be noted, is unusually long as compared with those of most living species of *Tilia*.

The leaf originally called *Platanus aspera* Newberry, from Bridge Creek, Oreg., and referred by LaMotte to *Tilia oregona*, is a small leaf of *T. aspera*, because it has the long, coarse teeth and the conspicuously asymmetric base that characterize the latter species.

Occurrence.—Miocene, on Sucker Creek, near the Idaho-Oregon boundary.

Nyssa hesperia Berry

Nyssa knowltoni Berry. Brown, U. S. Geol. Survey Prof. Paper **186**: 184, pl. 62, figs. 1–3, 1937. [Not *Nyssa knowltoni* Berry, U. S. Geol. Survey Prof. Paper **154**: 261, pl. 59, fig. 7, 1929.]

Nyssa hesperia Berry, U. S. Geol. Survey Prof. Paper **170**: 42, pl. 13, figs. 9–11, 1931.

With the acquisition of new material from the Latah formation at Spokane, Wash., it becomes apparent that the specimens figured by me as *Nyssa knowltoni* in 1937 differ so markedly in form and secondary venation from the type described by Berry in 1929 that they should be segregated from the latter and retain the name *N. hesperia*. Whether the type of *N. knowltoni* is in reality a *Nyssa* is problematical. Its form and venation find counterparts in some of the leaves of the living *Magnolia acuminata* and also in the entire, somewhat asymmetric leaflets of *Rhus toxicodendron*.

CHANGES OF NAME AND NEW COMBINATIONS

Acer aquilum Chaney (Contrib. from Walker Mus. **2** (5): 178, pl. 17, figs. 4, 5; pl. 18, fig. 1; pl. 19, fig. 1, 1920)—*Acer negundoides* MacGinitie.

Acer completum Chaney (idem, 179, pl. 18, fig. 2)—*Acer negundoides* MacGinitie.

Acer merriami Knowlton (U. S. Geol. Survey Bull. **204**: 74, pl. 14, fig. 7, 1902) = *Platanus dissecta* Lesquereux.

Acer septilobatum Oliver (Carnegie Inst. Washington Pub. **455** (1): 25, pl. 4, figs. 1, 2, 1934) = *Acer bendirei* Lesquereux. The coarse marginal teeth distinguish this species from the *circinnatum* type to which it was likened, and relate it to the *macrophyllum* type. I can match Oliver's septilobate leaves with specimens of *macrophyllum* I collected near You Bet, Calif., in 1936.

Acer septilobatum Oliver. Dorf (Carnegie Inst. Washington Pub. **476** (2): 122, pl. 3, fig. 5, 1936) = *Acer scottiae* MacGinitie.

Acer sp.? Newberry (U. S. Geol. Survey Mon. **35**: 115, pl. 46, fig. 8, 1898) = *Cedrela merrilli* (Chaney) Brown, n. comb.

Amelanchier magnifolia Arnold (Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 89, pl. 4, figs. 1, 4, text figs. 2, 3, 1937) = *Amelanchier dignatus* (Knowlton) Brown.

Apocynum indiana MacGinitie (Carnegie Inst. Washington Pub. **416** (2): 66, pl. 12, fig. 1, 1933) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Cassia spokanensis Berry (U. S. Geol. Survey Prof. Paper **156**: 253, pl. 63, fig. 8, 1929) = *Cedrela pteraformis* (Berry) Brown.

Cedrela browniana Arnold (Amer. Midland Naturalist **17** (6): 1019, fig. 11, 1936) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Cedrela trainii Arnold (idem, 1018, figs. 1, 2) = *Cedrela oregoniana* (Lesquereux) Brown n. comb.

Cedrela pteraformis (Berry) Brown (part) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Cercidiphyllum crenatum (Unger) Brown. Chaney and Elias (Carnegie Inst. Washington Pub. **476** (1): 35, pl. 4, figs. 4, 5, 1936) = *Populus lamottei* Chaney & Elias.

Diospyros elliptica Knowlton (U. S. Geol. Survey Bull. **204**: 83, pl. 16, figs. 5, 1902) = *Castanopsis convexa* (Lesquereux) Brooks.

Fagus? *bonnevillensis* Chaney (Contrib. from Walker Mus. **2** (5): 167, pl. 11, fig. 1, 1920) = *Fagus washoensis* LaMotte.

Ficus? *oregoniana* Lesquereux. Knowlton (U. S. Geol. Survey Bull. **204**: 56, pl. 10, fig. 3, 1902) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Libocedrus sp. Dorf (Carnegie Inst. Washington Pub. **476** (2): 108, pl. 1, fig. 4, 1936) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Liriodendron trilobatum Chaney (Contrib. from Walker Mus. **2** (5): 173, pl. 14, fig. 4) = *Acer negundoides* MacGinitie.

Nymphaea diatoma MacGinitie (Carnegie Inst. Washington Pub. **416** (2): 55, pl. 7, fig. 1, 1933) = *Nymphaeites nevadensis* (Knowlton) Brown, n. comb.

Nymphaeites diatoma (MacGinitie) Arnold (Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 85, 1937) = *Nymphaeites nevadensis* (Knowlton) Brown, n. comb.

Nyssa knowltoni Berry (part) = *Nyssa hesperia* Berry.

Philadelphus bendirei (Knowlton) Chaney. Arnold (Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 88, pl. 3, fig. 4, 1937) = *Sassafras hesperia* Berry. Arnold's leaf figured as *Philadelphus bendirei* is a fragment of an unlobed leaf of *Sassafras hesperia*.

Picea? sp. Chaney (Contrib. from Walker Mus. **2** (5): 159, pl. 5, fig. 2, 1920) = *Betula fairii* Knowlton.

Pinus knowltoni Chaney. Mason (Carnegie Inst. Washington Pub. **346** (5): 148, pl. 2, fig. 3, 1927) = *Cedrela merrilli* (Chaney) Brown, n. comb.

Pinus monticolensis Berry. LaMotte (Carnegie Inst. Washington Pub. **455** (5): 110, pl. 5, figs. 1, 4, 1936) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Pinus russelli LaMotte (Carnegie Inst. Washington Pub. **455** (5): 110, pl. 5, figs. 2, 3, 1936) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Populus lindgreni Knowlton. LaMotte (Carnegie Inst. Washington Pub. **455** (5): 115, pl. 5, fig. 1, 1936) = *Populus washoensis* Brown, new name. The type of *P. lindgreni* Knowlton has numerous, relatively small, somewhat crenate, rounded, marginal teeth, whereas the specimen figured by LaMotte has few, large, dentate, blunt-pointed teeth, and a longer, slenderer petiole.

Pseudotsuga masoni MacGinitie. LaMotte (Carnegie Inst. Washington Pub. **455** (5): 111, pl. 2, figs. 6, 7, 1936) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Quercus duriuscula Knowlton. Dorf (Carnegie Inst. Washington Pub. **476** (2): 114, pl. 2, fig. 8, 1936) = *Quercus columbiana* Chaney.

Quercus spokanensis Knowlton (U. S. Geol. Survey Prof. Paper **140**: 37, pl. 19, fig. 3, 1926) = *Castanea orientalis* Chaney.

Quercus sp., unnamed leaf. Berry (U. S. Geol. Survey Prof. Paper **156**, pl. 50, fig. 15, 1929) = *Salix spokanensis* (Berry) Brown.

Rhus diluvialis Arnold (Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 93, pl. 5, fig. 4, 1937) = *Acer osmonti* Knowlton.

Rhus merrilli Chaney (Carnegie Inst. Washington Pub. **346** (4): 125, pl. 16, figs. 1, 2, 1927) = *Cedrela merrilli* (Chaney) Brown, n. comb.

Rhus payettensis Knowlton (U. S. Geol. Survey Ann. Rept. **18** (3): 733, pl. 101, figs. 6, 7, 1898) = *Fraxinus idahoensis* Brown.

Sapindus affinis Newberry? MacGinitie (Carnegie Inst. Washington Pub. **416** (2): 60, 1933) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Sapindus oregonianus Knowlton (U. S. Geol. Survey Bull. **204**: 79, pl. 15, fig. 3, 1902) = *Castanopsis convexa* (Lesquereux) Brooks.

Sapindus oregonianus Knowlton. LaMotte (Carnegie Inst. Washington Pub. **455** (2): 37, pl. 1, figs. 2, 3, 5; pl. 2, figs. 1–4; pl. 3, figs. 2, 4, 5, 1935) = *Cedrela oregoniana* (Lesquereux) Brown, n. comb.

Scale. Chaney (Contrib. from Walker Mus. **2** (5): 181, pl. 22, fig. 5, 1920) = *Libocedrus praedecurrens* Knowlton.

Spathyema? *nevadensis* Knowlton (U. S. Geol. Survey Ann. Rept. **21** (2):

211, pl. 30, figs. 17, 18, 1900) = *Nymphaeites nevadensis* (Knowlton) Brown, n. comb.

Sterculia aceroides Knowlton (U. S. Geol. Survey Prof. Paper **131**: 191, pl. 43, fig. 12, 1923) = *Mahonia marginata* (Lesquereux) Arnold.

Tilia sp. Arnold (Contrib. Mus. Paleont., Univ. of Mich. **5** (8): 94, pl. 5, fig. 1, 1937) = *Tilia aspera* (Newberry) LaMotte.

Tilia oregona LaMotte (Carnegie Inst. Washington Pub. **455** (3): 45, pl. 1, fig. 6, 1935. [*Platanus aspera* Newberry, U. S. Geol. Survey Mon. **35**: 102, pl. 59, fig. 3, 1898]) = *Tilia aspera* (Newberry) LaMotte.

Unknown plant. Knowlton (U. S. Geol. Survey Ann. Rept. **21** (2): 212, pl. 30, figs. 16, 24, 25, 1900) = *Nymphaeites nevadensis* (Knowlton) Brown, n. comb.

ZOOLOGY.—*The histology of nemic esophagi.* VIII. *The esophagus of representatives of the Enoplida.*[1]

B. G. CHITWOOD, Bureau of Animal Industry, and M. B. CHITWOOD.

This paper is the eighth of a series (Chitwood and Chitwood, 1934–1936) describing the esophagi of representatives of various groups of the Nematoda. In previous papers representatives of the suborders Rhabditina, Strongylina, Ascaridina, Chromadorina, and Monhysterina have been studied. The present paper deals with representatives of the three suborders of the Enoplida, namely, Enoplina, Dorylaimina, and Diocotophymatina. Of the free-living representatives of this group only *Enoplus*, *Oncholaimus*, *Thoracostoma*, *Cylicolaimus*, and *Dorylaimus* have received any attention by previous authors and even these were not studied from the standpoint of nuclear distribution and nuclear constancy. Among the parasitic forms *Hexamermis*, *Trichuris*, *Trichinella* and *Capillaria* have been studied, but recent observations (Chitwood, 1935) make it necessary to reinvestigate the esophagi of the trichuroids and mermithoids from the comparative standpoint. References to the results of previous authors will be made in the text wherever closely related forms are treated.

The nomenclature and general approach in this paper is the same as that in previous papers and is explained in Part I of the series. As in the sixth paper of the series, data are presented in tabular form, wherever possible, in order to avoid extended descriptions.

Prionchulus muscorum (Mononchidae)

The esophagus of this species is cylindrical, only slightly larger at the posterior end than at the anterior end, and its proximal end surrounds the basal part of the stoma. Grossly, the anterior part differs from the posterior part in being completely muscular, the posterior part containing lobulations of the esophageal glands. The lumen varies with the region of the esophagus but retains a peculiarly modified triradiate character throughout its length.

[1] Received August 13, 1937.

This is due to 6 thickenings of the esophageal lining which serve as attachment points for the radial muscles.

The esophagus cannot clearly be subdivided into regions homologous with those of rhabditids, but in general the muscular part is comparable to the corpus and the glandular part to the bulbar region. There are 36 radial muscle nuclei arranged in 6 groups, the first and second groups (r_{1-12}) being anterior to the nerve ring, and the fourth, fifth, and sixth groups (r_{13-36}) posterior to the nerve ring. The nuclei of the first two groups are considerably smaller than those of the remaining groups.

There are 9 marginal nuclei arranged in 3 groups, the first group (m_{1-3}) being immediately anterior to the third group of radial nuclei (r_{13-18}), the second (m_{4-6}) lying between the fourth and fifth groups of radial nuclei (r_{19-24} and r_{25-30}) and the third group (m_{7-9}) near the base of the esophagus and near the level of the sixth group of radial nuclei (r_{31-36}).

There are 44 nerve cell nuclei, 25 being situated anterior and 22 posterior to the fourth group of radial nuclei. The peculiarities of the pattern of distribution of nerve cell nuclei are distinctive and, with modifications, characteristic of the Enoplina and close relatives.

Five esophageal gland nuclei are present, 1 (g_1) in the dorsal sector and 2 (g_{2-4}) in each of the subventral sectors. The dorsal nucleus lies anterior to the others, near the fourth group of radial nuclei (Fig. 2) while the subventral nuclei are arranged in tandem and posterior to the fifth group of radial nuclei. Each esophageal gland possesses a separate opening close to the nucleus.

The esophago-intestinal valve consists of a short internal triradiate layer of tissue outside of which there is a circular layer, the whole containing 22 nuclei.

Tripyla papillata (Tripylidae)

The esophagus of this species is cylindrical throughout, terminating in a complex, lobular, esophago-intestinal valve. The stoma is rudimentary, the stomatal region being entirely surrounded by esophageal tissue; the lumen is simple, triradiate, and the lining without thickened attachment points for the radial muscles which are dispersed throughout the sectors rather than concentrated in special areas.

There are 36 radial nuclei, 12 marginal nuclei, 45 nerve cell nuclei, 5 gland cell nuclei and 1 nucleus (s_1) of undetermined character. The relative position of most of the nuclei is essentially the same as in *Prionchulus* except that there are 4 groups of marginal nuclei instead of 3, the fourth group being situated anterior to the first group of radial nuclei; the dorsal esophageal gland nucleus (g_1) is situated posterior to n_{39} in *Tripyla* whereas in *Prionchulus* it is anterior to n_{28}.

The dorsal gland nucleus is the largest nucleus of the esophagus; the gland in which it lies opens through the small dorsal denticle at the base of the stomatal region; throughout the anterior part of the esophagus the gland is small and occupies only a small part of the dorsal sector, but becomes lobed and extensive in the posterior part of the esophagus. The nuclei of the first pair of subventral glands are but little larger than the radial nuclei, and those of the second pair are intermediate in size between the first pair of subventral gland nuclei and the dorsal gland nucleus. The first pair of subventral glands have orifices near the level of the dorsal gland orifice, while the second pair appears to have separate orifices situated near the nerve ring, a short distance anterior to their nuclei; no subventral gland tissue extends anterior to the fifth group of radial nuclei.

The posterior lobed structure (commonly termed the "pseudobulb,") at the base of the esophagus apparently represents an unusual development of the esophago-intestinal valve and does not correspond to the base of the esophagus as commonly supposed. The external, lobed part of this structure contains 7 large nuclei and the internal part of this structure contains about 96 small nuclei; some of these nuclei lie in a triradiate tissue surrounded by the external lobed layer, while the others lie posterior to this structure; the anterior (internal) portion is continuous posteriorly with the intestine. The above-described formation is homologous with the "pseudobulb" of *Trilobus* and does not correspond to the bulbar region of other nematodes.

Prismatolaimus sp. (Tripylidae)

The prismatolaim esophagus resembles that of *Tripyla* in being cylindrical and terminating in a massive esophago-intestinal valve; here, however, the resemblance ceases. There is a well developed cylindroid stoma surrounded only at its base by esophageal tissue, and there are three inconspicuous teeth projecting from the base of the stoma which are very similar to those of the oncholaims. The lumen is simple, with very faint indications of terminal dilation of the radii; the lining is unmodified but the radial muscles are concentrated rather than dispersed as in *Tripyla*.

The radial nuclei (30 in number) as well as the marginal and nerve cell nuclei are arranged in a pattern somewhat closer to that found in *Eurystomina* than to that occurring in any other form. The five subequal esophageal gland nuclei are located in the posterior part of the esophagus, and a gland duct extends anteriad through the center of each sector to the anterior end where each opens into the stoma through an orifice in the corresponding tooth. Orifices of the second pair of subventral glands, if separate from the first pair, are probably situated near the nerve ring.

The esophago-intestinal valve is triradiate, massive and apparently contains 13 nuclei.

Aliamus sp. (Alaimidae)

The esophagus of this form consists of a rather elongate anterior part and a moderately short, wide, glandular posterior part. Since the stoma is rudimentary, the stomatal region is surrounded by esophageal tissue. A complete enumeration of the nuclei was not possible. There are 5 subequal esophageal gland nuclei, the nucleus of the dorsal gland being slightly larger than the nuclei of the subventral glands; the orifice of the dorsal gland is situated at the base of the stomatal region while those of the subventral glands are in the posterior part of the esophagus. The radial muscles are concentrated but no attachment points are present. The esophago-intestinal valve is short, triradiate, and appears to contain 9 nuclei.

Metoncholaimus pristiurus (Oncholaimidae)

The esophagus of *Metoncholaimus pristiurus* is cylindrical, and esophageal tissue surrounds only the base of the stoma. Grossly, the anterior and posterior parts of the esophagus are very similar; the part of the esophagus anterior to the nerve ring is uniformly muscular while in the part posterior to the nerve ring the muscle tissue is broken up to a slight extent by lobulations of the esophageal glands. The lumen is simple, closed and triradiate throughout, and the cuticular lining is thin and without modified regions for the attachment of muscles.

There are 12 marginal nuclei arranged in 4 groups of 3 nuclei each, this distribution being similar to that in *Tripyla* except that the third group of marginals is between the third and fourth groups of radial nuclei instead of between the fourth and fifth groups of radials as in *Tripyla*. The radial nuclei are only 27 in number; they are arranged in 4 groups of 6, and 1 group of 3 radial nuclei each. The first three groups undoubtedly correspond to the first 3 groups of radial nuclei in other forms; the fourth group corresponds to

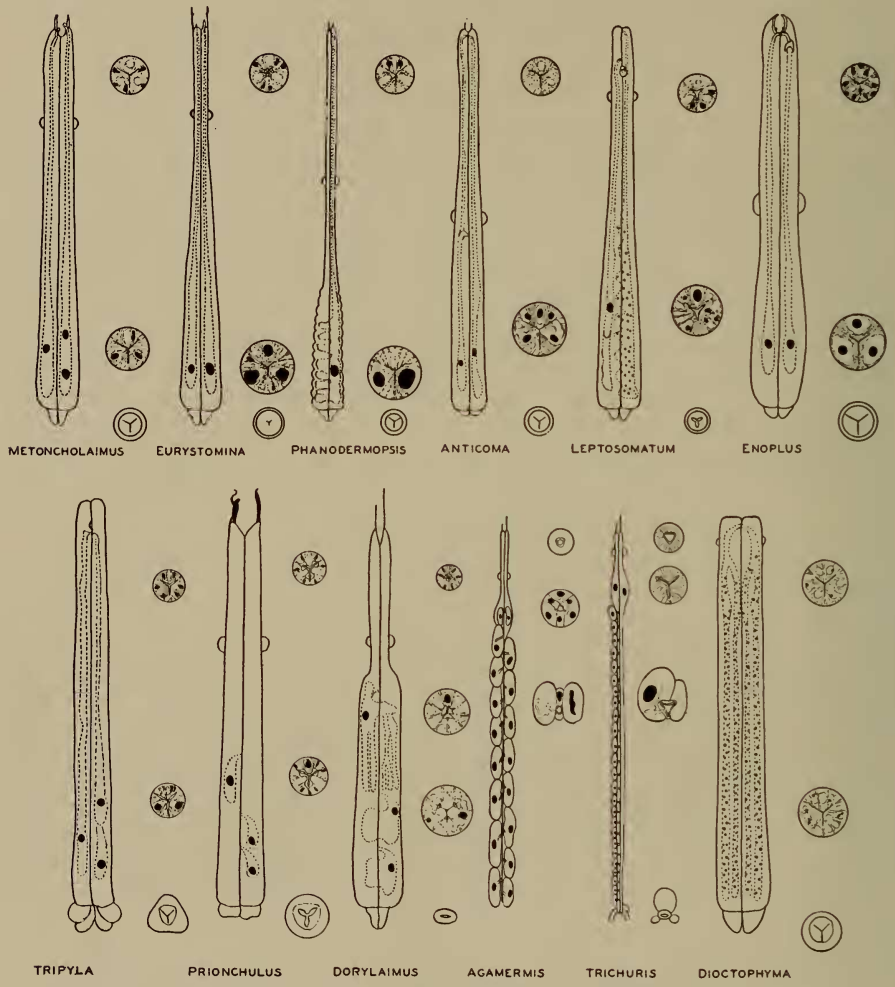

Fig. 1.—Diagrams of esophagi in the Enoplida.

the fifth group in other forms. The last group (r_{25-27}) is composed obviously of giant nuclei resulting from the failure of one nuclear division (Fig. 2). There are 43 nerve cell nuclei which correspond in general to the nerve cell nuclei described in previous forms; the chief differences from forms such as *Tripyla* is that there is 1 additional nucleus (n_{43}) in the mid-dorsal row an-

terior to the peculiar dorsal group (n_{29-32}) and there are 2 less subdorsal nerve cell nuclei at the posterior end of the esophagus (n_{43-44} of *Tripyla*).

Three esophageal glands open into the stoma through the 3 teeth. From their orifices posteriorly, each gland is represented by a small strand of tissue containing the duct in the center of each sector extending approximately to the level of n_{30-31}; posterior to this level they become branched and enter other intermuscular regions of the sectors. Rauther (1907) described *Oncholaimus* sp. (*?vulgaris*) as having 5 esophageal glands, 1 dorsal, 2 lateral, and 2 ventral. The lateral glands according to Rauther, open into the lumen some distance from the anterior end of the esophagus. In *Metoncholaimus pristiurus*, however, the present writers observed 1 dorsal and 4 subventral glands, all 5 nuclei being approximately the same size. In so far as the writers have been able to observe, the 2 subventral glands of each sector have but 1 orifice and their cytoplasm is continuous. If additional orifices are present, they are probably situated near the subdorsal margins of the subventral sectors near n_{30-31}.

The esophago-intestinal valve is elongated, triradiate and consists of an internal trilobed layer containing radial fibers, and a double external layer of circular fibers; the whole is inclosed in a trilobed mass of tissue. The nuclei are numerous (number not determined). A single large nucleus, similar to those of the radial muscle tissue of the esophagus, is situated at the junction of the esophagus and the esophago-intestinal valve.

Eurystomina americana (Oncholaimidae)

The esophagus of this species is of the type generally termed "conoid"; the anterior end is narrow and muscular, gradually increasing in diameter posterior to the nerve ring, the posterior third being wide, glandular, and cylindrical. The lumen is simple, triradiate, but the esophageal lining carries paired cuticular thickenings in the form of attachment points for the radial muscles; these thickenings, similar to those of *Prionchulus*, *Dorylaimus*, *Ironus* and *Cryptonchus*, extend from the anterior end of the esophagus to a short distance posterior to the nerve ring or approximately to the beginning of the glandular part of the esophagus.

The number (12) and arrangement of marginal nuclei is like that in *Tripyla* and *Oncholaimus*. There are 44 nerve-cell nuclei as in *Tripyla* and *Prionchulus*, the first 28 of which are arranged as in those forms, while the remainder differ in many respects in their distribution. Only 30 radial nuclei are present, these being arranged in 5 groups of 6 each. Only 3 nuclei have been identified with certainty as belonging to the esophageal glands; all three of these nuclei are gigantic, the right subventral being considerably larger than the other two. All three glands open through teeth into the cavity of the stoma, the right subventral tooth, like the right subventral gland, being much larger than the other two. In some series there appear to be 2 additional small subventral gland nuclei situated anterior to the large ones.

The esophago-intestinal valve contains only 8 nuclei; the anterior part is triradiate in cross section while posterior part is dorso-ventrally flattened.

Enoplus communis v. *meridionalis* (Enoplidae)

The esophagus of *Enoplus* is cylindrical, slightly enlarged posteriorly, and shows moderate "vesiculation" in the glandular region. Since the stoma is reduced—the stomatal region being indicated by the large bifurcate teeth—this region is entirely surrounded by esophageal tissue. The lumen is simple

and the esophageal lining unmodified (i.e., without cuticular thickenings) throughout the length of the esophagus.

There are 12 marginal nuclei, arranged approximately as in *Tripyla*. Only 33 radial muscle nuclei are present and of these the first 30 comprise the first 5 groups of radial nuclei which correspond to the first 5 groups of *Tripyla*, while the last group of 3 nuclei (r_{31-33}) apparently represents the 6 nuclei (r_{31-36}) composing the sixth group of radial nuclei in that form. The nerve cell nuclei, 44 in number, correspond to the 44 nerve cell nuclei of *Prionculus* and *Tripyla*, but their arrangement differs considerably. There are 3 large similar esophageal-gland nuclei (gl_{4-5}) and 2 smaller subventral gland nuclei (g_{2-3}). Just posterior to the latter an additional pair of ventrolateral nerve cell nuclei (s_{1-2}) are present.

The three large esophageal glands have their orifices at the base of the teeth as Rauther (1907) has already shown in *Enoplus* sp. The vesiculate appearance of the esophagus when viewed in toto is due to the separation of radial muscle fibers by gland tissue. The cytoplasm of the glands is relatively greater in proportion to the muscular tissue than in any of the forms previously described.

The esophago-intestinal valve is short, consisting of an internally trilobed and an externally circular part; the entire valve contains 12 or 13 nuclei (actual number not ascertainable).

Anticoma litoris (Enoplidae)

The esophagus of *Anticoma* is cylindrical and similar to that of *Enoplus;* the anterior part surrounds the stomatal region. Since all of the nuclei have their homologues in *Enoplus*, they are arranged in a practically identical pattern (Fig. 2) and further description seems unnecessary. The gland orifices all appear to be situated at the anterior end of the esophagus, the 2 small subventral glands ending in the marginal regions of the dorsal sector. The esophago-intestinal valve is like that of *Enoplus*.

Rhabdodemania minima (Enoplidae)

The esophagus of *Rhabdodemania* is also like that of *Enoplus*, except that the orifice of the dorsal gland is some distance from the anterior end of the esophagus; the small subventral glands (g_{2-3}) extend nearly to the anterior end as in *Anticoma*, and the large subventral glands (g_{4-5}) have swollen ampulla near the level of their orifices.

Leptosomatum elongatus v. *acephalatum* (Enoplidae)

The esophagus of *Leptosomatum* is grossly conoid, of smooth contour and internally vesiculate. The lumen is simple, triradiate, and the lining thick but unmodified. The relative proportions of muscular and glandular tissue give to the esophagus a consistency somewhat like that observed in *Eurystomina* or *Enoplus*.

There are 2 groups of 3 marginal nuclei, 3 groups of 6 radial nuclei and 18 nerve cell nuclei anterior to the nerve ring as in *Eurystomina* and *Enoplus*. Posterior to the nerve ring nuclear identification becomes extremely difficult due to a great increase in the number of these structures, there being approximately 105 nuclei in the remainder of the esophagus. The ventral gland nuclei have apparently undergone multiple division, since nuclei lie in all possible positions and have little or no definite arrangement. The numerous small nuclei extend into the dorsal as well as the subventral sectors, although

the dorsal gland nucleus has retained its individuality. There is no evidence of atypical division such as nuclear budding, for the small nuclei are all of about equal size. The subventral esophageal gland orifices are near the anterior end of the esophagus while that of the dorsal gland is situated somewhat posterior.

Leptosomatum is provided with pigment spots or "ocelli" which are generally considered to be situated dorsal to the esophagus; the spots are acorn-

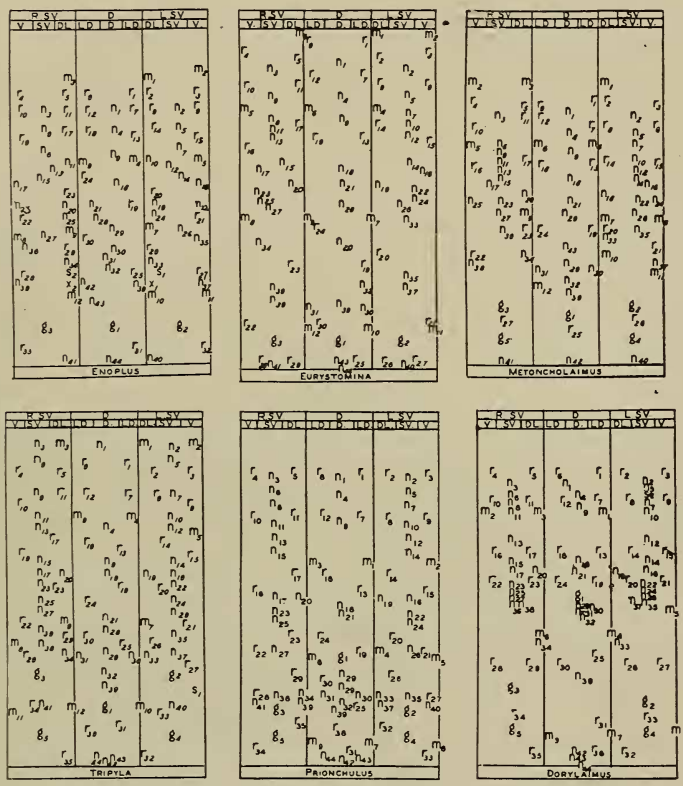

Fig. 2.—Tables of nuclear distribution in the Enoplida.

shaped and contain a distinct lens. Schulz (1931) described such ocelli in *Parasymplocostoma formosum*, stating that the lens is a continuation of the external cuticular covering of the body and that the presence of a special cell lying outside of the esophagus is responsible for this formation. In the present form, such is not the case. The pigment spot and lens form a swelling in the wall of the esophagus and are clearly of esophageal derivation. This is a peculiar situation in the origin of photoreceptors, if such they be, and supplies definite evidence of the homology of this type of ocellus with the pigment spots of forms such as *Enoplus*.

Cryptonchus nudus (Ironidae)

The esophagus of *Cryptonchus* grossly resembles that of *Dorylaimus* since it is clearly divisible into a narrow anterior muscular part and a wide pos-