



Observations on the terrestrial leech *Haemopsis septagon* Sawyer & Shelley, 1976 (Annelida: Hirudinea) from the Outer Banks, North Carolina, USA, with a revision of the species

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Abstract

The terrestrial leech *Haemopsis septagon* Sawyer & Shelley, 1976, is indigenous to the Great Dismal Swamp and environs of northeastern North Carolina and southeastern Virginia, USA. Ever since its discovery in 1895 at Lake Drummond in the Dismal Swamp, this elusive species has been recognized as taxonomically aberrant. For example, it is the only jawed leech in the United States with seven annuli between gonopores, and the only one with sixteen complete (5-annulate) segments, both highly conserved characters in the Hirudinidae.

The discovery of two populations of *H. septagon* in the Albemarle Peninsula in the Outer Banks region of North Carolina afforded an opportunity to investigate the taxonomy and biology of this inadequately characterized species. Its description in this study is the first comprehensive account of the external and internal anatomy of this species since its incomplete original description in 1976. This study is also an opportunity to correct errors in the incomplete original description, and to elucidate morphological and developmental variability of taxonomic significance. Evidence is presented for the first time of a possible aquatic or semi-aquatic form of *H. septagon*.

These Albemarle individuals were compared to the holotype from Durham County, NC, specimens from southeastern Virginia and a terrestrial leech recently reported from southern New Jersey. All of these fall within the variability demonstrated in this study for the Albemarle populations, and are accordingly recognized as the same species, *H. septagon*. Consequentially, *Haemopsis ottorum* Wirchansky & Shain, 2010, is recognized as a junior synonym of *Haemopsis septagon*.

Key words: Albemarle Peninsula, terrestrialism, *ottorum*, Dismal Swamp, tidewater Virginia

Introduction

The terrestrial leech *Haemopsis septagon* Sawyer & Shelley, 1976, was first discovered at Lake Drummond near the center of the Dismal Swamp, south of Norfolk, Virginia, USA. On 7 June 1895 vertebrate zoologist A. K. Fisher of the U. S. Department of Agriculture (later Bureau of Biological Survey) collected two specimens during his expedition to the then unexplored Dismal Swamp (Fisher 1895a,b).

Over the next six decades other specimens were found in or near the Dismal Swamp at very infrequent intervals, most notably during 1957–61 by the French émigré Roger Rageot of the now defunct Norfolk Museum of Natural History. A local naturalist with an intimate knowledge of the Swamp, Rageot acquired unique skill for finding this elusive leech (Mitchell & Liebman 2007). He sent several living and preserved specimens to J. P. Moore (1869–1965), the doyen of leech taxonomists. At the age of 92 Moore was preparing to describe it as a new species but this account was never published (Moser 2011). Consequentially, one of the largest terrestrial invertebrates in the United States remained in obscurity until 1976. Since the brief description over forty years ago this leech continues to be rarely encountered in spite of its superlative size, by far the largest leech species in the Atlantic coastal plain, reaching relaxed lengths of 150 mm or more.

In an ongoing ecosystematic study of the Hirudinea of the Albemarle-Pamlico region of the Outer Banks, North Carolina, two populations of *H. septagon* were discovered on the Albemarle Peninsula, a massive wetlands

contiguous with the Dismal Swamp (Sawyer 2010). Since 2010 specimens of varying sizes have been encountered at irregular intervals and at different times of year, affording a rare opportunity to broaden our understanding of the taxonomy and biology of this remarkably elusive leech.

Interestingly, these two populations, both in southern Tyrrell County, are about 2 km apart but represent very different microhabitats. One is terrestrial, being a sandy ridge separating adjacent blackwater swamps. Perplexingly, the other microhabitat is aquatic, being located below a small man-made culvert which blocks their passage upstream.

The following study is based on these specimens and constitutes the first comprehensive revision of *H. septagon*. A detailed description of this fresh material is an opportunity to correct errors in the incomplete original description, as well as to elucidate morphological and developmental variability of taxonomic significance.

Materials and methods

Reference material. In this taxonomic study specimens of *H. septagon* were examined from two localities in southern Tyrrell County, NC. Each specimen had been frozen immediately upon collection until such time they could be preserved in 5% formalin. After fixation, the specimens were measured at relaxed length, and wet weight recorded. All reference material is retained in the collections of the Medical Leech Museum under deposition numbers prefixed by HS.

The first (terrestrial) locality is on private land on Stephen's Ridge, Gum Neck (35.721446, -76.101951) where the following specimens were collected: **HS-1** and **HS-2**, April/May 2010, 7 am, light rain, two adjacent specimens crawling in grass, 91 mm and 88 mm, respectively; **HS-4**, 9 January 2016, crawling in yard, very large specimen, 115 mm, 6.4 g; **HS-5**, 4 May 2016, immature juvenile under board at water's edge of swamp, 54.5 mm, 0.5 g.

The second (aquatic) locality is 1.67 km distance at Cooper's corner adjacent to FWB Church, Gum Neck (35.712759, -76.114115) where the following specimens were collected: **HS-3**, spring 2015, in water below drainage culvert, large specimen, 113 mm, 6.0 g; **HS-6**, 15 June 2017, a *light-colored form crawling on land 15 metres from water*, 91 mm, 3.0 g; **HS-7**, early summer 2017, in water below drainage culvert, mature specimen with clitellum, 109 mm, 5.2 g. Additional sight records have been noted below the culvert at this locality.

In several respects a natural distinction exists between light-colored terrestrial specimens on the one hand (HS-1, HS-2, HS-4, HS-5, HS-6), and melanistic aquatic specimens on the other (HS-3, HS-7) (Fig. 1). This difference in pigmentation is accentuated particularly after freezing and subsequent fixation in 5% formalin. Significantly, the melanism of aquatic forms is manifested internally as well as externally. For example, in aquatic specimen HS-3, the sheath surrounding the ventral nerve cord is so heavily pigmented that the precise location of some ganglia within the sheath is obscured. This is in contrast to the barely pigmented sheaths found in lighter, terrestrial specimens. Another intriguing difference is prominence of segmental sensilla in aquatic forms (see Fig. 3A). On the other hand in this paper no significant morphological differences between terrestrial and aquatic forms are evident (see Figs. 4, 7). By way of caution, since the newly discovered "aquatic" form of *H. septagon* is known only from one locality which may have unusual environmental circumstances its distinctive aquatic or semi-aquatic character requires clarification from future workers.

Methodology. The methodology employed in this study is similar to that described in detail in a recent paper on another jawed leech species from this region (Sawyer 2019). External features, especially annulation, gonopores and other features of taxonomic significance, were recorded for each specimen listed above. The jaws and teeth of selected specimens were examined and photographed following a mid-ventral cut of the mouth region. The teeth of some individuals were stained with Haematoxylin (Harris).

A mature, well-preserved specimen (HS-4) from the terrestrial population is described below in external and internal detail. In addition, an immature specimen (HS-5) from the same terrestrial population was examined in order to elucidate developmental factors of taxonomic significance. Furthermore, a mature, darkly pigmented specimen (HS-3) from the aquatic population was dissected to establish possible inter-population variability. The segmental and annular nomenclature used throughout this study follows that of Sawyer (1986: 54–66; 2019: 191).

Following a mid-dorsal incision each specimen was dissected under noncarbonated water in a wax-bottomed dissecting tray using a Wild M7A stereo microscope with a Volpi Intralux 4000 light source, aided by a Lapsum Spot Point LED lamp, with ultraviolet capability. During dissection photographs of the digestive and reproductive

systems were taken at appropriate stages for future reference and tracing onto Bristol board or heavyweight tracing film. Images were taken with digital cameras of increasing magnification: 1) Conrad Electrics, Mirazone MZ902, DP-M14; 2) Yuanj MC5000 eyepiece camera for stereo microscope; and 3) Bresser LCD MP Microscope for prepared slides. Measurements were taken by Ocular Micrometer Model WF 10X.

Results

Description of *H. septagon* from Albemarle Peninsula

A representative specimen of *H. septagon* is described in comprehensive detail below. This mature specimen (HS-4) from the terrestrial population at Stephen's Ridge serves as 'archetype' for the Albemarle region, against which meaningful comparisons can be made for variability within the Albemarle region.



FIGURE 1. *Haemopsis septagon* Sawyer & Shelley, 1976. Terrestrial and “aquatic” forms from the same (Cooper’s corner) locality in Tyrrell County, Albemarle Peninsula, North Carolina. Upper, light-colored terrestrial individual (HS-6) found crawling on land 15 m from water. Lower, melanistic aquatic individual (HS-7) found in a nearby small stream. Both had been frozen prior to fixation in 5% formalin. Anterior to right. Scale bar: 10 mm.

External features (HS-4). This large bulky specimen was frozen immediately upon capture, and fixed three months later in 5% formalin in which it is stored. As fixed, the body is elongated and noticeably flattened throughout its length, with its greatest width at the posterior end. This posterior region displays a lateral widening faintly reminiscent of stubby lateral ‘wings’. The maximum width is maintained for about half the length of the animal and then narrows perceptibly toward the head which is noticeably broad and rounded. The diameter of the caudal sucker is slightly less than half the width of the posterior end of the body, i.e. relatively small for the size of the animal. The male gonopore is well forward in the body, being located about one quarter from the tip of the head. Dimensions: length, 115 mm; maximum width (posterior end), 16.5 mm; length from male gonopore to tip of head, 27 mm; width at level of male gonopore, 9.5 mm; width of head, 6.5 mm; diameter of caudal sucker, 7.5 mm; length of exposed penis, 4.0 mm; total body wet weight, 6.4 g.

Pigmentation. As fixed in 5% formalin without any exposure to ethanol, the specimen is uniformly grey in color, being somewhat darker on the dorsum. From a lateral perspective the contrast between the dorsum and venter gives the appearance of a light marginal line on each side. The darker pigment of the dorsum is attributable to blackish flecks from near the head along the entire length of the body. These flecks are irregular, random (non-metameric) and not overpowering, thereby giving a grey rather than black appearance. There are virtually no flecks on the venter. From a distance, a very faint, inconsequential darkish stripe is barely perceptible along the mid-dorsal line.

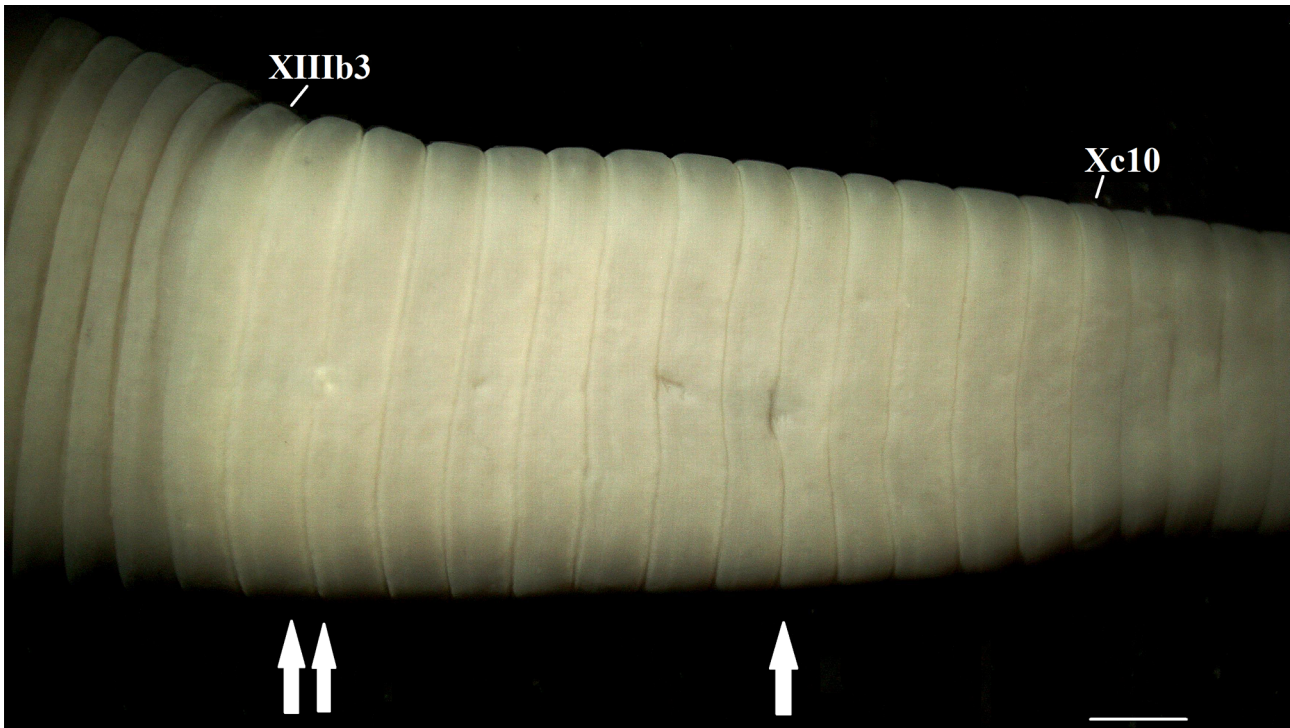


FIGURE 2. *Haemopsis septagon* Sawyer & Shelley, 1976. Clitellar region (HS-7). Ventral view. The clitellum extends all or part of 15 annuli, from Xb5(c10) to XIIIa2(b3), inclusively. Gonopores are separated by 7 annuli. The male opening at XIb5/b6 is indicated by a single arrow; the female opening at XIIIb1/b2 is indicated by two arrows. Scale bar: 2.0 mm.

Genital region. The male gonopore is clearly located in the furrow XIb5/b6. It is circular and not a slit. From this gonopore a short, conspicuous length of penis protrudes anteriorly for three full annuli. This structure is uniformly cylindrical and translucent enough to reveal a helical coil within. The tip is blunt, rather than tapering, and exudes a very long cuticle-like thread.

The most taxonomically significant attribute of *H. septagon* is the position and nature of the female gonopore which is unique among jawed leeches in the United States. The female gonopore of this specimen is located on the b1 annulus of segment XIII, approximately six and one-half annuli posterior to the male (Fig. 2). It is manifest as a relatively small, raised nipple-like structure. In spite of its size no clitellum is evident in this specimen, either externally or internally.

Nephridiopores. Seventeen pairs of nephridiopores are discernible on the ventral side of segments VIII to XXIV, inclusively, invariably on the posterior edge of the b2 annulus. Some are more visible than others.

Sensilla. Sensilla are useful landmarks in determining annulation, but in this specimen they vary considerably in appearance (see Fig. 3). Those at the cephalic end of the body are particularly difficult to discern, whereas those at the caudal end are clearer, especially on the dorsum.

Eyes. This specimen has the number and arrangement of eyes characteristic of the family Hirudinidae, namely five pairs in an arc. However, the mouth is closed and distorts their apparent arrangement. Nonetheless, the eyes are clearly located on segments II, III, IVa1+a2, Va1+a2 and VIa2. There are two annuli between eyes 4 and 5.

Oral Sucker. In this specimen the mouth is tightly closed by infolding of the first four segments, I–IV. The ventral rim of the oral sucker consists of a single fused annulus Va1+a2+a3, which divides dorsally into two annuli, namely Va1+a2 and Va3. Similarly, segment VI consists of two annuli on the venter (VIa1+a2, VIa3) and three annuli on the dorsum (VIa1, VIa2 and VIa3), as delineated by faint dorsal and ventral sensilla. Segment VII consists of three annuli which encircle the body, namely VIIa1, VIIa2 and a broadened VIIa3. Segment VIII consists of four annuli which also encircle the body, namely a broadened VIIIa1, along with VIIIa2, VIIIb5 and VIIIb6. The first pair of nephridiopores are clearly located ventrally on the posterior edge of VIIIa1(b2). Taxonomically significant, the two adjacent annuli VIIa3 and VIIIa1 are characteristically broadened, and serve as a useful landmark, even from a distance.

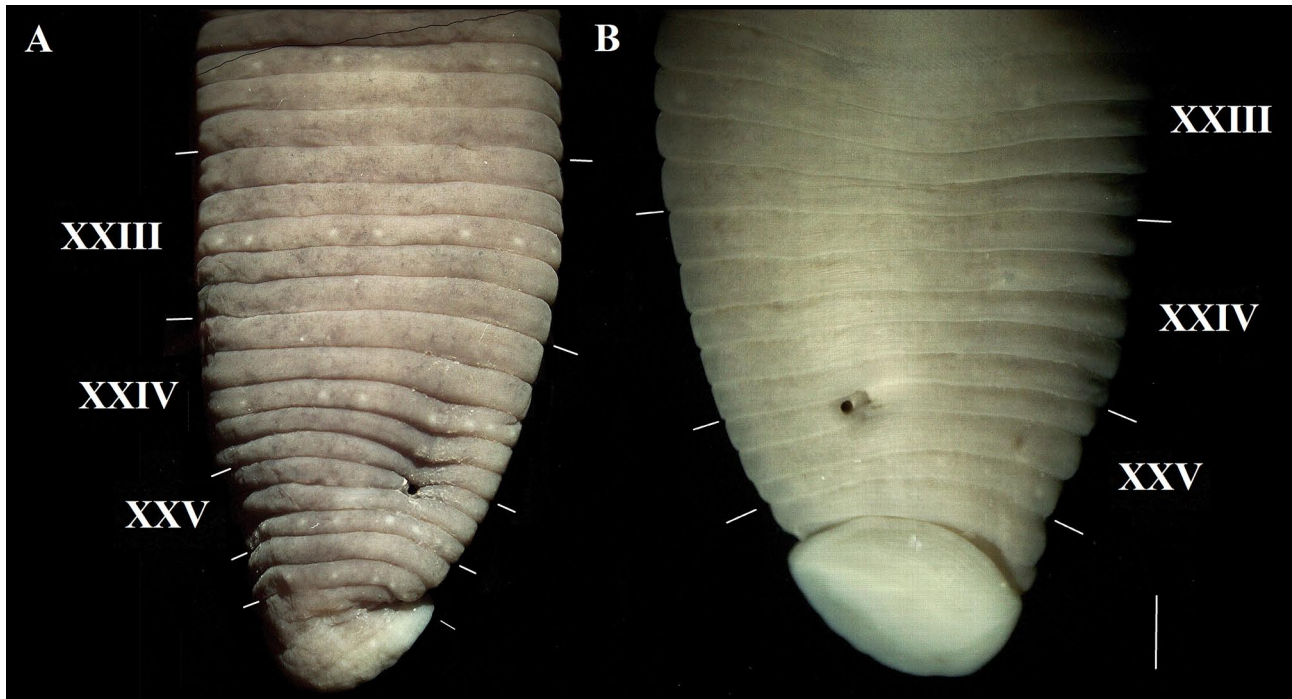


FIGURE 3. *Haemopsis septagon* Sawyer & Shelley, 1976. Taxonomically significant caudal annulation. As shown in this individual (HS-7) segment XXIV bears 5 annuli, with the result that this species has 16 complete (5-annulate) segments (IX–XXIV, inclusively). All other hirudinid species from the mid-Atlantic coastal plain have the more usual 15 complete segments, i.e. segment XXIV bears only 4 annuli. **A.** Dorsal. **B.** Ventral. Scale bar: 2.0 mm.

Caudal Sucker. The caudal sucker is noticeably smaller than the posterior end of the body and is roughly circular in diameter. In this specimen it is facing ventrally, and involves a short distance of unnatural curvature at the caudal extremity of the body.

Fortunately, annulation in the caudal region can be delineated with confidence because in this specimen the sensilla on each of the respective a2 annuli stand in sharp relief to the darker background pigmentation. Furthermore, the four nephridiopores on the b2 annulus of segments XX–XXIII, inclusively, are useful landmarks in that they are inexplicably large and dark. By way of summary, segments XXIII and XXIV have five annuli each, namely b1, b2, a2, b5 and b6, respectively (see Fig. 3). Segment XXV has three annuli which, to judge from the sensilla, consists of XXVb1, XXVb2 and XXVa2+a3. Segment XXVI is comprised of 2 annuli, and XXVII of one annulus. The anus is large and no post-anal annulus is evident.

Annulation. Annulation is determined by the presence of sensilla and eyes on the notional a2 annulus, along with the ventral position of nephridiopores invariably on the b2 annulus. In this specimen dorsal annulation is: Segment I, 1 annulus; II, 1; III, 1; IV, 2; V, 2; VI, 3; VII, 3; VIII, 4; IX–XXIV, 5; XXV, 3; XXVI, 2; XXVII, 1. Of taxonomic significance, this specimen has 16 complete (i.e. 5 annulate) segments (IX–XXIV). This feature sets *H. septagon* apart from a sympatric jawed leech *Philobdella floridana* (Verrill, 1874) which has the more usual 15 complete segments (IX–XXIII) (Sawyer 2019).

Internal features (HS-4)

Digestive tract (Fig. 4)

Foregut. The digestive tract of this species is essentially a straight tube and consists of a buccal cavity, pharynx, crop, intestine and rectum. In this specimen the cephalic sucker is tightly closed like a mitten, and somewhat distorted due to freezing prior to fixation. After teasing, the sucker reveals a field of labial sensory cells on the anterior-most annuli (see also Fig. 9A).

The mouth itself is an elliptical gaping opening edged by a fleshy, somewhat corrugated surround. Anterior to the mouth the sucker component is quite smooth. Dissection along the ventral midline reveals the anterior portion of the pharynx (Fig. 5). This consists of about 13 longitudinal ridges which anastomose loosely at the anterior extremity to form three low relatively unsubstantial jaws located in mid-dorsal and two ventro-lateral positions. Each jaw bears indistinct scars of dental plaques which dislodged with the buccal cuticle.

From the mouth exudes a large portion of tough translucent cuticle which evidently lined the foregut in life (Figs. 6B, 9A, bc). Attached to this cuticle are three equidistant plaques bearing white teeth. These were isolated and examined under a monocular microscope. Each of the three sets of teeth is clearly distichodont and accurately counted, consisting of 14, 15 and 15 pairs of teeth, respectively. Most of the teeth are contiguous with its partner and elongated away from the midline, but the last pair or two are more rounded and do not touch. Each pair of teeth in a plaque is separated by a short gap from adjacent pairs, especially at the less developed portion of the plaque. By way of caution, future workers must take into account the possible artifactual loss of teeth during preservation in this species.

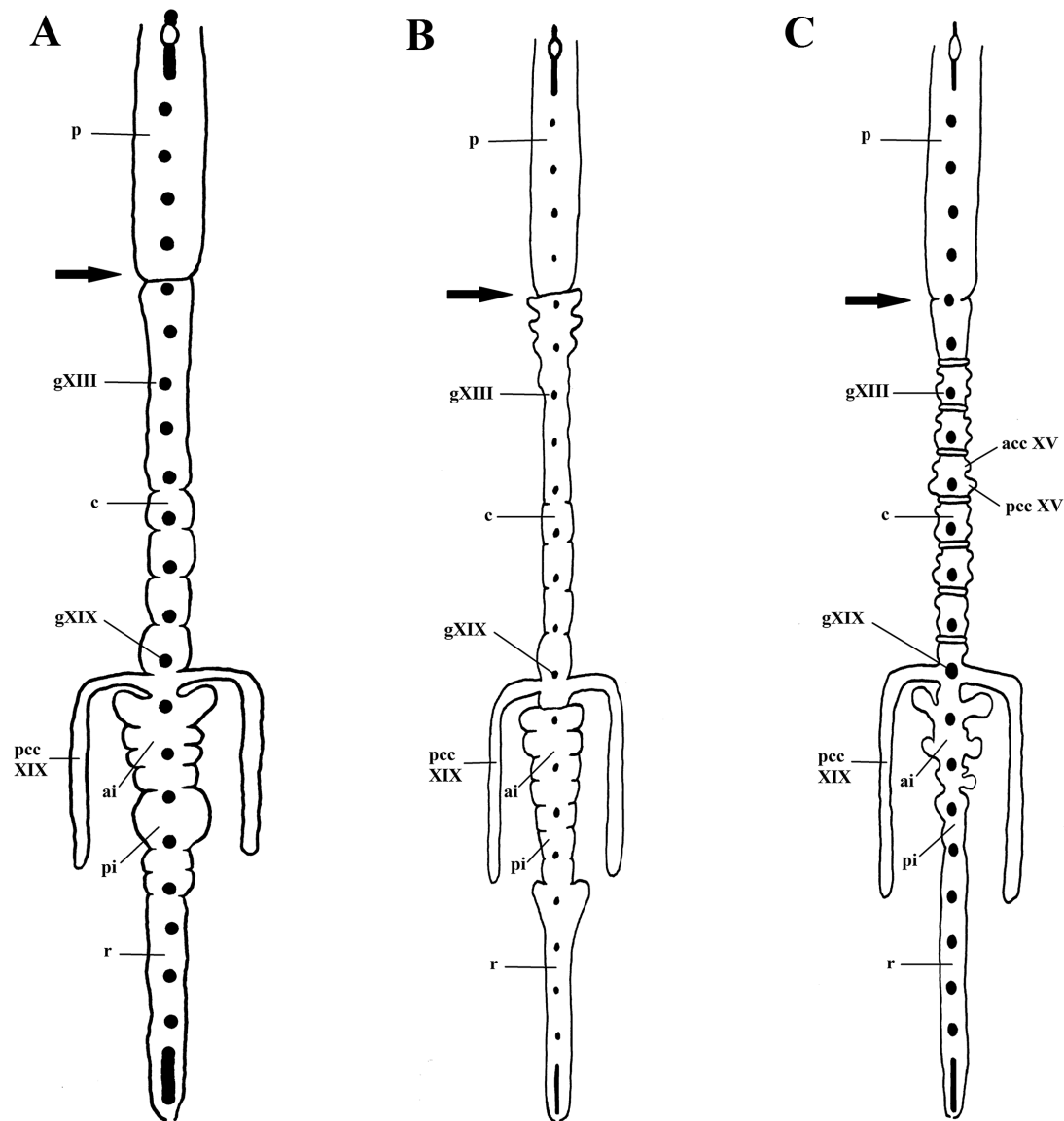


FIGURE 4. *Haemopsis septagon* Sawyer & Shelley, 1976. Digestive tract of specimens from the Albemarle Peninsula, North Carolina. Comparison of the guts. **A.** Terrestrial individual (HS-4). **B.** “Aquatic” individual (HS-3). **C.** Juvenile individual (HS-5). Of taxonomic significance, the pharynx in each case is prominently wide in relation to the crop, and extends posteriorly to ganglion XI (arrow), a unique feature among mid-Atlantic Hirudinidae. Furthermore, in each case the intestine consists of anterior and posterior regions, respectively (see text). Note the crop of the juvenile is segmentally compartmentalized and displays distinct anterior and posterior crop caeca per segment, a feature almost non-existent in adults (see also Fig. 8). acc XV, anterior crop caecum of segment XV; ai, anterior intestine; c, crop; gXIII, ganglion of segment XIII; gXIX, ganglion of segment XIX; p, pharynx; pcc XV, posterior crop caecum of segment XV; pcc XIX, posterior crop caecum of segment XIX; pi, posterior intestine; r, rectum.

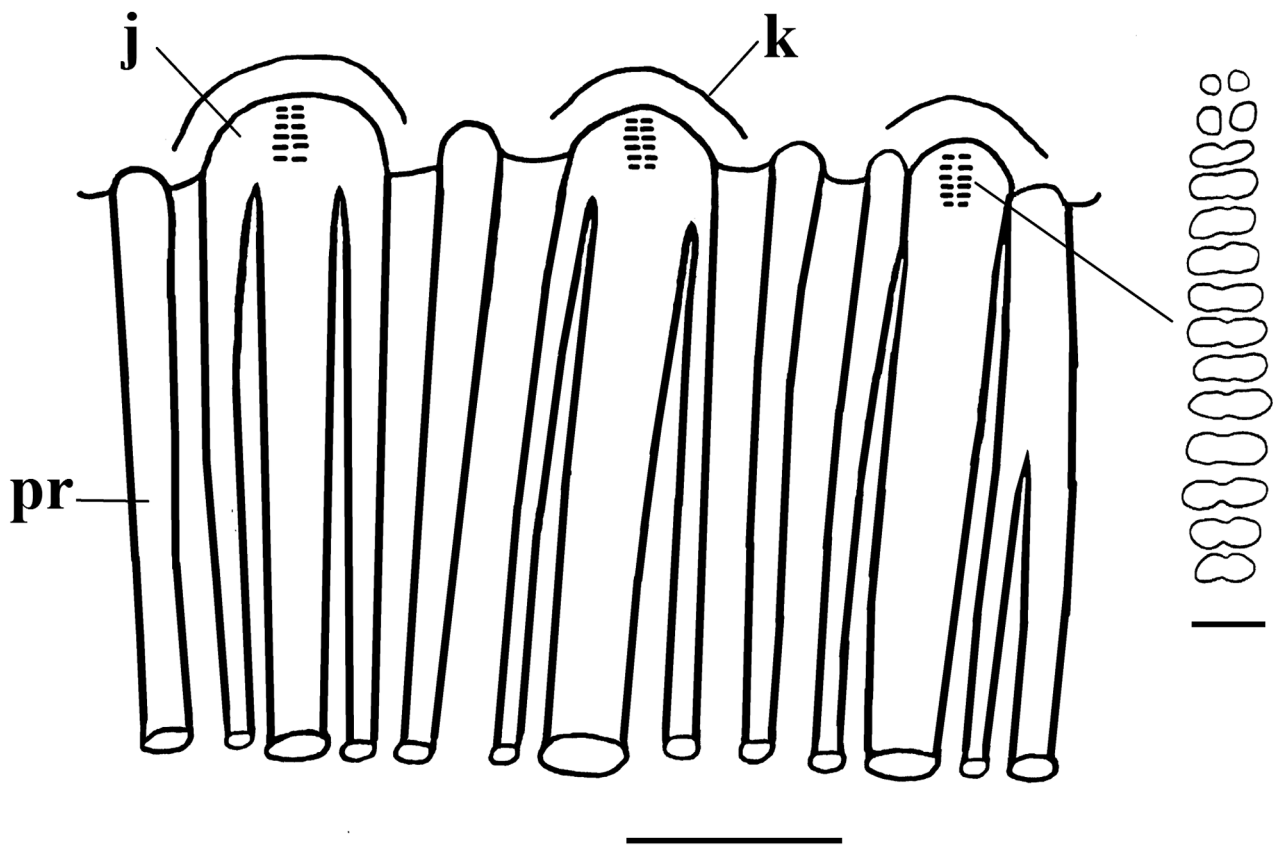


FIGURE 5. *Haemopsis septagon* Sawyer & Shelley, 1976. *Haemopsis septagon* (HS-4). Anterior pharynx and associated structures, cut along mid-ventral line. j, jaw at anterior extremity of coalesced pharyngeal ridges; k, crypt housing jaw; pr, pharyngeal ridge. Scale bar: 3.0 mm. Inset: enlarged plaque of 14 distichodont teeth at rim of jaw. Inset scale bar: 10 μ m.

Each jaw typically forms from the fusion of three longitudinal ridges of the pharynx, with the central ridge being largest and the basis of each jaw. One ventro-lateral jaw was incompletely fused at the anterior extremity such that the jaw was mainly formed from two ridges only. Between each jaw is a smaller ridge or two which terminate independently.

Small, diffuse unicellular cell bodies, presumably salivary in nature, are noticeable in the anterior pharyngeal region. Unlike *Philobdella floridana* (Verrill, 1874), their ductules are not bundled into conspicuous tracts leading to the jaws (see Sawyer 2019).

The sub-pharyngeal brain is noticeably widened and from each side projects an expansive circum-pharyngeal commissure. Thus, the esophageal opening is compatible with swallowing large prey. Ganglion VII is linked to the sub-pharyngeal brain via a very short nerve connective, in marked contrast to the long nerve connective linking it to ganglion VIII.

The pharynx dominates the foregut and is difficult to extricate from the muscular body wall of this region. The structure itself consists primarily of a thick layer of circular muscles which essentially define the pharynx. It is a large, elongated structure which extends posteriorly to approximately 80% of the distance between ganglia X and XI where it abruptly opens into the crop. Once freed from the body wall, the pharynx is dorso-ventrally flattened (4.5 mm in width) with sides which are more or less parallel throughout its length (20.0 mm).

Internally, the pharynx bears about 13–14 low longitudinal ridges which extend the entire length of the pharynx with little anastomosis. At the posterior end these ridges terminate abruptly as an integral part of a tight sphincter which seals off the non-muscular crop.

Midgut. The crop is a thin-walled tube which extends from just anterior to ganglion XI, to anterior to ganglion XX. This tube displays inconspicuous segmental constrictions which demarcate functional compartments, most evident in the gut lumen. These constrictions occur between the ganglion and the testisacs, and are most noticeable externally in segments XV through XVIII, inclusively. The last such compartment, in segment XIX, is perceptibly wider than the others, and is replete with contents clearly visible through the gut wall.

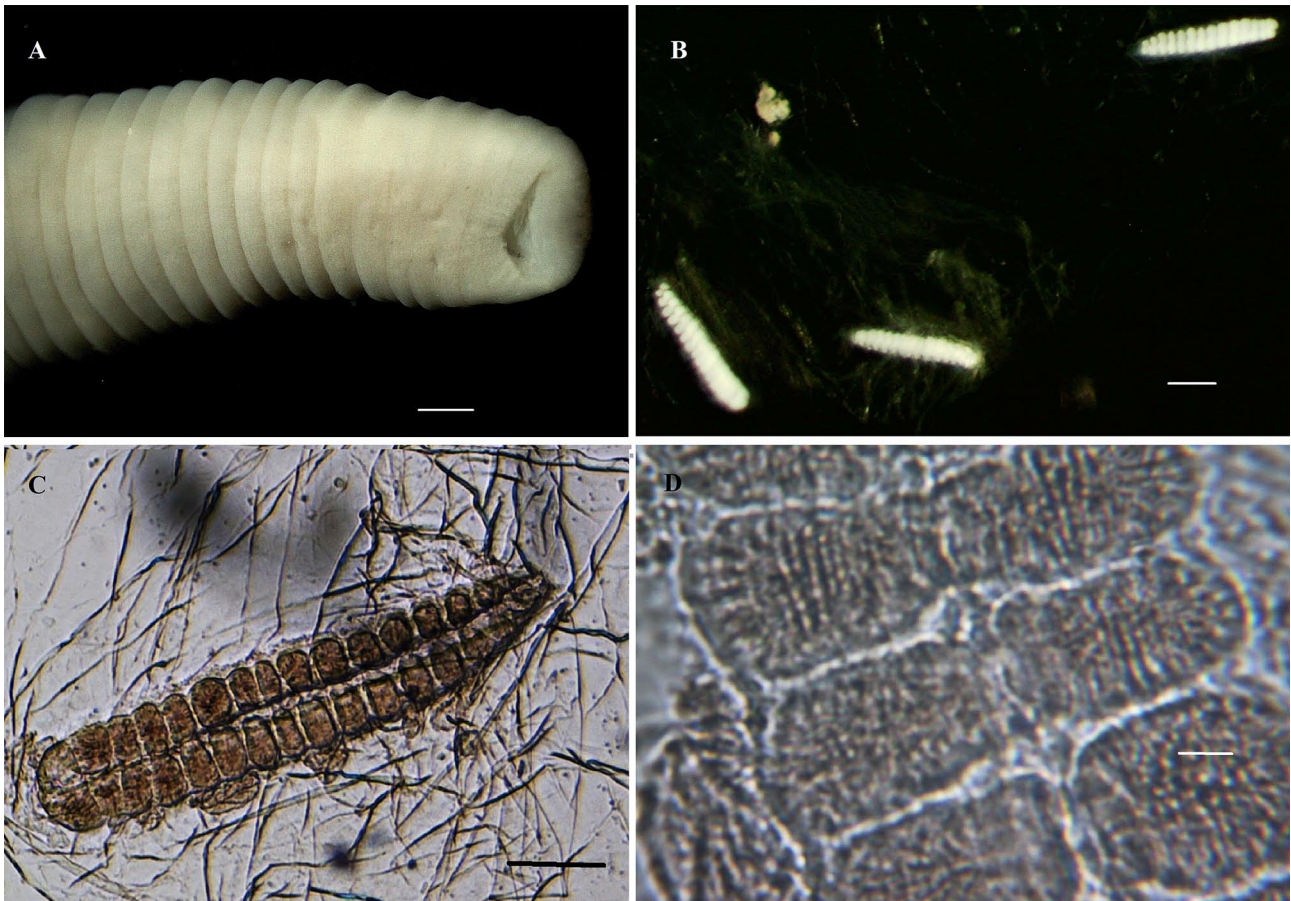


FIGURE 6. *Haemopsis septagon* Sawyer & Shelley, 1976. Mouth and distichodont teeth. **A.** Underside of head showing wide mouth with a prehensile upper lip (HS-6). **B.** Dislodged cuticle removed from the buccal cavity bearing three sets of distichodont teeth (HS-4), reflected light. (See also Fig. 9A). **C, D.** Increasingly higher magnifications of one of the jaws shown in B, transmitted light. Scale bars: A, 1.0 mm; B, 0.1 mm; C, 50 μ m; D, 2.5 μ m.

In this specimen the crop displays some irregular contortions along its length, in part due to deformation from adjacent reproductive structures, but there are no true bilaterally paired caeca. The exception is a pair of narrow, tubular posterior caeca which originate laterally from the aforementioned compartment in segment XIX. The initial portion of each caecum is incongruously narrow before widening and extending ventro-laterally to about half-way between ganglia XXIII and XXIV. Along most of its length this posterior caecum lies dorsal to and is intricately deformed by the last three functional testisacs (T8–T10).

Throughout its length the lining within the midgut bears some rugosity not evident externally. At the aforementioned external constrictions, the crop wall folds inward into loose sphincters which define crop compartments. The inner wall of most such compartments bears several irregular longitudinal ridges.

Intestine and rectum. The intestinal region originates abruptly just anterior to ganglion XX. In the lumen, the midgut opens into the intestine via a tight sphincter. The wall of the intestine is thicker, more opaque and in this specimen more orange in color than that of the translucent midgut. At this level the intestine widens and has an anterior bulbous caecum-like projection. Behind this the intestine displays another three widened compartments more or less defined by muscular constrictions. These four swellings are probably not true caeca, and do not appear to be strictly metameric.

Of taxonomic significance, the intestine is divided into two regions, best differentiated internally (Fig. 4A, ai, pi). The anterior intestine is larger and characterized by capacious villi-like ridges encircling the inner intestinal wall. The anterior intestine is opaque and opens via a sphincter into the translucent posterior intestine, a thin-walled, smooth-lined swelling lying between ganglia XXII and XXIV. The posterior intestine continues further as three increasingly smaller smooth-lined compartments. The last of these enters via a sphincter into the relatively narrow straight rectum. The external wall of the latter in dissection has an opaque ‘hairy’ appearance. On its ventral floor

the rectum bears a series of obliquely longitudinal ridges. The rectum terminates at the anus at segment XXVII. The posterior intestine and the rectum are generally associated with a loose, external layer of circular muscles.

Gut Contents. The mouth of this specimen exudes one or two membranous tubes associated with conspicuous sand grains, along with some flocculent material. Such material occurs throughout the lumen of the pharynx.

Throughout its length the midgut contains a whitish material of irregular size and shape, some flocculent as found in the lumen of the pharynx but comprised mostly of more compact, elongated pieces, some giving the appearance of being vestiges of earthworms. Interspersed amongst this material are discrete, fragile packets of sand grains, possibly derived from gut contents of ingested earthworms. The posterior caeca contain white flocculent matter.

Unexpectedly, the only intact oligochaete ingested by this specimen lies coiled in the posterior extremity of the midgut, in the crop compartment of segment XIX from which the posterior caeca originate (see Fig. 9B). Numerous sand grains are visible through the body wall of this large earthworm which is preserved intact in the Medical Leech Museum. The anterior intestine, posterior intestine and the rectum contain flocculent material along with numerous sand grains and strings of presumptive oligochaete cuticle. Some of the sand grains are compacted together.

Nephridia. Seventeen pairs of nephridia (N1–N17) lie in segments VIII–XXIV, inclusively. Each nephridium is comprised of two parts, a compact body and a bladder. These are positioned lateral to a line defined by the vas deferens. In midbody segments the nephridial body lies anterior to the bladder which in turn lies just anterior to the respective ganglion (opening externally on the b2 annulus). The nephridial bodies of the first three nephridia (N1–N3) are less compact and relatively inconspicuous. Starting at Nephridium 4 of segment XI the nephridia are conspicuous structures with large tightly coiled bodies, which serve internally as useful segmental landmarks (see Fig. 8, n).

Of possible taxonomic significance in their detail, the nephridia of the ten testicular segments (XIII–XXII) are linked anatomically to the testisacs such that the anterior-most or ‘initial lobe’ of the nephridial body attaches to the lateral wall of the testisac. Interestingly, it actually attaches to the testisac of the preceding segment, e.g. Testis 1 of segment XIII is linked to Nephridium 7 which opens externally in segment XIV.

Reproductive structures (HS-4).

The following description of the reproductive system of specimen HS-4 is an opportunity to confirm, clarify and extend anatomical details not presented in the original description of *H. septagon*. For example, the holotype of this species reportedly has 11 pairs of testisacs (Sawyer & Shelley 1976: 86). In contrast, the Albemarle specimen (HS-4) has only ten functional pairs (T1–T10), in segments XIII–XXII, inclusively. Vestiges of an eleventh pair do lie in segment XXIII, but testicular tissue per se is lacking, and the vas deferens in this segment is disorganized to the point of atrophy.

Male system (Fig. 7A). Each testisac in HS-4 is a bulbous structure which lies at a level posterior to its respective ganglion, but sometimes the bilateral counterparts in a segment are slightly skewed. The vas efferens is much whiter in color and emerges from the posterior surface of the testisac. In general the testisacs are in close proximity to the crop, and the last three testisacs (T8–T10) lie immediately under, and contiguous with, the extended posterior caecum of segment XIX. The anterior lateral surface of the testisac is typically attached to the initial arm of the body of the nephridium which itself lies in the next following segment.

The vas efferens proceeds laterally to join the equally conspicuous vas deferens. The latter lies in the ventral floor between the testisacs and the nephridia, and proceeds anteriorly as a thick, white wavy line which narrows at about the level of ganglion XII. The left vas deferens turns laterally at XI/XII, about the level of the male gonopore, and then posteriorly to enter the anterior medial face of the left epididymis. The right vas deferens does not recurve but continues straight to enter the anterior medial face of the right epididymis. This difference in trajectories of the two vasa deferentia is attributable to displacement of the left epididymis a half segment to the posterior (Fig. 7A, e, vd). Thus, in this specimen the left ejaculatory bulb/epididymis complex is centered at the level of ganglion XII, whereas the right complex is centered at XI/XII.

Each epididymis is a large, white tightly coiled structure about one and one-half times the mass of the ejaculatory bulb, and in the case of the right epididymis extends a short distance beyond the posterior end of the ejaculatory bulb. The ejaculatory bulb is a sleek, muscular (shiny) cigar-shaped structure which frames the anterior edge of the epididymis. It is a relatively straight structure, with little or no curvature. In this specimen the two bulbs have a lateral-medial orientation in situ, whereas in the holotype they have an anterior-posterior orientation (see Sawyer & Shelley 1976, fig 7B).

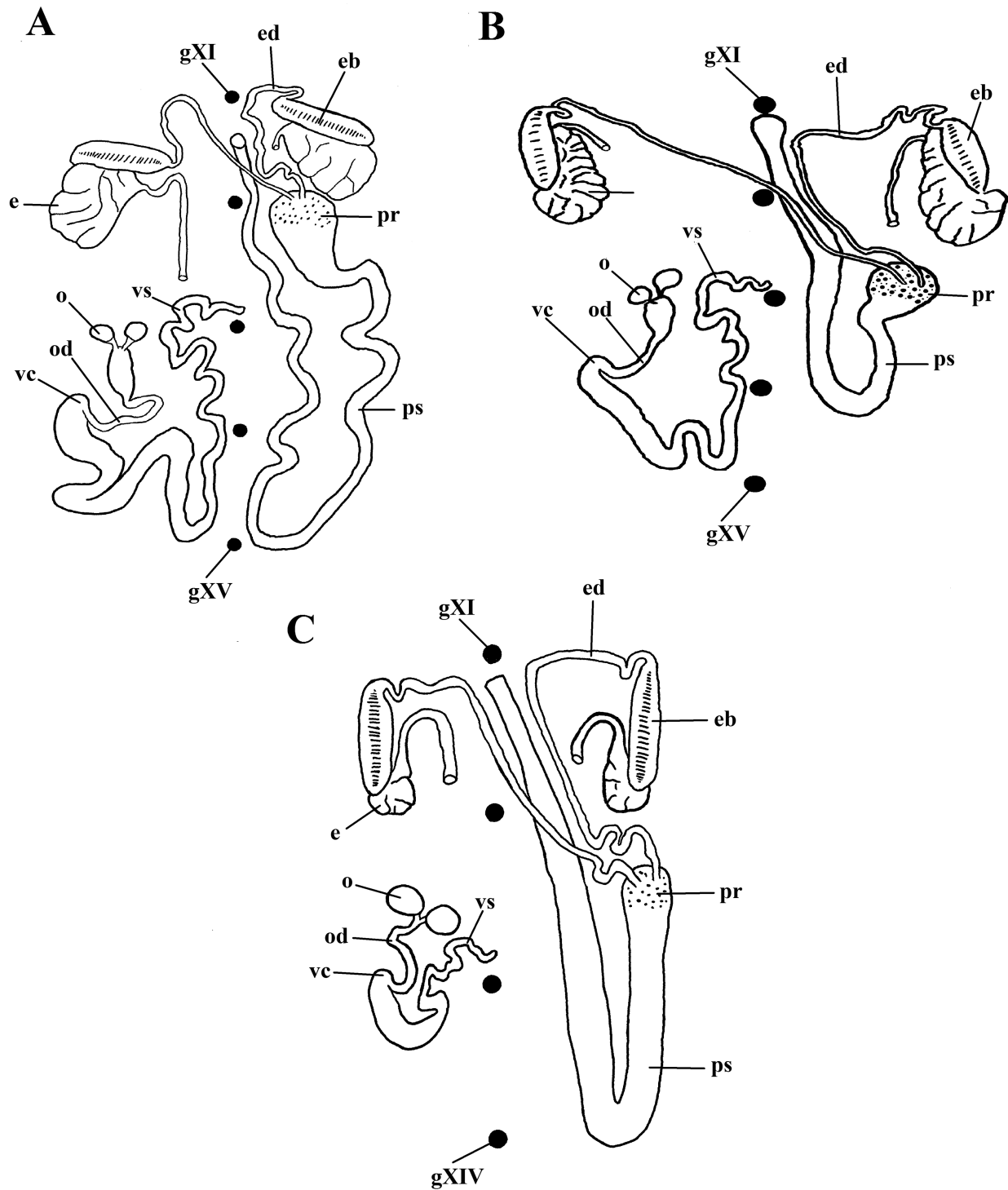


FIGURE 7. *Haemopis septagon* Sawyer & Shelley, 1976. Reproductive system of *Haemopis septagon* from the Albemarle Peninsula, North Carolina. Comparison of the reproductive structures of **A.** terrestrial individual (HS-4), **B.** “aquatic” individual (HS-3), and **C.** juvenile individual (HS-5). For clarity the intertwining male and female ducts are separated and drawn semi-schematically to same relative scale. Note as the individuals mature the penis sheath and vaginal stalk extend progressively to the posterior, coupled with increased twisting of these structures. The simplest condition is found in the juvenile. In this species precise location of the point of flexion of the penis sheath and vaginal stalk is not species specific per se and therefore is of little taxonomic significance. e, epididymis; eb, ejaculatory bulb; ed, ejaculatory duct; gXI, ganglion of segment XI; gXV, ganglion of segment XV; gXIV, ganglion of segment XIV; o, ovisac; od, common oviduct; pr, prostate; ps, penis sheath; vc, vaginal caecum; vs, vaginal stalk.

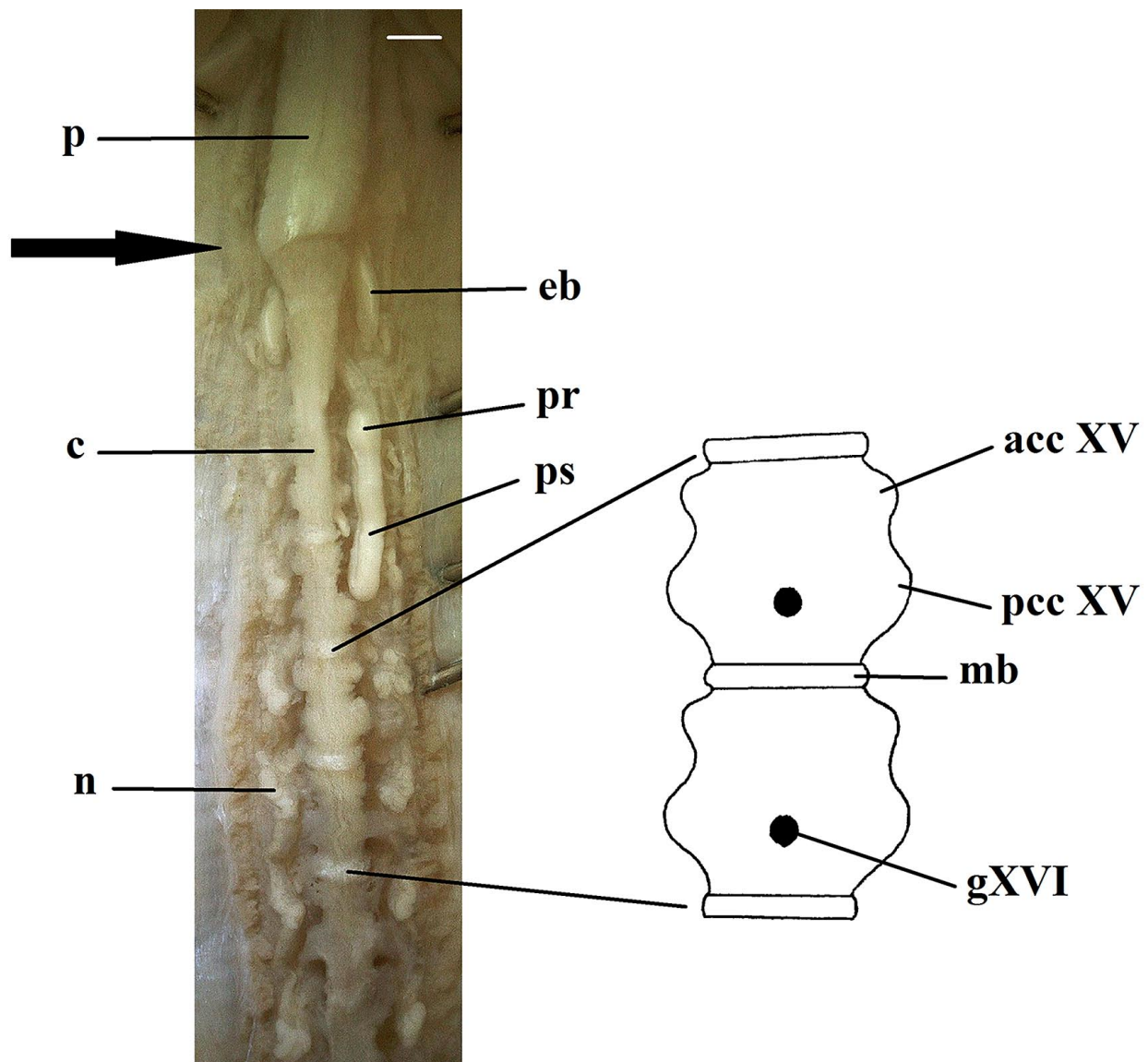


FIGURE 8. *Haemopsis septagon* Sawyer & Shelley, 1976. Dissected juvenile specimen from Albemarle Peninsula, North Carolina (HS-5) showing the mid-body crop is compartmentalized by sphincter-like muscle bands. Inset: schematic enlargement of consecutive segments XV and XVI, respectively, displaying anterior and posterior crop caeca per segment. Arrow indicates posterior position of pharynx (at segment XI). acc XV, anterior crop caecum of segment XV; c, crop; eb, ejaculatory bulb; gXVI, ganglion of segment XVI; mb, muscle band; n, nephridium of segment XVI; p, pharynx; pr, prostate; ps, penis sheath. Scale bar: 1.0 mm.

From the anterior, medial tip of each ejaculatory bulb arises a characteristically long ejaculatory duct. This proceeds anteriorly and medially toward ganglion XI. As the left ejaculatory duct approaches the ganglion it angles postero-medially to cross the mid-line under the ventral nerve cord just behind the male gonopore. It continues for about the same length again to enter the base of the prostate. The right ejaculatory duct has a similar trajectory but is more coiled. Both enter the base of the prostate independently but close together within the glandular region.

The prostate is a large conspicuous structure which in this specimen lies to the right of the crop. Its anterior face is encased in glandular tissue. The penis sheath proceeds from the posterior face of the prostate and winds posteriorly nearly as far as ganglion XV before turning anteriorly and eventually entering the ventral midline to emerge at the male gonopore at XIb5/b6. The penis sheath is a tubular structure with circular striations. It is of uniform diameter throughout its length and contains the penis which in this specimen protrudes a short distance through the male gonopore.

Female system (Fig. 7A). Paired ovisacs lie near the ventral floor to the left of the ventral nerve cord behind the level of ganglion XIII. Short oviducts join the common oviduct which is initially widened before becoming a

narrow, twisting tube. The common oviduct in turn enters the relatively wide and flattened vagina a short distance below its tip thereby creating a poorly defined vaginal caecum. A very long vaginal stalk (“vaginal duct” in Sawyer & Shelly 1976: 87) emerges imperceptibly from the vagina and proceeds posteriorly to the level of XV before turning anteriorly. It gradually narrows and twists its way to the ventral mid-line to emerge at the female gonopore on XIIIb1. Unlike the penis sheath, the vaginal stalk is not cylindrical, and its walls contort spatially along its path. Some loose heterogeneous material is evident through the walls of the ovisacs, vagina and vaginal stalk. The vaginal stalk and penis sheath intertwine along much of their paths, and together represent a large elongated bundle to the right of the crop which conforms spatially.

Variation within the Albemarle populations of *H. septagon*

Collectively, the specimens in this study from the Albemarle Peninsula represent a unique opportunity to address the question of variability within the species *H. septagon*. Using the foregoing description of HS-4 as a cornerstone, similarities and discrepancies in other Albemarle specimens are highlighted below and in the figures.

Comparison of external characters is based on examination of all specimens available to this study (HS-1 to HS-7, inclusively), whereas assessment of internal characters is based on dissections of three selected specimens, representing an immature individual (HS-5), a mature terrestrial individual (HS-4) and a mature “aquatic” individual (HS-3), respectively (Figs. 4, 7). Analysis of anatomical features demonstrate the probability that the terrestrial and aquatic forms in this study represent the same species, *H. septagon*.

The immature specimen (HS-5) may be of particular taxonomic significance in that early development can reflect unsuspected phylogenetic affinities. A case in point is the presence of two sets of crop caeca per segment in immaturity (Figs. 4C, 8, acc, pcc), a feature not clearly manifested in adults (HS-3, HS-4) (Fig. 4A, B). In any case its digestive and reproductive organs are relatively simple (Figs. 4C, 7C), from which the adult configuration can be derived during the maturation process.

Variation of external features

Gonopores. In all specimens the gonopores are separated by more than 6.5 annuli. In only two individuals are they separated by the eponymous 7 annuli, and these differ in detail. For example, in specimen HS-7 both gonopores are located in the furrows (XIb5/b6 and XIIIb1/b2), whereas in HS-3 the gonopores are located on the rings (XIb5 and XIIIb1). With only one or two exceptions the male gonopore is located in the furrow XIb5/56, and is manifested variously from an inconspicuous discolored slit to a circular pore. As a rule the female opening is located on the posterior half of annulus XIIIb1. Expression of the female gonopore varies with the size of the animal, from a simple, unraised slit in the smallest specimen to a raised nipple in the largest specimens. Thus, the raised nipple previously purported to be characteristic of this species is frequently not manifested, notably by immature individuals.

Clitellum. In this study only one leech, an aquatic individual collected in early summer (HS-7), has a clitellum (Fig. 2). In this case the clitellum is a conspicuous band in that its lighter color contrasts against otherwise dark pigmentation. This structure comprises all or part of 15 annuli, from the posterior half of annulus Xb5(c10) to the anterior half of annulus XIIIa2(b3), respectively.

Pigmentation and sensilla. Unquestionably, this species is cryptically darkish in life, but the only living specimen (HS-5) I observed in this study turned uniformly light grey after preservation in 5% formalin. In fact, there is discernible variation in retained pigmentation following fixation, particularly in terrestrial specimens.

One consequence of the dark pigmentation in aquatic specimens is that their segmental sensilla are conspicuous (Fig. 3). This includes the ventral surface, especially in post-genital segments. Distinct sensilla are useful landmarks which make precise determination of segmental annulation easy to ascertain in these individuals. On the other hand in the lighter terrestrial specimens segmental sensilla are variously indistinct, and often obliterated.

Based on limited observations, the sensilla in aquatic specimens may be more anatomically developed than those in the terrestrial specimens, possibly suggesting more reliance on these sensory structures in an aquatic micro-environment. In aquatic individual HS-3 nine pairs of sensilla (S1–S9) are arranged in stereotypic positions along the a2 annulus. The S1 sensillum lies a short distance on either side of the dorsal midline. Sensilla S4 and S5 lie dorsally and ventrally, respectively, in paramarginal positions. Interestingly, the S9 sensillum which lies a short distance on either side of the ventral midline differs from the other eight pairs of sensilla in being elongated, obliquely

angled, and consistently more anterior on the a2 annulus. This orientation suggests a unique function for these two mid-ventral sensilla.

Annulation. In the current study both terrestrial and aquatic specimens of *H. septagon* consistently have 16 complete (5-annulate) segments (IX–XXIV). This is attributable to caudal segment XXIV having 5 annuli, and segment XXV having 3 annuli, as determined by configuration of the sensilla-bearing a2 annuli in these respective segments (Fig. 3). Future researchers are cautioned, however, that this important determination can only be made with confidence on well-preserved specimens of *H. septagon* with prominent sensilla and nephridiopores. In virtually all specimens examined from the Albemarle region there are consistently 24 annuli from the male gonopore (XIb5/b6) to and including the fused annulus defining the ventral rim of the oral sucker (Va1+a2+a3) (see Fig. 9A).

Roughly half of the *H. septagon* in this study have no clear annulus behind the invariably large anus. In others there is some sort of fleshy tissue behind the anal opening. This may be interpreted as partial eversion of the rectum in such individuals, and could be taxonomically misleading.

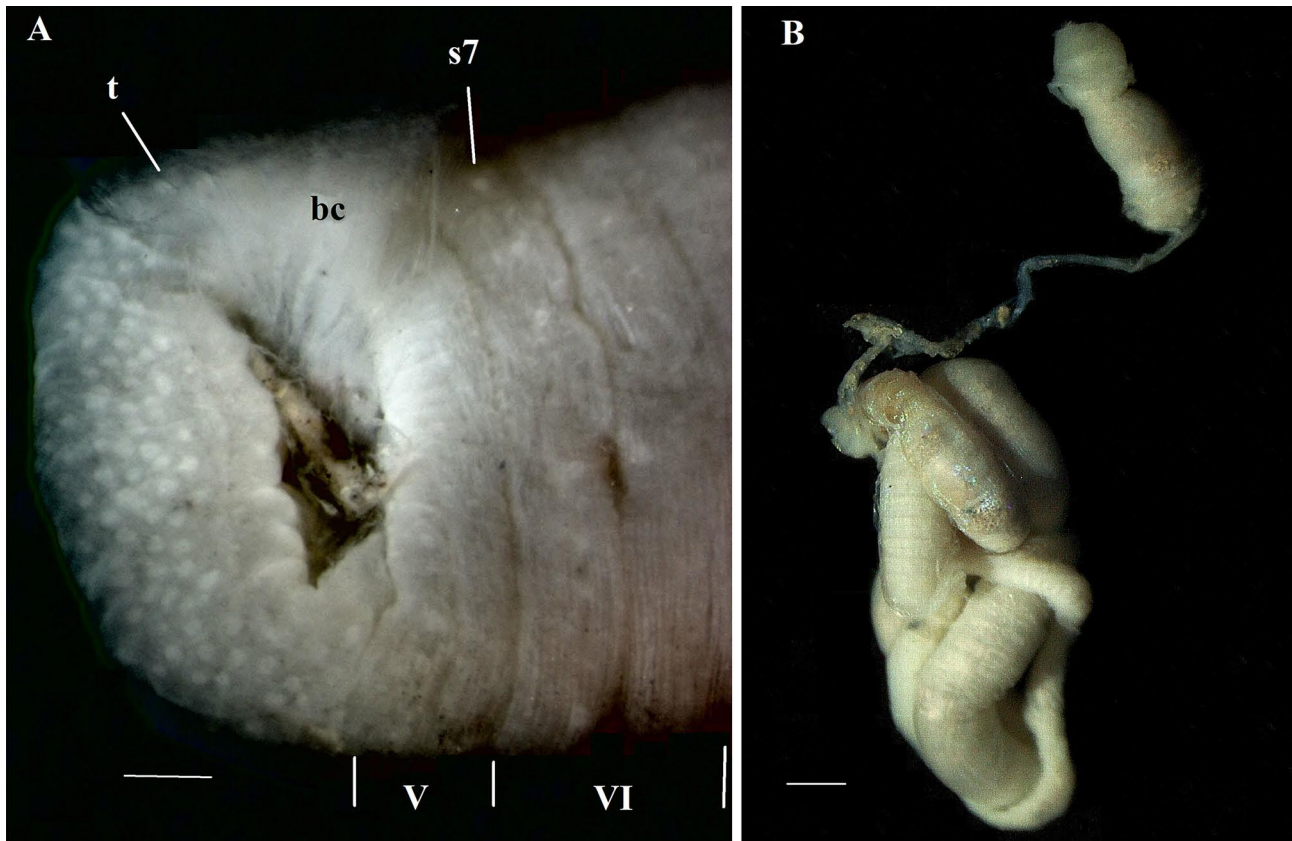


FIGURE 9. *Haemopsis septagon* Sawyer & Shelley, 1976. **A.** Mouth of individual HS-7 showing labial sensory structures or “taste” receptors concentrated along dorsal lip. These apparently function to detect earthworms (see Simon & Barnes 1996). Note dislodged cuticle exuding from buccal cavity. **B.** Earthworm found in crop of another individual (HS-4). bc, buccal cuticle; s7, sensilla 7 of segment VI; t, “taste” receptor. Scale bars: A, 0.5 mm; B, 2.0 mm.

Variation of digestive tract (Fig. 4)

Foregut. The foreguts of all dissected individuals are similar to that described in detail for the reference specimen (HS-4) with only minor variation in the number (12–14) of longitudinal ridges of the pharynx and specific detail of their anastomosing to form the jaws.

Midgut. The crop is essentially a long tube in all dissected specimens, but displays noteworthy individual differences. Unlike the mature specimens, the crop of the immature individual (HS-5) displays two pairs of small, but distinct, caeca per segment throughout its length, from segment XIII to XIX, inclusively (Figs. 4C, 8, acc, pcc). In each segment the posterior pair of caeca is larger and centered on the respective ganglion. Furthermore, each set of caeca is demarcated by a well-formed muscular sphincter, positioned just posterior to the respective ganglion, thereby creating well-defined segmental crop compartments. These sphincters are inconspicuous constrictions in mature specimens HS-3 and HS-4.

Vestiges of the two pairs of caeca per segment are discernible in the anterior gut of the aquatic specimen (HS-3). In this individual the region of crop immediately behind the pharynx consists of two pairs of small caeca, one pair between g. XI and g. XII, and one pair between g. XII and g. XIII. The rest of the crop lacks caeca.

Intestine and rectum. In all specimens the intestine is a conspicuous structure with lateral swellings. In the immature individual (HS-5) these swellings are paired digitiform caeca whereas in the mature specimens they are better described as bulbous lobes. In all cases the intestine is demarcated into anterior and posterior portions, most evident within the lumen (Fig. 4, ai, pi). The rectum is similar in all specimens.

Variation of reproductive structures (Fig. 7)

In this study certain components of the reproductive anatomy of *H. septagon* are invariant in both immature and mature specimens, whereas other structures change significantly in size, location and/or cellular differentiation as the animal matures. The invariant characters can be considered landmarks of taxonomic significance. These include location of the prostate, ejaculatory bulbs, testisacs and ovisacs, as well as presence of a small vaginal caecum. The more plastic structures include the penis sheath and vagina stalk, and their respective points of flexion. As an individual matures the penis sheath and vaginal stalk coil and flex progressively toward the posterior (Fig. 7C, B, A). Accordingly, the precise point of flexion of either the penis sheath or vaginal stalk is not taxonomically reliable in this species.

Testisacs. The basic number of testisacs in *H. septagon* from the Albemarle region is 11 pairs, with each testisac positioned close to ganglia XIII to XXIII, respectively. However, the number of functional testisacs is subject to variation from 10 to even 12.

The testisacs are among the last components of the male reproductive system to develop. In the immature individual HS-5 the testisacs are strikingly underdeveloped, but 11 pairs of liver-colored primordial testisacs are clearly discernible in the correct positions. In this individual each testisac primordium is round and flattened, rather than spheroidal, with blunt irregularly digitiform processes extending from the medial face. The vas deferens is a conspicuous white linear structure running along the ventral floor. In this immature specimen it is remarkably broad and anastomosing, seemingly without a discrete longitudinal duct. At segmental intervals a similarly broad vas efferens proceeds antero-laterally from the vas deferens to join the posterior portion of the primordial testisac.

In mature specimen HS-4 the presumptive eleventh testisac is neither fully formed nor functional. At the position where T11 should be located, there is only flattened primordial tissue with no connection to the vas deferens, which terminates at T10 in this specimen. On the other hand in specimen HS-3 there is superfluous primordial tissue located at what would be T12 but there is no connection to the vas deferens, which terminates at T11.

Penis sheath. In all cases the penis sheath contains a long muscular structure originating in the ventral floor behind g. XI. From here it proceeds posteriorly some distance before flexing and returning anteriorly to join the enlarged prostate located between g. XII and g. XIII. The proximal arm (gonopore end) of the penis sheath is always longer than the distal arm (prostate end).

In the immature specimen (HS-5) both arms of the penis sheath are straight and flex at g. XIV (Fig. 7C, ps). In the mature individuals (HS-3, HS-4) both arms of the penis sheath are noticeably longer, with the points of flexion at XIV 1/4 and XV, respectively. With such lengthening the ratio of short to long arms of the penis sheath changes from approximately 1:2 in immaturity to approaching 1:1 when fully mature. The prostate is capped with gland cells in mature specimens, but such gland cells are lacking in the immature specimen (HS-5).

Ejaculatory bulb, epididymis and ejaculatory duct. All specimens have a cigar-shaped ejaculatory bulb located between g. XI and g. XII. In mature individuals (HS-3, HS-4) this structure is muscular and opaque, whereas in the immature individual (HS-5) the ejaculatory bulb has transparent walls which reveal the absence of content (spermatozoa). The ejaculatory bulbs are typically oriented anterior to posterior (HS-3, HS-5), as in the original description, but in one individual (HS-4) both ejaculatory bulbs display a medial-lateral orientation (7A, eb).

In all specimens the epididymis extends at least a little beyond the distal end of the ejaculatory bulb. However, this coiled structure varies considerably in prominence with maturation. In the immature individual (HS-5) the epididymis is relatively inconspicuous with few coils and extends only slightly beyond the end of the ejaculatory bulb. It runs only about half-way along the postero-medial surface of the ejaculatory bulb. In both mature individuals dissected the epididymis is massive and extends conspicuously beyond the end of the ejaculatory bulb. It is cradled by virtually the full medial surface of the ejaculatory bulb. In all cases the ejaculatory ducts are lengthy, a taxonomically significant feature, with a trajectory always posterior to the level of g. XI. Interestingly, only in the immature individual HS-5 do the ejaculatory ducts coil conspicuously near point of entry into the prostate.

Vaginal caecum, common oviduct and vaginal stalk. In general, the female reproductive system of all dissected specimens from the Albemarle conforms to that described above for the reference specimen (HS-4) (Fig. 7). Especially noteworthy in this context is the presence of the small vaginal caecum even in the immature specimen (HS-5).

However, the common oviduct and vaginal stalk change as the animal matures. In immaturity the common oviduct coils noticeably along much of its length whereas in mature individuals the common oviduct coils little (HS-4) or not at all (HS-3). Furthermore, the anterior portion of the common oviduct in mature individuals is encased with small, whitish gland cells in mature individuals. Such cells are absent in the immature specimen. Finally, the flexion of the vaginal stalk is at XIII 1/3 in the immature specimen, whereas in both mature individuals the flexion is considerably more posterior, toward g. XV.

Comparison of *H. septagon* from the Albemarle Peninsula with the holotype

Sawyer and Shelley (1976) originally described *H. septagon* from Durham County, NC, approximately 325 km west of the Albemarle populations. In most respects the holotype (USNM 51539) falls within the variability shown in this study for specimens from the Albemarle Peninsula. However, there are some external and internal discrepancies which extend the taxonomic concept of this species.

In life, the bodies of the Albemarle specimens are not as firm nor muscular as that described for the holotype. Thus, the muscularity of *H. septagon* is probably overstated in the original description. Background pigmentation in the Albemarle population is quite variable, and minor differences from the holotype are of little taxonomic significance. A faint mid-dorsal stripe is not characteristic of the Albemarle specimens, and its purported presence in the holotype is probably misleading.

Importantly, this Albemarle study introduces a developmental dimension to the taxonomy of *H. septagon*. For example, the holotype is described as lacking crop caeca. In contrast, the immature specimen (HS-5) from the Albemarle region displays two pairs of crop caeca per segment throughout most of the length of the crop (Figs. 4C, 8). The taxonomic implication is that in *H. septagon* paired crop caeca are lost during maturation.

For similar developmental reasons, the positions of flexion of the penis sheath and the vaginal stalk ('vaginal duct' in Sawyer & Shelley 1976: 87, 88) are not inherently diagnostic as purported in the holotype. As shown in the Albemarle specimens such positions move posteriorly with maturation, and therefore are not inherently reliable taxonomic characters in this species.

[By way of correction, the original description of *H. septagon* contains several typographical errors as follows: XIIa3 should read VIIa3; VIIa1 should read VIIIa1; and XIIb1 should read XIIIb1 (see Sawyer & Shelley 1976: 85–86). In addition, in their fig. 6 E the segment should be labeled XII rather than XI. Internally, the anterior tip of the prostate is correctly positioned "immediately behind ganglion XII" in the narrative (p 87), but misleadingly drawn in their fig 7B.]

Comparison of *H. septagon* from the Albemarle Peninsula with specimens from southeastern Virginia

H. septagon has been known from southeastern Virginia since 1895 (including specimens USNM 21192, 42650, 42724, 42649). Five or six of these specimens were examined in life and after preservation by J. P. Moore (see Moser 2011). Of historic importance, Moore gave considerable (unpublished) anatomical detail on two specimens collected by A. S. Fischer on 26 June 1895 at Lake Drummond, Dismal Swamp. At the time Moore was working at the Academy of Natural Sciences of Philadelphia, but after his death in 1965 his collection was transferred to the Smithsonian (Meyer 1968).

Significantly, Moore clearly stated in his personal notes dated 26 June 1958 that the original specimen collected in 1895 had sixteen complete segments (i.e. segments IX–XXIV are 5-annulate), a taxonomically significant feature found consistently in specimens from the Albemarle Peninsula, as well as in the holotype. Furthermore, all specimens examined by Moore had seven annuli separating the male and female gonopores at XIb5/b6 and XIIIb1/b2, respectively, with the usual minor variation in position. At least one specimen displayed the female opening associated with a nipple-like papilla.

Fortunately, Moore dissected one large specimen (collected 4 Apr 1955, vicinity of Magnolia, VA, 110 mm) to determine internal features. This specimen agreed internally with the Albemarle specimens in most respects. However, both the penis sheath and vaginal stalk extended more posteriorly than observed in the Albemarle specimens. In the Virginia specimen the flexion is in segment XVI for the penis sheath, and in segment XVII for the vaginal stalk, respectively.

Comparison of *H. septagon* from the Albemarle Peninsula with specimens from southern New Jersey

About 2003 William Ott made a totally unexpected discovery of a large terrestrial leech in his lawn in Alloway, New Jersey (Donovan 2009). Wirchansky & Shain (2010) found additional specimens in two other localities, all in the southern part of the state (Wirchansky 2009). Recognizing its novelty to New Jersey, they described it as a new species, *Haemopsis ottorum* Wirchansky & Shain, 2010.

At the time little was known about the morphological parameters of *H. septagon* as a biological species, apart from the brief original description. The analysis of variability within the Albemarle specimens in this paper demonstrates that taxonomically there is remarkably little to distinguish the terrestrial leech from New Jersey from *H. septagon*. For the following reasons *H. ottorum* is herein considered a junior synonym of *H. septagon*.

The authors distinguished the New Jersey leech from *H. septagon* primarily as follows: presence of white-tipped sensilla, lack of lateral stripes, very large epididymis twice size of the ejaculatory bulbs, and relatively straight vaginal ducts. Each of these characters falls within the variability of *H. septagon* presented in this paper. Pigmentation of *H. septagon* is unreliably variable, and therefore of little taxonomic significance in this species. Note for example two particularly dark specimens from the Albemarle Peninsula (HS-3, HS-7) in which the lighter sensilla are highlighted by contrast (see Fig. 3). Furthermore, the size of the epididymis and certain other features of the reproductive systems vary according to size and state of maturation. In one mature Albemarle specimen (HS-4) the large size of the epididymis is virtually indistinguishable from that in the New Jersey holotype (see Fig. 7A, e).

In two respects the New Jersey specimens appear to lie outside the variability found in the Albemarle specimens, namely in having 10 distichodont teeth and a length of 300 mm. The former was based apparently on a single specimen and not illustrated as in this paper (Fig. 6b–d). Moreover, loss of teeth during preservation must be considered. In any case number of teeth is a technically challenging character requiring convincing data. It is unclear if the reported length was based on a properly relaxed specimen. The Albemarle specimens were exaggeratedly extensible in life.

Furthermore, the New Jersey leech closely resembles *H. septagon* in the following taxonomically significant characters: 7 to 7½ annuli between gonopores, with the female gonopore on a raised ‘nipple’; 16 complete segments (IX–XXIV, see fig 3 of Wirchansky & Shain 2010); and lengthy pharynx extending to about ganglion XI (see fig 2 of Wirchansky 2009). In the New Jersey holotype the penis sheath flexes at ganglion XIV, and the vaginal stalk at ganglion XVI, both within the parameters of *H. septagon* from North Carolina and Virginia.

Wirchansky and Shain (2010) add significantly to understanding *H. septagon* as a biological species. They extend its geographic range 450 km to the north and, for the first time, found it sympatric with, and taxonomically distinct from, the widespread northern leech *Haemopsis marmorata* (Say, 1824) which it superficially resembles.

Biology and distribution

H. septagon is probably more common than current records indicate. This may be attributable to its remarkable elusiveness and propensity for inhospitable habitats. Ecologically, this species has been found in a diversity of wetland environments, including shrub bogs (locally known as “pocosins”) characteristic of the vast Albemarle region, riverine swamps, barrier islands, and even local damp depressions. There is evidence in this study that some populations, or at least some individuals (HS-3, HS-7), may be aquatic or semi-aquatic (see Introduction). In all likelihood *H. septagon* will prove to be amphibious, but with undoubted tendency toward terrestriality.

Virtually all sightings to date have been in the daytime. However, it is probably not a truly diurnal species in that nocturnal activity cannot be excluded. This predominantly terrestrial leech is most frequently encountered for-

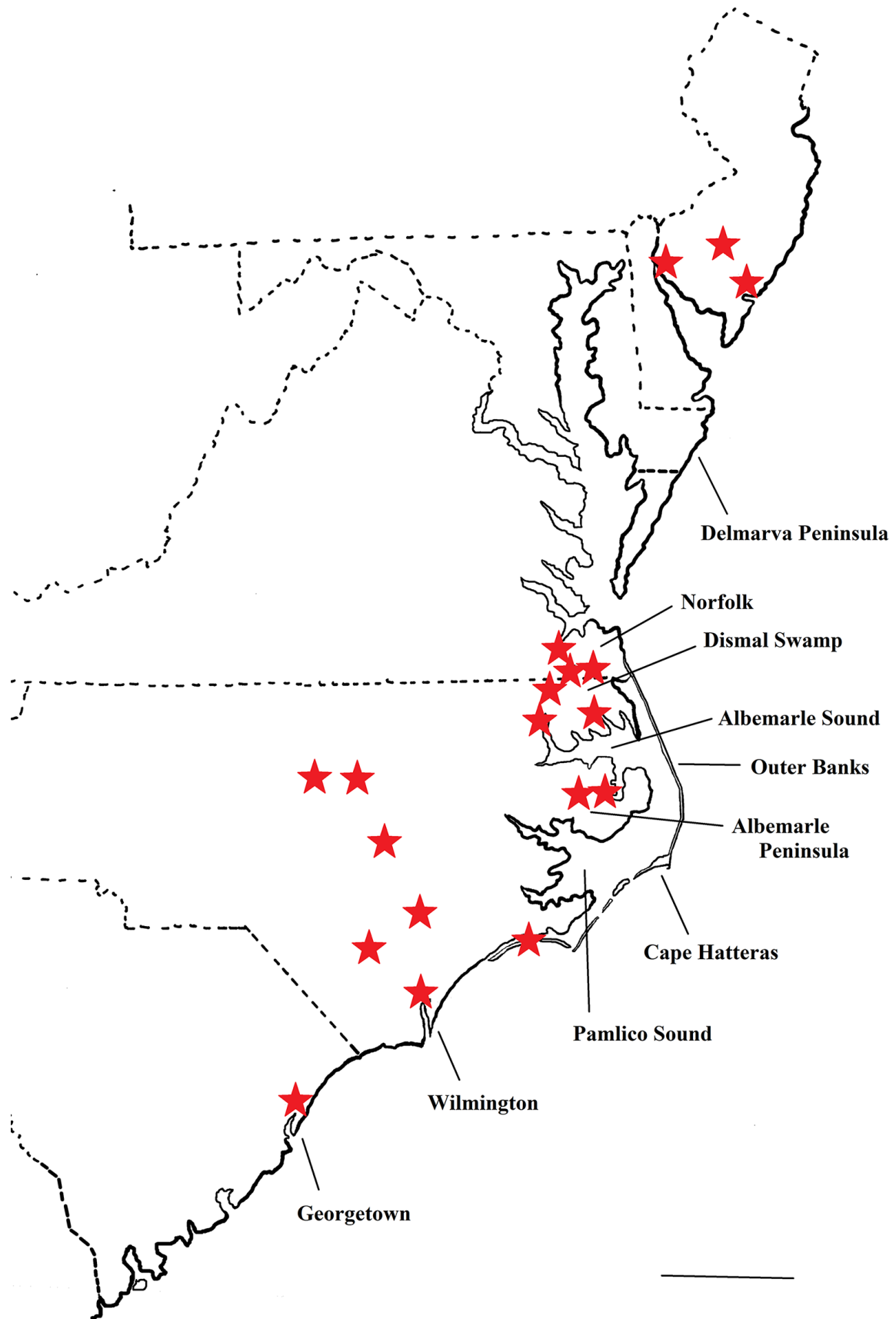


FIGURE 10. *Haemopsis septagon* Sawyer & Shelley, 1976. Map of locality records. *Haemopsis septagon* is currently known from the mid-Atlantic coastal plain from South Carolina to southern New Jersey. Scale bar: 100 km. See **APPENDIX** for compilation of locality records.

tuitously, crawling in damp grass, or even on roads following a rain. In this study it was typically found early in the morning foraging in grass during a light rain or drizzle (HS-1, HS-2, HS-4). With experience the most productive way to collect this species is by looking in and under rotten logs, or under pieces of wood (HS-5) (pers. obs.).

Throughout its range *H. septagon* feeds on oligochaetes. In inland North Carolina its diet is well established as earthworms (Shelley 1977; Shelley *et al.* 1979). This predilection is confirmed in this study in that a partially digested earthworm was found in the crop of a large specimen (HS-4) from the Albemarle Peninsula (Fig. 9B). Similar dietary observations were made on the New Jersey populations (Wirchansky 2009; Wirchansky & Shain 2010). Whether it consumes other prey organisms is unknown.

There is morphological evidence in this study that *H. septagon* may use chemoreception to forage for its prey. This is suggested from highly developed labial sense organs or “taste” receptors concentrated on the dorsal lip of this species (Fig. 9A). Similar sensory structures were shown by behavioural and ablation studies to account for foraging for earthworms in *Haemopis marmorata* (see Simon & Barnes 1996).

With respect to seasonality *H. septagon* can be active more or less throughout the year, but about half of all sightings to date have been in March and April. Based on 38 specimens with known dates in this and previously published studies, the breakdown of monthly encounters is as follows: Jan (1), Feb (2), Mar (8), Apr (11), May (1), June (6), July (3), Aug (1), Sept (4), Oct (0), Nov (0) and Dec (1).

Reproduction in this species is largely unknown. However, a clitellum, normally a prelude to cocoon deposition, has been reported in two specimens to date, both in early June. These were a specimen (82 mm) from Lake Drummond, Dismal Swamp, found on 7 June, and a specimen (HS-7, 109 mm, 5.2 g) from the Albemarle region collected “in early summer” (Fig. 2). Juveniles of *H. septagon* have been reported on 19 April (Shelley *et al.* 1979) and 4 May (HS-5).

As revised in this paper the geographic distribution of *H. septagon* has been extended north to southern New Jersey (Fig. 10). In this context this elusive species should be sought in the intervening Delmarva Peninsula. One center of abundance and the focus of this study is the peaty wetlands of the Dismal Swamp and contiguous swamps of the Albemarle region and southeastern Virginia. It also lives in some numbers well up the flood plain of the Neuse River in the general Raleigh-Durham area (Shelley 1977; Shelley *et al.* 1979). Further south it extends up the flood plain of the lower Cape Fear River to at least Bladen County (White Lake). In South Carolina a single record locates it in coastal Georgetown County (Plantersville).

Taxonomic revision

The foregoing descriptions of *Haemopis septagon* from the Albemarle Peninsula, along with critical comparisons with those from the holotype, Dismal Swamp, southeastern Virginia and southern New Jersey, revealed that these disparate populations share a number of external and internal features of taxonomic significance. Taken together these key characters can serve as the basis for a taxonomic revision of the species *H. septagon*, summarized succinctly as follows:

Haemopis septagon Sawyer & Shelley, 1976. Revised

Synonymy:

Haemopis septagon Sawyer & Shelley, 1976; Shelley 1977; Shelley *et al.* 1979.

Haemopis ottorum Wirchansky & Shain, 2010.

Diagnosis. Eyes 5 pairs in characteristic hirudinid arc; 16 complete (5-annulate) segments (IX–XXIV); male and female gonopores separated by 6 ½ to 7 annuli, typically at XIb5/b6 and XIIIb1/b2; typically 14–16 distichodont teeth per jaw; known from mid-Atlantic coastal plain, from South Carolina to southern New Jersey (Fig. 10).

Description. Terrestrial, semi-terrestrial or amphibious; predaceous on oligochaetes; length of adults up to at least 150 mm; pigmentation concolor with no metameric patterns, basically olive green in life, with or without irregular black specks dorsally (and sometimes ventrally); jaws low and rounded; at least one pharyngeal ridge terminating between each jaw; lengthy pharynx, extending to ganglion XI; adult crop basically a long irregular tube

without bilateral caeca, except a pair of posterior caeca extending from segment XIX to XXIV (NOTE: In juvenile specimens there are two sets of distinguishable crop caeca per segment, not evident in adults) (see Fig. 8); intestine comprised of two parts (see Fig. 4); ejaculatory bulb and epididymis well developed; ejaculatory ducts lengthy and tortuous; small vaginal caecum, even in juveniles; segments VII, 3-annulate; VIII, 4-annulate; the two adjacent annuli VIIa3 and VIIIa1 characteristically broadened; XXIV, 5-annulate; XXV, 3-annulate; female gonopore sometimes with a nipple-like protuberance, commonplace in adults but not juveniles; penis sometimes everted externally; male opening penetrates ventral body wall behind ganglion XI and the female opening penetrates immediately anterior to ganglion XIII; prostate located in segment XII and the ovisacs at ganglion XIII; penis sheath and vaginal stalk increasingly long and coiled as animal matures, with flexion from ganglion XIII 1/2 in juveniles to as far as ganglion XVI in mature adults; epididymis extending well beyond ejaculatory bulb in mature adults (much smaller in juveniles); 11 (10–12) pairs of testisacs, in segments XIII to XXIII, inclusively.

Discussion

Although recognized from the outset as taxonomically aberrant based on gonopores alone, *H. septagon* was assigned initially to the genus *Haemopsis* Savigny, 1822, rather than proliferate yet another new genus based on limited information (Sawyer & Shelley 1976). A generic revision was later anticipated (Sawyer 1990) but again deferred because of inadequate knowledge of this elusive leech. In the current paper a much better understanding of *H. septagon* as a biological species supports a stronger case that this terrestrial, mid-Atlantic species stands apart from other members of the genus *Haemopsis*. However, the taxonomy of this diverse, possibly paraphyletic, genus is problematic and cannot be pursued further here.

Of particular interest in this context is another American terrestrial leech *Haemopsis oenops* (Grube, 1871), senior synonym of *Haemopsis terrestris* (Forbes, 1890), a species of the lower Mississippi River drainage (see Sawyer 1972). Although its gonopores are separated by the conventional 5 annuli, it deviates from other *Haemopsis* in having 17 complete segments (VIII–XXIV), and a lengthy pharynx reaching to ganglion XI. It is tempting to assign *H. septagon* as a sister species of *H. oenops*. However, by way of caution and to avoid the possibility of convergence due to terrestriality, this question must be deferred pending a comprehensive study of *H. oenops* as a biological species. Interestingly, this reputedly terrestrial leech also has an aquatic form (see Moore 1901: 531–532; Moore 1912: 112–114).

With respect to broader taxonomic kinships, *H. septagon* may have affinity with certain hirudinids from South America and even Asia. For example, the genus *Semiscolex*, a Latin American group typically has 6–7 annuli between gonopores. Similarly, the pharynx of other South American hirudinids extend to segment XI or beyond. Intriguingly, a group of Asian terrestrial leeches (*Gastrostomobdella*) has anterior and posterior intestines shown in this paper to be present also in *H. septagon* (see Fig. 4, ai, pi). However, these suspected higher relationships cannot be pursued further here (Sawyer 1986: 455–457, 679, 681, 789–793; see also Ocegüera-Figueroa 2006).

From the long view *Haemopsis septagon* is best interpreted as a relict carnivore successfully adapted to conditions of an ancient, resilient wetland ecosystem defining the mid-Atlantic coastal plain. In this context the extension of the range of this species from South Carolina to southern New Jersey, as proposed in this paper (Fig. 10), takes on a broader perspective. This distribution is unique for any hirudinid leech and in itself hints of an ancient past in that it broadly overlaps the distribution of the primeval Carolina Bays, peculiar wetland features characteristic of this same region (see Sawyer 2010: 2, 14–20, 48–49, 217).

The terrestrial habit of *H. septagon* undoubtedly reflects adaptive response to several aspects of living in peaty wetlands characteristic of the Dismal Swamp/ Albemarle Peninsula region. One is the low levels of oxygen attributable to organic decomposition (Chapman *et al.* 2004). In the Dismal Swamp, for example, the dissolved oxygen concentration is typically less than 1.0 mg/L (Speiran *et al.* 2015). Another factor is that this region typically vacillates between submerged swamp on the one hand and dry woodland on the other depending on seasonal precipitation (illustrated in Sawyer 2010: 168). Finally, an overriding biological factor is localized availability of earthworms under these same environmental constraints.

As a category terrestrial worms are commonly subject to accidental introductions in soil, such as with potted plants. A case in point is the carnivorous flatworm *Bipalium kewense* originally from Southeast Asia (Sluys 2016). This large worm can be confused with *H. septagon* by the inexperienced, and has already established itself in the remote Albemarle Peninsula (June 2002, per. obs.).

In this context the question arises whether *H. septagon* itself is a non-native species, and/or whether its range has expanded in recent times due to human influence. The best evidence it is truly a native species is that it was first found in 1895 at Lake Drummond in the Dismal Swamp (see Introduction). This was, and continues to be, one of the least influenced habitats by human activity in eastern United States. On the other hand whether an apparent increase in recent sightings, especially in urbanized areas such as the Raleigh-Durham conurbation, is due to human influence should be investigated. An intriguing case in point may be the discovery of *H. septagon* at an erstwhile landfill site in Wake County (Wake Audubon 2015).

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APPENDIX

Locality records for *Haemopsis septagon*. Following is a compilation of known locality records for *H. septagon* from various sources, including published accounts and museum specimens, in addition to records presented in this study (see Fig. 10).

SOUTH CAROLINA. Georgetown County (1.6 km ne Plantersville, 23 July 1933, coll: C. E. Burt, USNM 20016, S&S 1976). **NORTH CAROLINA. Bladen County** (White Lake, 25 March 1933, 1 specimen, 46 mm, coll: A. S. Pearce); **Carteret County** (Theodore Roosevelt State Natural Area, Bogue Banks, NCRID, 7 Mar 2008, photographed by Patricia McNeese); **Duplin County** (“13.6 km ne Kenansville, Goshen Swamp near NC hwy 11, 1 adult, 6 March 1976, NCSM P177”, Shelley *et al.* 1979); **Durham County** (Type locality: New Hope Creek flood plain of NC highway 54, 0.8 km w. NC highway 751, 28

Dec 1973, USNM 51539, S&S 1976. Other records from the upper Neuse River basin, especially Wake and Durham Counties, can be found in Shelley *et al.* 1979 and in NCSM); **Gates County** (Merchants Mill Pond State Park, 21 Apr 2018, F. Williams, www.dpr.ncparks.gov/photos/fromNRID.php?pid=40555); **Hertford County** (Harrellsville, NCSM 29, S&S 1976); **Johnston County** (Ward Street, Smithfield, 1 adult, 10 Apr 1977, NCSM P224); **New Hanover County** (“Wilmington”, 19–24 May 1924, 1 specimen 109 mm, coll: George S. Myers. California Academy of Sciences CASIZ 004813, C. Piotrowski, pers. comm.); **Pasquotank County** (“Elizabeth City, crawling on ground near service station, 1 adult, 8 Mar 1975, NCSM P186”, Shelley *et al.* 1979); **Tyrrell County** (Gum Neck, see **Reference material**); **Wake County** (NWD Landfill Park/Abbott’s Creek Greenway, 19 June 2015, photographed, Wake Audubon 2015); **County Unspecified** (‘Eyre’, 3 June 1924, USNM 42557, S&S 1976). **VIRGINIA. Chesapeake City County** (Lake Drummond, Dismal Swamp, 2 specimens, USNM 48259, 82 mm, USNM 48359, 86 mm, 7 June 1895, coll: A. S. Fisher (Moser 2011); ‘Norfolk Swamp, Gum Swamp’, 25 Sept 1959, 2 specimens labeled as ‘*Haemopsis grandis*’, coll: R. Rageot, USNM 42649; ‘Dismal Swamp’, Oct 1957, observed in life by J. P. Moore, fixed 14 Dec 1957, cf USNM 42650); **Suffolk City County** (Vicinity of Magnolia, 1 specimen, 110 mm, 4 Apr 1955, coll: R. Rageot, dissected by J P Moore; Holland, on roadside, 19 July 1961, 1 specimen labeled as ‘*Haemopsis marmorata*’, coll: G. M. Boush, USNM 42724); **County Unspecified** (“Five Forks”, 29 Mar 1949, USNM 21192, S&S 1976). **NEW JERSEY. Salem County** (Alloway, USNM 1125241); **Camden County** (Winslow); **Atlantic County** (Pomona), Wirchansky & Shain 2010, as *Haemopsis ottorum*.