A CONTRIBUTION TO OUR KNOWLEDGE OF THE ANATOMY OF THE FRESH-WATER MUSSELS OF THE DISTRICT OF COLUMBIA

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All of the North American fresh-water mussels are contained in the family Unionidae, of which five genera are native to the District of Columbia. These are Lampsilis, Strophitus, Anodonta, Alasmidonta, and Elliptio. The genus Lampsilis has four species native to the District of Columbia—L. cariosus Say, L. ochraceus Say, L. radiatus Gmelin, and L. nasutus Say. Strophitus has one local species: S. undulatus Say. Anodonta has one: A. cataracta Say. Alasmidonta has three: A. undulata Say, A. heterodon Lea, and A. marginata Say. Elliptio is represented by two local species: E. complanatus (Solander) Dillwyn and E. productus Conrad.

In the following anatomical descriptions are given the differences exhibited by five local species, namely, Lampsilis ochraceus, L. nasutus, Anodonta cataracta, Elliptio complanatus, and E. productus.

ANATOMY OF LAMPSILIS OCHRACEUS SAY

Plate 1, figs. 1 to 10

DESCRIPTION OF THE SHELL

Plate 1, figs. 1, 2, and 4

The shell is elliptical with full beaks which are sculptured with a few straight, stout ridges. Posteriorly from the beaks a well-developed posterior ridge begins and curving slightly down the middle of the shell ends in a blunt point halfway up the height of the shell. The outside is dull, tawny-brownish, usually smoky and feebly rayed.

The interior of the shell is pearly gray, iridescent, often growing into a deep rose along the margin of the shell.

The left valve has two small pseudocardinal teeth in front of the beak cavities and two thin, lateral hinge teeth. The right valve has two pseudocardinals opposite each other (with a pit between) and one high thin lateral.
The muscle scars of both shells are identical, forming shallow cicatrices on the interior face of the shell. The anterior adductor scar lies in front of the pseudocardinal teeth and is somewhat oval in outline. At the termination of the lower pseudocardinal tooth is the anterior retractor muscle scar which is deeper than the anterior adductor scar and continuous with it. Below the impression of these two muscles is the small circular impression of the protractor pedis muscle. At the termination of the lateral hinge tooth is the scarcely visible oval scar of the posterior adductor muscle. Directly above it is the impression of the posterior retractor muscle which is small and circular and often invisible. A very faint line runs about a quarter of an inch from the margin of the shell from the anterior to the posterior adductor muscle. It is the impression of the pallial line muscles, small muscles inserted along the margin of the mantle.

In the beak cavities there is an irregular number of very small scars, one of which is a deep elliptical scar in the apex of the cavity and is the impression of a small dorsal mantle muscle.

**Mantle**

Plate 1, fig. 3

The mantle lobes are separated for almost the length of the posterior adductor muscle in the formation of the dorsal mantle aperture. They are then united for about 3 mm. before separating to form the exhalent siphon. The tentacles of the exhalent siphon are rudimentary while those of the inhalent siphon are from 1 to 2 mm. in length.

The pigmentation of the dorsal mantle aperture and of the siphon is heavy, growing fainter and disappearing as the margins continue anteriorly.

The lack of pigmentation along the entire mantle edge, exclusive of the siphons, the absence of tentacles beyond the inhalent siphon but rudimentary tentacles at the exhalent siphon and a more elongate form of body distinguish this species from *L. nasutus*.

**Muscular System**

Plate 1, fig. 8

The largest muscles are the anterior and the posterior adductor muscles, great cylindrical masses of fibers situated on a line with each other on the dorsal portion of the body, piercing the mantle as they traverse the body to their attachment on the valves. Their functioning keeps the valves closed.

The remaining muscles are the anterior and the posterior retractors, the protractor pedis, two small muscles inserted in the cavities of the beak, and the small muscles of the pallial line. In alcoholic specimens, the anterior retractor muscle is very small and circular in appearance, with its point of insertion just posterior to the upper
portion of the anterior adductor muscle. This muscle passes downward to the anterior ventral portion of the foot with its greatest development in the anterior portion.

The posterior retractor muscle lies on the anterior ventral portion of the posterior adductor muscle. At this point it is a compact cylinder of fibers which after a short distance spreads diagonally through the body and foot and supplies the thick musculature of the foot. These muscles are antagonistic to the protractor pedis muscle which lies just at the base of the anterior adductor muscle and presents, with the mantle intact, a crescent-shaped form. With the mantle removed, it is seen to be fan-shaped, spreading outward over a large portion of the body and foot. By its play the foot is capable of great expansion. The two small muscles with their attachments in the beak cavities serve to retain there the dorsal portion of the body. The pallial line muscles are inserted along the edge of the mantle and form a delicate connection between the mantle and shell.

The muscular system of the remaining species is the same as for *L. ochraceus*.

**Labial palps**

Plate 1, fig. 7

The labial palps surround the mouth and consist of two pairs of thin contractile flaps which are subtriangular in shape with an inner and outer palp on each side of the body. Their edges are attached dorsally and are free ventrally. The outer edge of the outer palp is attached to the mantle, with the inner edges of each palp united, and the outer edge of the inner palp attached to the body mass. Anteriorly the palps are attenuated and at their confluence directly under the anterior adductor muscle give contour to the oral orifice with the attenuated portion of the outer palp forming the upper lip and that of the inner palp forming the lower lip.

The exterior faces of the palps are smooth. The inner faces are strongly furrowed transversely for about three-quarters of the distance, where the transverse furrows terminate abruptly and longitudinal furrows begin and continue to the mouth where they curve inward and pass into the gullet. These ridges bear cilia which sweep along the food brought into the mantle cavity at the inhalent siphons. The cilia on the transverse ridges check undesirable substances and send them back into the mantle cavity, while the cilia of the longitudinal furrows sweep the desirable food into the mouth.

**Gills and reproductive system**

Plate 1, figs. 6, 7, and 9

The noticeably semicircular form is the only peculiarity of the gills of *L. ochraceus*. The marsupium occupies the hinder portion of the outer gills.

The glochidia are hookless.
The mouth is immediately below the anterior adductor muscle. It is oval in shape and leads by a short gullet into the stomach, which is of irregular shape, but more oval than globular, with plications on its inner surface, and lies just posterior to the anterior adductor muscle. Surrounding the stomach are the digestive glands, hepatopancreas, a brown, spongy mass made up of minute tubes in clusters whose orifices open into the stomach. The intestine is given off from the left posterior portion of the stomach and, in alcoholic specimens, is about 3 mm. in diameter. It descends obliquely through the visceral mass with a slight curve almost to the posterior margin of the foot where it curves dorsally following the line of the foot margin. It is narrowest here, about 1 mm. in diameter. At a point midway between the dorsal and ventral portions of the body mass the curve proceeds anteriorly and continues in an oblique line until at a point below the anterior portion of the renal organ it turns to the right and then backward, still following the curve of the foot, and continues anteriorly for about two-thirds of the length of the body where it is attached to the visceral mass. Turning again to the right side of the body, it continues dorsally and posteriorly, keeping to the right of the portion descending from the stomach. It continues anteriorly for a short distance where it again turns and passing upward becomes very broad—about 5 mm. in diameter. From this point the wall is produced into a fold (typhlosole) continuing through the rectum. Approaching the dorsal surface in an oblique line it grows gradually smaller until it turns abruptly backward and passes into the pericardium; leaving the visceral mass, the intestine or rectum passes through the heart over the posterior adductor muscle, and bending dorsally terminates with the anus in the suprabranchial chamber.

The labial palps and alimentary system are the same for all species.

**Nervous System**

Paired nerve centers or ganglia, with their emanating branches and commissural cords connecting the ganglia, form the nervous system. There are three nerve centers, an anterior, a visceral, and a posterior, supplying the respective portions of the body, which are called the cerebral ganglia, the pedal ganglia, and the posterior ganglia.

The cerebral ganglia are paired and lie bilaterally symmetrically on each side of the body in front of the protractor pedis muscle.
They are very near the surface, being exposed by removing the film of the mantle. A single ganglion is roughly triangular with the apex directed downward and a little anteriorly. From the most anterior end there is a stout cerebral commissure which passes over the gullet to connect with the ganglion of the other side. From the anterior ventral portion three large nerves arise. The most anterior one bifurcates after a short distance, one branch passing around the most anterior edge of the mantle and the other descending to the anterior portion of the mantle. Behind this nerve descends another, also bifurcating after a short distance and supplying also the anterior mantle area. The last of these three nerves, after bifurcating, divides and redivides to supply the remaining anterior portion of the mantle. At the middle anterior portion of this ganglion a nerve arises which passes to the anterior adductor muscle, supplying it with its branches. Posteriorly the ganglion narrows to pass into the posterior commissural cord which passes upward through the visceral mass into the renal organ where it runs parallel with the commissural cord of the opposite ganglion. After leaving the renal organ the two commissures spread out to pass around the tendons of the posterior retractor muscle, after which for a short distance they run close together and pass into the posterior ganglion. From the inward central portion of the cerebral ganglia the pedal commissural cord arises at right angles, then turns abruptly down, passes through the protractor pedis muscle, and descends deep into the center of the foot to meet the pedal ganglion. On the dorsal portion of the cerebral ganglion are two very small nerves which supply the protractor pedis and the anterior retractor muscle. The labial palps receive a filamentous nerve supply from a branch of the anterior mantle nerve.

The pedal ganglia lie at a slightly elevated angle deep in the ventral part of the visceral mass near the center. They are exactly contiguous and present a bilobed appearance, though they are not fused.

At the anterior end the stout commissural cord to the cerebral ganglion arises. From the posterior end two large nerves are given off. The inner, after bifurcating, traverses the whole length of the body mass. The outer nerve bifurcates, sending its branches, which also fork, to the muscles of the foot. On the outer edge of the ganglion two forking nerves arise and continue to the musculature of the foot. From the inward portion of the ganglion at the center a nerve arises at right angles and supplies the viscera.

At the posterior nerve center the paired ganglia have become fused into a single bilobate mass which is situated on the ventral surface of the posterior adductor muscle. From the anterior end four nerves pass. The two inner or mesial ones are the commissural
cords which pass to the cerebral ganglia. The two outer ones pass parallel for a short distance with the commissural cords and then turning abruptly backward continue along the junction of the gills supplying them with its numerous branches. At the posterior portion a gigantic nerve arises which separates into three large branches. The central branch supplies the inhalent siphon, the inner or mesial branch the posterior portion of the mantle, and the outer branch the exhalent siphon.

The nerves emanating from the ganglion often vary with the individual mussel. A certain nerve may be entirely lacking or exceedingly large or very delicate. The most constant arrangement however, is the one given above and shows no variation for different species.

**EXCRETORY SYSTEM**

Plate 1, fig. 9

The excretory system for all five species exhibits no peculiarities.

**CIRCULATORY SYSTEM**

Plate 1, fig. 10

The circulatory system of *L. ochraceus* and of the other species included in this study shows no variation. From the ventricle proceed two aortae, one passing anteriorly and above the rectum, though almost contiguous with it; the other passing posteriorly enters the visceral mass below the rectum. They are the anterior and posterior aortae from which numerous arteries arise. The anterior aorta, on entering the visceral mass, curves outward and slightly to the right, then passes downward and a little posteriorly gives off a large artery, which passes into the mantle. The main branch continues its downward anterior course and near the center of the visceral mass divides into three large arteries which pass in and out among the folds of the intestine. Just before the curving main branch begins its downward course a large artery is given off which curves downward back of the anterior adductor muscle and curves posteriorly, to supply, with its numerous veins, the ventral portion of the body mass. From this artery, a little before it reaches the anterior adductor muscle, ascends a branch which passes into the muscle, supplies the mouth and anterior portions of the body.

The posterior aorta bifurcates just before reaching the posterior adductor muscle, sending one branch to the muscle and to the region of the pericardium and the rectum. The other branch passes over the muscle and enters the mantle, continuing ventrally to meet the anterior mantle artery. The blood supply of the mantle is continually oxygenated by the current of water which bathes the inner face of the mantle. It is, therefore, returned directly to the auricles without passing through the gills.
ANATOMY OF LAMPSILIS NASUTUS SAY

Plate 2, figs. 1 to 10

DESCRIPTION OF THE SHELL

Plate 2, figs. 1, 2, 4

The shell is not shiny and ranges in color from dark brown to olive green; it is thin to moderately solid, elongated, and has a distinct posterior ridge, which generally is curved down the middle. The anterior ventral margin curves broadly to the base which is full behind the center, attenuating to a long point halfway up the height of the shell.

The highly characteristic beaks are low and sculptured with fine close ridges, looped in front and following the paralleling longitudinal axis of the shell behind. (Pl. 2, fig. 5.) The exterior surface shows irregular growth lines, with sometimes vertical bars just back of the center, representing the growth of the shell over the gills while distended with fry. Young shells are finely rayed, while in the adult shell the rays are less distinct or entirely invisible.

The interior of the shell is iridescent and lustrous and may be bluish-white, lurid, flesh-tinted, or purplish. The left valve has two pseudo cardinal teeth and one lateral hinge tooth, which is nearly straight and very delicate. The right valve has one pseudocardinal tooth with a faint one above it and two lateral hinge teeth. The muscle scars are shallow, the anterior adductor scar being the more prominent. It is situated dorsally near the anterior margin of the shell and is oval shaped and very clear cut. The posterior adductor scar is a large faint oval impression just below the termination of the hinge teeth. Dorsal to it is the small circular impression of the posterior retractor muscle. On the posterior ventral margin of the anterior adductor muscle scar are two small irregular impressions, one dorsal. They are the anterior retractor and the protractor pedis muscle scars, respectively. Beginning at the most ventral point of the anterior adductor muscle scar, there is a thin faint impression running parallel with the margin of the shell and about one-fourth inch distant from it and ending at the base of the posterior adductor muscle. It is the pallial line impression and marks the insertion of the small pallial line muscles. There are two small pitted scars in the beak cavities which mark the insertion of the small dorsal muscles.

MANTLE

Plate 2, fig. 3

From the posterior adductor muscle the margins of the mantle are separated for the length of the muscle to form the dorsal mantle aperture. The edges reunite for a short distance and then separate again to form the exhalent siphon, the lower portion of which is
formed by the junction of the gills. It meets again, but is not fused, to form the upper part of the inhalent siphon and below this point is not united. The margins of both siphons are greatly thickened and pigmented, bearing on their inward surface numerous tentacles. In specimens preserved in alcohol the tentacles of the inhalent siphon have an average length of 3 mm., while the tentacles of the exhalent siphon are smaller and not so numerous. From the inhalent siphon the tentacles continue on the inward margin of the mantle to a median point, growing smaller and diminishing in number until the last several tentacles are about 5 mm. apart. The margin from this point to its junction over the anterior adductor muscle diminishes in thickness and is free from tentacles. The edge of the mantle is distinctly pigmented along its entire course. This pigmentation is very heavy at the siphons and at the posterior tentacle-bearing portion.

**GILLS AND REPRODUCTIVE SYSTEM**

Plate 2, figs. 6, 7, and 9

The gills are elongated with the inner lamellae continuous with the visceral mass anteriorly. There are about 10 gill filaments between the septa of that portion of the gills which serves as a marsupium and about 20 septa between that which does not, so that a gill or a part of one with more numerous septa than other portions is indicative of a marsupium and therefore of the female mussel. There is a very inconspicuous longitudinal furrow passing around the base of the inner gills and is caused by a very slight invagination of the gill filaments. The inner or mesial gills have no such groove, for the filaments are smoothly curved as they bend upon themselves at the base. This furrow is present in the gills of both sexes. In *L. nasutus* the gravid gill protrudes much beyond the original base of the filaments. This condition is readily seen by the projection of the bulging gills beyond the chitinous rods of the filaments which have a clear-cut line of termination. This projection beyond the filaments is not uniform, for the septa are continuous with the stretched area, checking at their points of insertion the bulging, and therefore giving a scalloped or beaded appearance to the edge of the gill.

In *L. nasutus* the posterior portion of the outer gills is specialized to form the marsupium.

The glochidia are of the hookless type.

**BEAK SCULPTURE**

Plate 2, fig. 5

**ANODONTA CATARACTA Say**

Plate 3, figs. 1 to 10

In the genus *Anodonta* the male and female shells are alike, the beak sculpture is coarse and the embryos fill the entire gills, forming
smooth pads. The inner lamellae of the inner gills are free from the visceral mass. Hinge teeth are absent and the muscle scars faint. The shell is rather thin, evenly rounded in front and somewhat biangular behind and is very slightly winged in the postero-dorsal region. The beaks are rather full, the sculpture consisting of a moderate number of concentric ridges which are usually doubly looped. The surface is usually covered with irregular growth lines. The exterior is generally shining, greenish-yellow, yellow-green or olive, usually banded with darker color and often faintly rayed. The interior is bluish-white and not shining. There are no small, dorsal muscles in *Anodonta*.

**Mantle**

Plate 3, fig. 3

The mantle edge is strongly pigmented at the siphons. The connection of the mantle edge runs nearly the length of the posterior adductor muscle, restricting the dorsal mantle aperture to a very short slit and causing it to lie behind the anterior adductor muscle. The tentacles of the inhalent siphon are large with some of them forking. The exhalent siphon has no tentacles.

**Gills and reproductive system**

Plate 3, figs. 6, 7, and 9

The gills are semicircular with the inner lamellae of the inner gills free from the visceral mass. The entire outer gill serves as a marsupium. During the breeding season the water tubes of the marsupium are divided longitudinally into three tubes with the two outer tubes facing the inner and outer lamina. It is only the central tube which contains embryos. This threefold division of the water tubes is present only during the breeding season.

The glochidia of *A. cataracta* are of the hooked type.

**Beak sculpture**

Plate 3, fig. 5

*Elliptio productus* Conrad and *Elliptio complanatus* (Solander) Dillwyn.

In this genus three species of the *fisherianus* group, *Elliptio productus*, *E. fisherianus*, and *E. lanceolatus* have been thought to occur in the District of Columbia. Close examination of both shell and morphology shows that there is no constant distinction, and it is therefore thought that the only representative of this, the *fisherianus* group, in the District of Columbia is *E. productus* Conrad.

The group of *fisherianus* is distinctive in the manner of gill attachment, for the outer lamina of the inner gill, instead of having the usual connection to the visceral mass, is free.
**ELLIPTIO COMPLANATUS**

Plate 4, figs. 1 to 10

**SHELL**

Plate 4, figs. 1, 2, and 4

The shell of *Elliptio complanatus* has an elongate trapezoidal shape, with the dorsal and ventral margins nearly parallel. The posterior ridge which is well developed and generally double, ends in a point at the base, while the anterior end is rounded.

The surface of the shell is marked by irregular growth lines which are smooth in the young shell and rough in the old. In color it ranges from tawny green to greenish brown.

In *E. complanatus* there is no marsupial bulge distinguishing the female shell. The interior may be white, straw-color, salmon, or various shades of purple.

In the left valve there are two nearly straight lateral hinge teeth and two irregular pseudocardinals, while in the right valve there is one lateral hinge tooth and one stumpy pseudocardinal with a faint one above it.

From the base of the anterior adductor scar just in front of the pallial line impression, there is a delicate groove which passes downward and curves around the base of the shell representing the course of the mantle artery.

**MANTLE**

Plate 4, fig. 3

The only variation in the mantle is a heavier pigmentation at the siphons. The anterior and posterior adductor muscles are very large with the anterior muscle assuming a distinct quadrilateral shape. The body is roughly trapezoidal in shape.

**GILLS AND REPRODUCTIVE SYSTEM**

Plate 4, figs. 7, and 9

The gills are semicircular with the marsupium occupying the entire outer gills.

The glochidia are hookless.

**BEAK SCULPTURE**

Plate 4, fig. 5

**ELLIPTIO PRODUCTUS**

Plate 5, figs. 1 to 10

**SHELL**

Plate 5, figs. 1, 2, and 4

The shell is elongated, ranging in color from dark reddish brown to olive green and is rather thin. The beaks, which in the adult shell are generally eroded, are low. In very young shells there is a
definite beak sculpture so characteristic that it is a reliable means of classification. In *E. productus* the beak sculpture consists of strong, longitudinal, corrugated ridges.

The posterior ridge is well developed, curved down the middle, ending behind the center in a long, drawn-out point near the median line with the point often turned up. From the beaks in a radial direction are heavy, irregular growth lines.

The interior of the shell is iridescent and is purplish or whitish and shows muscular scars. In the left valve on the dorsal surface are two stumpy pseudocardinal teeth and two strong lateral hinge teeth. In the right valve is one pseudocardinal and one lateral tooth.

**MANTLE**

Plate 5, fig. 3

The mantle edge at the dorsal mantle aperture and the siphons is pigmented, but not heavily so. The dorsal mantle aperture extends almost the length of the posterior adductor muscle, while the connected portion between this aperture and the exhalent siphon is about as long as the inhalent siphon. Both siphons bear tentacles. The body is slender and elongate.

**GILLS AND REPRODUCTIVE SYSTEM**

Plate 5, figs. 6, 7, and 9

The gills are very much elongated, with the outer pair serving as a marsupium and forming a smooth pad when filled with embryos. The glochidia are hookless.

**BEAK SCULPTURE**

Plate 5, fig. 5

**EXPLANATION OF PLATES**

**Figure 1**

1. Hinge line.
2. Beaks.
3. Growth lines.
4. Dorsal margin.
5. Anterior end.
6. Posterior end.
7. Ventral margin.

**Figure 2**

1. Lateral hinge teeth.
2. Posterior retractor muscle scar.
3. Posterior adductor muscle scar.
4. Pseudocardinal tooth.
5. Anterior retractor muscle scar.
6. Anterior adductor muscle scar.
7. Protractor pedis muscle scar.
8. Pallial line muscles scar.

**Figure 3**

1. Anterior retractor muscle.
2. Anterior adductor muscle.
3. Protractor pedis muscle.
4. Pallial line muscles.
5. Foot.
7. Ventricle.
8. Left auricle.
9. Renal organ.
11. Dorsal mantle aperture.
12. Posterior adductor muscle.
13. Exhalent siphon.
15. Dorsal mantle muscles.
1. **Pseudocardinal teeth.**
2. **Anterior retractor muscle scar.**
3. **Anterior adductor muscle scar.**
4. **Protractor pedis muscle scar.**

**Figure 4**

5. **Pallial line muscles scar.**
6. **Lateral hinge tooth.**
7. **Posterior retractor muscle scar.**
8. **Posterior adductor muscle scar.**

**Figure 5**

**Beak sculpture, enlarged.**

**Figure 6**

1. **Cross section of shell.**
2–3. **Glochidia, enlarged.**

**Figure 7**

1. **Left mantle lobe.**
2. **Labial palps.**
3. **Foot.**
4. **Outer gill.**

**Figure 8**

1. **Anterior retractor muscle.**
2. **Anterior adductor muscle.**
3. **Protractor pedis muscle.**
4. **Posterior retractor muscle.**

**Figure 9**

5. **Posterior adductor muscle.**
6. **Pallial line muscles.**
7. **Dorsal mantle muscles.**
8. **Gonads.**

**Figure 10**

1. **Cerebral ganglia.**
2. **Anterior adductor muscle nerves.**
3. **Cerebral commissure.**
4. **Anterior mantle nerves.**
5. **Pedal commissure.**
6. **Pedal ganglion.**
7. **Anterior visceral nerves.**
8. **Anterior visceral nerves.**
9. **Visceral nerves.**
10. **Posterior visceral nerves.**
11. **Posterior visceral nerves.**
12. **Posterior commissure.**
13. **Posterior ganglion.**
14. **Posterior mantle nerves.**
15. **Renal aperture.**
16. **Reno-pericardial aperture.**
17. **Ventricle.**
18. **Left auricle.**
19. **Anterior aorta.**
20. **Anterior adductor muscle artery.**
21. **Pedal artery.**
22. **Visceral artery.**
23. **Posterior aorta.**
24. **Posterior aorta.**
25. **Posterior mantle artery.**
26. **Posterior adductor muscle artery.**
27. **Anterior mantle artery.**

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**Plate 1**

*Lampsilis ochraceus* Say.

**Plate 2**

*Lampsilis nasutus* Say.

**Plate 3**

*Anodonta cataracta* Say.

**Plate 4**

*Elliptio complanatus* (Solander) Dillwyn.

**Plate 5**

*Elliptio productus* Conrad.
Lampsilis ochraceus Say

For explanation of plate see page 12
Lampsilis nasutus Say

For explanation of plate see page 12.
ANODONTA CATARACTA SAY

FOR EXPLANATION OF PLATE SEE PAGE 12
ELLIIPIO COMPLANATUS (SOLANDER) DILLWYN

FOR EXPLANATION OF PLATE SEE PAGE 12
ELLIPHTIO PRODUCTUS CONRAD

FOR EXPLANATION OF PLATE SEE PAGE 12