DEVELOPMENTAL MORPHOLOGY OF ROOTS AND SHOOTS OF *PODOSTEMUM CERATOPHYLLUM* (PODOSTEMACEAE – PODOSTEMOIDEAE)

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ABSTRACT. *Podostemum ceratophyllum* shows peculiar architectural characters that seem to apply to basal members of Podostemoideae. In contrast to more elaborate taxa of this subfamily, *P. ceratophyllum* fits into the classical root-shoot (CRS) model, with clearly distinguishable thread-like roots (with root caps and endogenous lateral roots), as well as stems and leaves. Root-born endogenous shoots initially develop a series of distichous leaves having one stipular sheath each. Shoot modules are terminated by double-sheathed leaves associated with stem branching and/or flower formation. Double-sheathed leaves of *P. ceratophyllum* have two boat-shaped stipular sheaths, each one containing a new leaf (as part of a daughter shoot) or a flower bud. Double-sheathed leaves are an evolutionary novelty of Podostemoideae, leading to branching types not known elsewhere in angiosperms. The vegetative architecture of *P. ceratophyllum* is similar to other American species of *Podostemum*.

Key Words: *Podostemum*, dithecous leaf, vegetative morphology, non-axillary branching, stem bifurcation, stipules

Podostemum ceratophyllum Michx. is the type species of the Podostemaceae (including Tristichoideae and Weddellinoideae), a relatively large aquatic family belonging to the Malpighiales clade in the eurosids I, perhaps related to Hypericaceae (= Clusiaceae; Savolainen et al. 2000; Soltis et al. 1999). The Podostemaceae contains about 46 genera and 280 species (Cook 1996a; Philbrick and Novelo 1993, 1995). Royen (1954) recognized 17 species of *Podostemum* in the Americas, although a monograph by Philbrick and Novelo (in prep.) will recognize only seven. There is growing evidence to support the hypothesis that the genus *Podostemum* is restricted to the New World (e.g., Kita and Kato 2001; Philbrick and Novelo, in prep.); Old World species once placed in *Podostemum* have been moved to other genera (e.g., Cook 1996a,b; Cusset 1992; but see Jäger-Zürn 1999, 2000a,b and Mathew and Satheesh 1997).

Although it is aberrant in terms of its temperate distribution, studies of *Podostemum ceratophyllum* have played an important role in our understanding of the morphology of plants in this intriguing family. Warming's (1881, 1882) accounts of the morphology of *P. ceratophyllum* represent some of the earliest detailed descriptions of the morphology of Podostemaceae. Even so, the developmental morphology of this species, indeed most species in the family, remains incompletely known. The purpose of this contribution is to present an account of the developmental morphology of *P. ceratophyllum* based principally on scanning electron micrographs. These observations will be discussed relative to the published literature (e.g., Graham and Wood 1975; Hammond 1936, 1937; Matthiesen 1908; Royen 1954; Warming 1881, 1882).

Interpretation of the vegetative body in Podostemaceae has been controversial. Consideration of the many aspects of the controversy are beyond the scope of this paper. The reader is referred to Rutishauser (1995, 1997) for a more thorough discussion. In this paper, we will use the structural terms "root," "shoot," "stem," "leaf." The use of these terms, however, does not imply a 1:1 correspondence (complete homology) with the organ categories of more typical angiosperms that show the classical root-shoot model (CRS model; Jäger-Zürn 2000a; Rutishauser and Huber 1991; Rutishauser 1995, 1997). We believe that these descriptive terms are best interpreted as structural categories with fuzzy borderlines that allow the recognition of intermediates or mosaic organs (cf. Rutishauser and Isler 2001). Some workers (e.g., Cusset 1992; Mohan Ram and Sehgal 1992, 1997, 2001; Schnell 1994) have used the neutral term "thallus" for the creeping structures that are called "roots" in the present paper. Herein the podostemaceous "root" is interpreted as a photosynthetic organ that serves an anchorage function, and from which endogenously formed shoots (with leaves) arise.

Plants of the family grow tenaciously attached to rocks or other solid substrata in river rapids and waterfalls. The geographic distribution, biology, and morphology of *Podostemum ceratophyllum* has attracted considerable attention (e.g., Capers and Les 2001; Graham and Wood 1975; Hammond 1936, 1937; Meiger 1976; Philbrick 1981, 1984; Philbrick and Bogle 1988; Philbrick and Crow 1983, 1992). Although few species of Podostemaceae occur in temperate regions, *P. ceratophyllum* has a broad range in eastern North America (as far north as eastern Canada) with disjunct portions of its range in the Dominican Republic and Honduras (Philbrick and Crow 1983; Royen 1954). The species has been shown to be important in the ecology of

rivers where it is the dominant macrophyte (Everitt and Burkholder 1991). Some river biota are closely dependent on the plant. The river-weed darter (*Etheostoma podostemone* Jordan, Percidae), a perch-like fish, occurs in habitats closely tied to *P. ceratophyllum* (Connelly et al. 1999). The plant has also been documented as providing important habitat for two fish species (amber darter, *Percina antesella* Williams and Etnier; Conasauga logperch, *P. jenkinsi* Thompson, Percidae) that are listed as federally endangered in the United States (U.S. Fish and Wildlife Service 1985). Human-induced changes in river flow and water quality have likely been factors that have lead to *P. ceratophyllum* being included on rare and endangered species lists for several states in the United States.

MATERIALS AND METHODS

The data presented in this study were derived from material collected from two populations of *Podostemum ceratophyllum* in the eastern U.S.: (1) Maine. York County, Mousam River, Kennebunk, 30 Aug 1981, *Philbrick 1148* (MEXU, NHA, WCSU, Z); (2) Pennsylvania. Cumberland County, Williams Grove, Yellow Britches Creek, 10 Oct 1981, *Philbrick 1166* (MEXU, NHA, WCSU, Z). Voucher specimens (pressed and/or liquid-fixed) are located in the herbaria listed above. The material used for this study was fixed and preserved in 70% ethyl alcohol. For scanning electron microscopy, the dissected shoot tips were critical-point dried (using acetone/carbon dioxide) and sputter-coated (Au-Pd). The micrographs were taken with scanning electron microscopes (Cambridge S4 and Hitachi S4000) at 20 kV.

RESULTS

The results will be presented in the following sequence: roots, shoots, leaf morphology and development, stipular sheaths, stem bifurcation, and flower position. These results are illustrated in Figures 1–27.

Dorsiventral roots with endogenous shoot buds and exogenous holdfasts. The roots of *Podostemum ceratophyllum* (Figures 1, 2) are green, thread-like structures that attach to submersed rocks. These slightly dorsiventrally flattened structures are provided with an asymmetric multicellular cap, resembling the calyptra of a typical root (Figure 2; Hammond 1937; Warming 1881). The roots have an oval outline
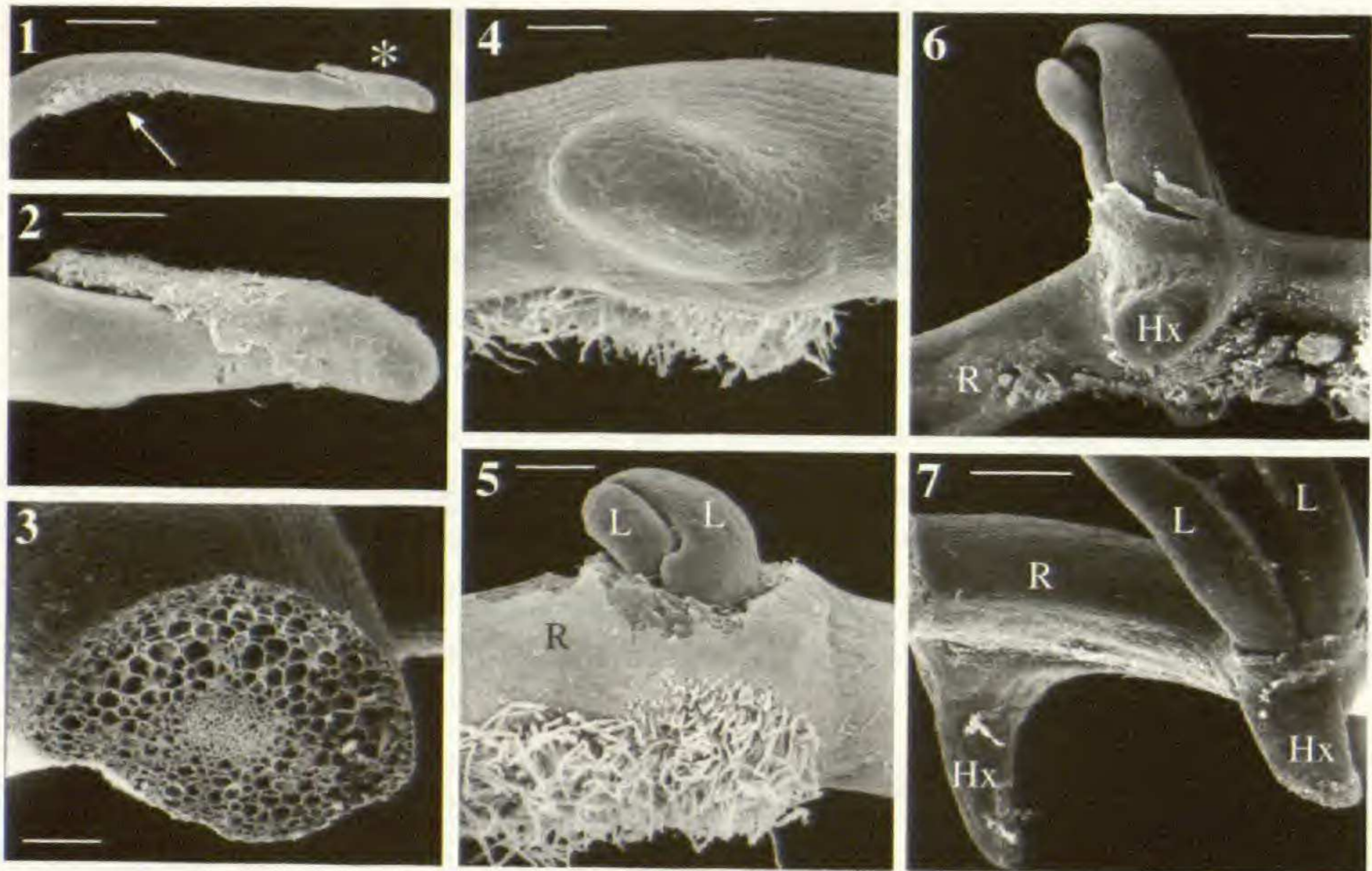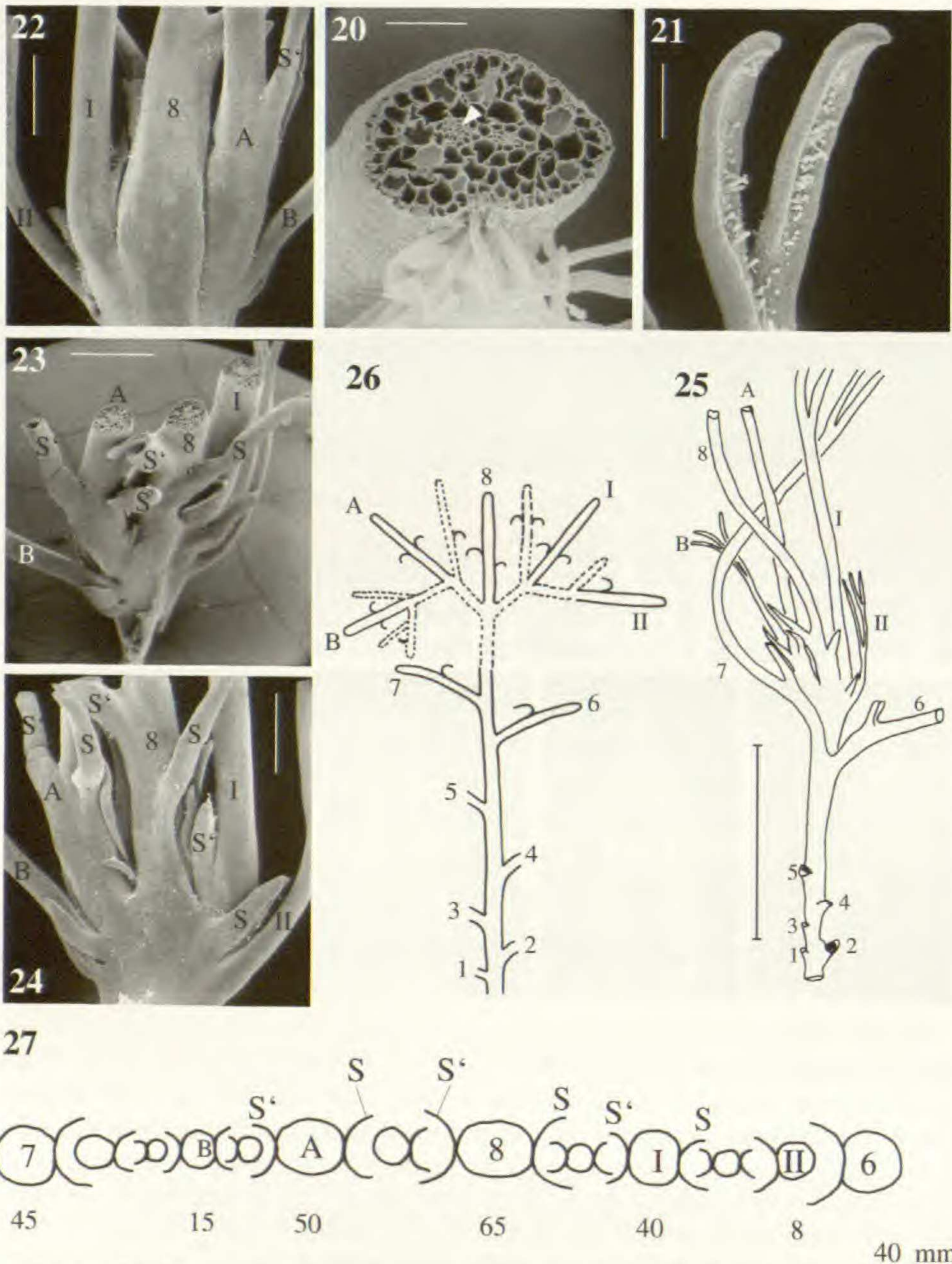
Figures 1–7. *Podostemum ceratophyllum.* Root structure with exogenous hold-fasts and endogenous shoots (*Philbrick 1148*). 1–2. Overview and close-up of root tip. Note asymmetric cap (asterisk). Arrow points to zone with adhesive hairs on ventral side. Scale bar = 1 mm and 300 μm, respectively. 3. Transverse section of slightly dorsiventral root. Note central vascular cylinder. Scale bar = 100 μm. 4. Distal portion of root, with protrusion along root flank due to endogenous formation of shoot bud. Note adhesive hairs on ventral surface. Scale bar = 100 μm. 5. Same root portion (R) as Figure 4; peripheral root tissue removed in order to show endogenously formed rosulate shoot with two young leaves (L). Scale bar = 100 μm. 6. Older root portion (R), with rosulate shoot protruding. Note the protruding exogenous holdfast (Hx) associated with the endogenous shoot bud. Scale bar = 200 μm. 7. Portion of a mature root (R), with two finger-like holdfasts (Hx) in alternate positions along the root flank, and endogenously formed rosulate shoot with elongate leaves (L). Scale bar = 200 μm.

when seen in transverse sections (Figure 3). There is a central vascular bundle with inconspicuous xylem elements that are often arranged in two basilateral poles (Hammond 1937, his Figure 3; Warming 1881, his Figure III/11, 15). Just behind the root tip, protrusions arise along the root flanks (Figure 4) that represent early stages of endogenous shoots. The first leaves of the endogenous shoot form while the shoot apex is still within the cortex, and protrude as soon as the cortex and epidermis are ruptured (Figures 5, 6). Finger-like holdfasts arise as multicellular exogenous outgrowths that are directed to the surface of the substratum (Figure 6). Holdfasts of *P. ceratophyllum* roots are opposite or alternate (Figure 7). The holdfasts have also been called haptera (singular hapteron; e.g., Rauh 1937; Warming 1881). They are associated with the endogenously formed shoots that arise in a more dorsal position along
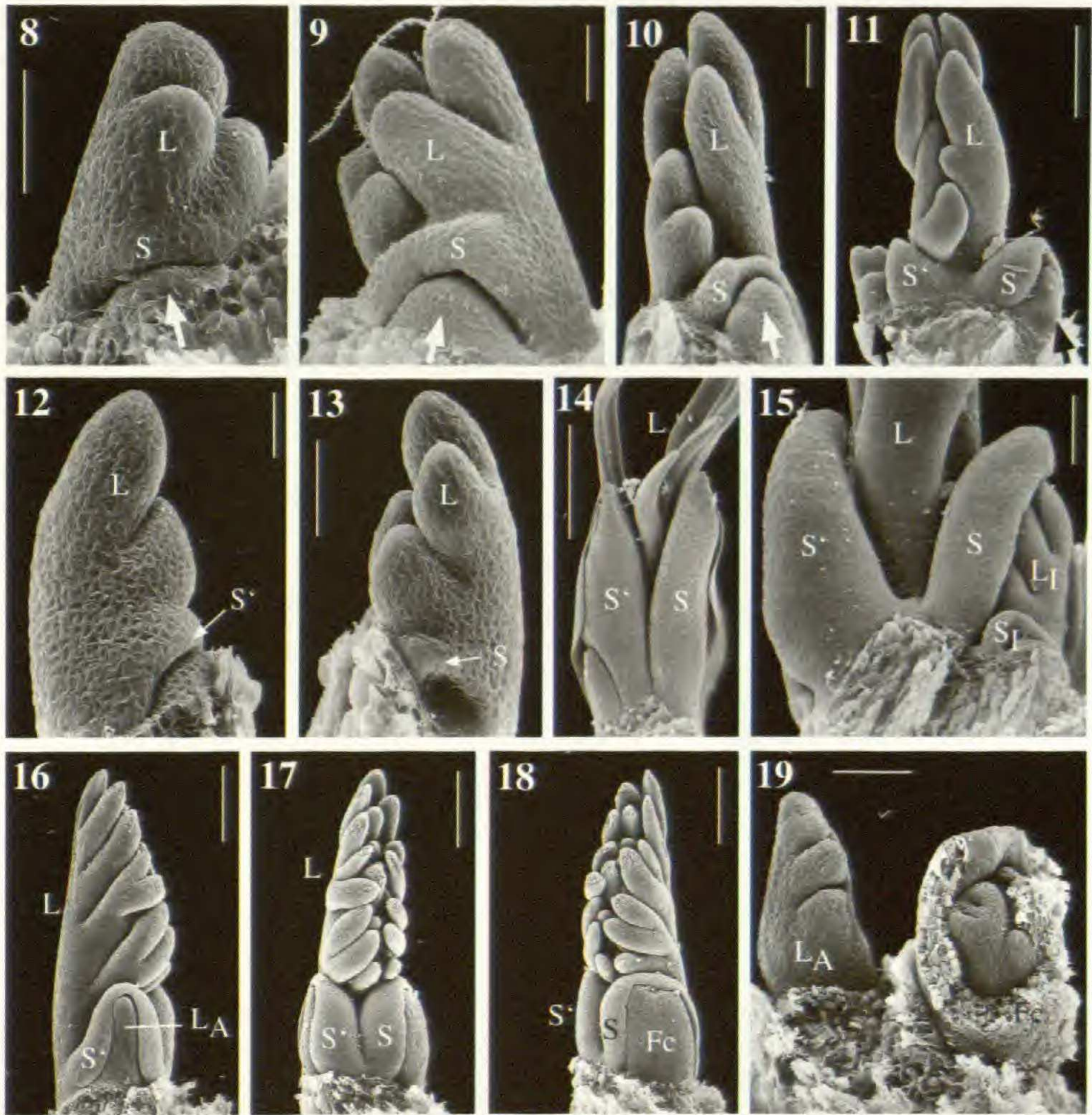
Figures 8–19. *Podostemum ceratophyllum.* Development of single-sheathed and double-sheathed leaves (8–15, *Philbrick 1148*; 16–19, *Philbrick 1166*). 8–10. Three developmental stages of single-sheathed leaves. Each leaf has only one stipular sheath (S) obliquely positioned relative to the orientation of the compound blade. The primary pinnae (L) arise as nearly hemispherical protrusions. Arrows point to initial stages of next younger leaves. Scale bars = 50 μm. 11. Young double-sheathed leaf, seen from upper (dorsal) side. There are two stipular sheaths adjacent to each other (i.e., in oblique lateral positions S, S'). Each sheath contains (covers) a younger leaf primordium (see black arrows). Scale bar = 100 μm. 12–13. Very young double-sheathed leaf seen from opposite sides. S and S' are the two primordial sheaths. Scale bars = 50 μm. 14–15. Proximal portion of two double-sheathed leaves. The two stipular sheaths (S, S') are adjacent to each other, and the base of the blade (L) occurs behind the sheaths. Further dissection has shown that the next younger leaf L_1 is again double-sheathed, with S_1 being its outer visible sheath. Scale bars = 500 μm and 100 μm, respectively. 16–18. Three different views of a half-grown double-sheathed leaf with a pinnate blade (L). Note that sheath S' is covering a daughter leaf (L_A) and sheath S contains a flower bud within a spathella (Fc). Scale bars = 250 μm. 19. Same specimen as Figures 16–18, after removal of the blade and the two sheaths in order to better observe the young leaf (L_A) and the young flower inside the spathella (Fc). Scale bar = 100 μm.

Figures 20–27. *Podostemum ceratophyllum.* Close-ups of blade segments and details of shoot branching associated with double-sheathed leaves (*Philbrick 1148*). 20. Transverse section of nearly mature blade segment with hairs arising from the concave surface. Arrowhead points to vascular bundle. Scale bar = 100 μm. 21. Two distal leaf blade segments of half-grown leaf (length 6 mm). Note hairs on concave surface. Scale bar = 250 μm. 22–24. Vegetative shoot tip after formation of seven leaves (upper portions removed). 22. Seen from "lower" side (toward substratum). Scale bar = 1 mm. 23. Seen from above. Scale bar = 1 mm. 24. Seen from "upper" side (away from substratum). View shown in Figure 24 is same as drawn in Figures 25 and 26. Double-sheathed leaf 8 is in terminal position, and additional ("lateral") leaves occur in both stipular sheaths (S, S‘) of leaf 8. For further explanation see

the root flanks (Figures 6, 7). Lateral roots are initiated as endogenous buds in the cortex of the mother root (Hammond 1937). Adhesive hairs grow out on the ventral side of the root, thus attaching it to the rock, especially in regions with shoot buds (Figures 4, 5; Warming 1881). The adhesive hairs in Podostemaceae have also been called root hairs or rhizoids (e.g., Hammond 1937; Rutishauser 1997).

Unbranched root-born shoots and their phyllotaxis. After protruding from the root cortex, each shoot bud is first rosulate with two or three leaves (Figures 5–7). As long as the shoot is unbranched the leaves arise along two ranks (i.e., they show distichous phyllotaxis). After the formation of additional leaves and internode elongation the stems may reach a length of over 10 cm, depending on the population (Hammond 1937). Vegetative shoots may produce a flower after the formation of 6–10 leaves (Graham and Wood 1975; Matthiesen 1908; Warming 1881, 1888).

Leaf morphology. The compound leaves of vegetative shoots reach a length of 3–30 cm. The blades are forked once or repeatedly (Figures 10, 16). Each spathulate to filiform subunit (blade segment) is longitudinally grooved, and is provided with a tiny vascular bundle. Short-lived hairs arise along the longitudinal groove or concave surface of the ultimate leaf segments (Figures 20, 21). The leaves along the unbranched stem are subtended by a single stipular sheath that embraces the node and is directed towards the shoot tip (Figures 8–10). Leaves next to branching sites of a stem have two stipular sheaths neighboring each other or obliquely opposite each other (Figures 11, 14, 15).

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Figures 26 and 27 and text. Scale bar = 1 mm. 25. Drawing of the same shoot tip as in Figures 22–24, with seven single-sheathed leaves (1–7) in two ranks along elongated stem, and double-sheathed leaf 8 in terminal position. Additional younger leaves are labeled I and II (right side), A and B (left side). Scale bar = 1 cm. 26–27. Schematic drawings of shoot tip, observed from the side and from above, respectively (same shoot as shown in Figures 22–25). The various double-sheathed and single-sheathed leaves are labeled, including their lengths in mm in Figure 27. Leaves A and B are the first outgrowths in the gap between leaf 7 (single-sheathed) and 8 (double-sheathed); leaves I and II belong to the gap between leaf 6 and 8. Areas drawn with dashed lines are more condensed than shown. The two sheaths of the three double-sheathed leaves (i.e., 8, I and A) are labeled as S and S', respectively.

Leaf development.   A bulge develops adjacent to the youngest leaf (arrow in Figure 8). This bulge, which may be viewed as a rudimentary shoot apical meristem, increases in size prior to giving rise to the next younger leaf (arrows in Figures 9, 10). In early developmental stages (leaf length ca. 200 μm) only three or four primordial pinnae (blade segments) are observable (Figures 8, 12, 13). A few additional lateral pinnae are subsequently initiated in basipetal order (Figures 9–11). In young leaves (ca. 1 mm long) the first-formed pinnae become subdivided by the formation of lateral pinnae along the rachis (Figures 11, 16). Subsequent differential elongation of the internal (non-terminal) segments of the compound leaf leads to the mature blade being dichotomously or subdichotomously divided. Both sheaths of a double-sheathed leaf are formed at about the same time when the leaf primordium is approximately 200 μm long (Figures 12, 13). Older developmental stages usually show two equal boat-shaped stipular sheaths which cover new leaf primordia or flower buds (Figures 11, 14, 16–18).

Position and development of the stipular sheaths in single-sheathed and double-sheathed leaves.   The sheath of a single-sheathed leaf is positioned obliquely relative to the "front" of the folded compound blade (Figures 8–10). In double-sheathed leaves the two stipular sheaths are adjacent to the left and the right set of pinnae, respectively (Figure 11). The two sheaths occupy obliquely lateral positions relative to the orientation of the young pinnae of the blade (Figures 11–18); neither sheath exactly occupies the site "in front" of the compound blade. The two stipular sheaths are adjacent to (i.e., obliquely opposite) each other. Seen from above, the two stipular sheaths of a double-sheathed leaf in *Podostemum ceratophyllum* form the two front corners of a triangle while the primordial leaf blade stands in the third ("rear") corner of this triangle (Figure 11).

Stem bifurcation and modular shoot construction.   The root-born shoot shown in Figures 25 and 26 has seven single-sheathed leaves in distichous order and a double-sheathed leaf (i.e., leaf "8") in terminal position. The first double-sheathed leaf is associated with the site of stem bifurcation. New shoot buds (i.e., new leaves) are formed within each of the two stipular sheaths of a double-sheathed leaf (e.g., leaf "8" in Figures 23–27), leading to stem bifurcation. Thus, the stem divides more or less symmetrically into two daughter shoots. Both sheaths of

a double-sheathed leaf give rise to a new daughter shoot. Leaves on the daughter shoots are visible in Figures 11, 14, and 15. Similar to the first-order shoot, both daughter shoots (= daughter modules) may again form single-sheathed leaves in distichous arrangement before terminating with another double-sheathed leaf, which initiates the next stem bifurcation. Due to repeated and accelerated stem bifurcation the shoots may appear "bushy" (i.e., with crowded leaves; Matthiesen 1908; Warming 1881). Consecutive branching can be accompanied by the production of a single leaf per branch, in which case the single leaf is double-sheathed. The "bushy" appearance develops when each of the consecutive daughter modules consists of only a single, double-sheathed, terminal leaf. When this occurs the first leaf of a daughter module, which is enclosed by one stipular sheath of a double-sheathed leaf, can itself be double-sheathed, indicating that successive branching has been initiated. Such a scenario is illustrated in Figure 15 where the daughter module on the right side has produced a double-sheathed leaf (L_1), with an outer stipular sheath (S_1) and an inner stipular sheath (not visible in the photograph).

The leaves of these truncated compound shoot systems are more or less arranged in one plane, as illustrated from different perspectives in Figures 22–25. This same compound branching system is illustrated schematically in Figures 26 and 27, as viewed from the side and top, respectively. Subsequent leaves and stem bifurcations are positioned within the plane of the seven distichously arranged leaves of the first order stem (Figures 25, 26). The next younger leaves ("A" on the left and "I" on the right side of Figure 27) are again double-sheathed. One of the next younger leaves ("B" on the left side) is again provided with two sheaths whereas an even younger leaf ("II" on the right side) has only one sheath.

Position of flowers. When flowering occurs, one of the two stipular sheaths of a double-sheathed leaf is occupied by a floral bud instead of a vegetative bud. Only one of the sheaths gives rise to a daughter leaf $(L_A$ in Figures 16, 19) whereas the other sheath is occupied by a flower bud covered by a spathella (Fc in Figures 18, 19). Mature shoots may have up to 12 flowers per shoot, arising from the "proximal" sheaths of double-sheathed leaves in the distal shoot region (Warming 1888, his Figure XIX/16–18).

DISCUSSION

***Podostemum ceratophyllum* and the classical root-shoot model (CRS model).** Warming (1881, 1882) gave a careful description of

the North American riverweed *P. ceratophyllum*. *Podostemum ceratophyllum* corresponds closely to the classical root-shoot model (CRS model) typical of most angiosperms (Mohan Ram and Sehgal 2001; Rutishauser 1997; Rutishauser and Huber 1991; Rutishauser and Isler 2001). According to the CRS model the plant body consists of roots and shoots, with leaves and stems as the shoot subunits. In contrast to many other members of the family, *P. ceratophyllum* has thread-like (i.e., only slightly flattened) roots with root caps and endogenous lateral roots.

The presence of stipular sheaths allows for the clear distinction between leaves and stems (Graham and Wood 1975; Hammond 1936, 1937; Rauh 1937; Royen 1954). Axillary branching in *Podostemum ceratophyllum* and most other Podostemoideae is replaced by a type of branching that is associated with double-sheathed leaves (see below).

Roots. As typical for all Podostemaceae, the seedling of *Podostemum ceratophyllum* lacks a long-lasting primary root. During seed germination the "radicle" emerges from the seed coat, bends toward and then flattens onto the substratum. The first structure that emerges from the seed coat may be seen as a short-lived primary root that produces the first adhesive hairs when contacting the substratum (Philbrick 1984). When the endogenously formed secondary root emerges from the base of the hypocotyl, the primary root has stopped growth (Hammond 1937). Mature roots of *P. ceratophyllum* (Figures 1 and 2) are thread-like, but slightly flattened and dorsiventral. Dorsiventrality is expressed by the root cap, which is oblique, and also by the eccentric vascular bundle and by the adhesive hairs that are restricted to the lower (ventral) side of the root. Lateral roots arise from endogenous buds along the root flanks. Similar roots (with caps and endogenous formation of lateral roots) are found in *Indotristicha ramosissima* (Wight) P. Royen, a member of subfamily Tristichoideae (Rutishauser and Huber 1991). In contrast to *P. ceratophyllum* and *I. ramosissima*, more elaborate roots of Podostemaceae (mainly Podostemoideae) lack a permanent cap. These are strongly dorsiventrally flattened and are often described as ribbon-like, crustose, or "foliose." These flattened photosynthetic organs have also been called "thalloid roots" or "thalli," thus avoiding use of the term "root" (Ota et al. 2001; Rutishauser 1997).

Various authors have discussed the apparent role of adhesive hairs ("rhizoids") in the attachment of roots of Podostemaceae to substrata. Jäger-Zürn and Grubert (2000) have reported that a microbial biofilm

also plays an important role in attachment of plants of Podostemaceae, and thus question the actual role that the adhesive hairs play.

Holdfasts. As typical for other species of *Podostemum*, *P. ceratophyllum* has exogenous finger-like structures that arise along the root flanks, associated with endogenous shoot buds (Moline 2001, see below). Hammond (1937: 21) compared the holdfasts to root tendrils that are "very sensitive to both gravity and contact, and they soon become firmly attached to the substratum by an adhesive secretion." Branched holdfasts in *P. ceratophyllum* were observed by Warming (1881). The exogenous holdfasts of probably all species of *Podostemum* in the New World stop growing after a few mm. They do not continue their growth and never become lateral roots. Exogenous lobes that develop into lateral roots, however, are found in *Polypleurum* and *Zeylanidium*, including *Z. subulatum* (Gardner) C. Cusset, which has been included in the genus *Podostemum* (as *P. subulatum* Gardner) by some authors (Mathew and Satheesh 1997; Rutishauser 1997; Suzuki et al. 2002).

Leaf initiation and lack of a proper shoot apical meristem. According to Hammond (1937: 27) there is no permanent shoot apical meristem in *Podostemum ceratophyllum*, either between the two cotyledons or at the end of the root-born shoots. While referring to the growth of monopodial stems with single-sheathed leaves Hammond wrote: "The leaves arise each from the base of the second older leaf, i.e., from the next older leaf in its rank." Our observations of the early stages of leaf initiation and the drawings given by Warming (1881, his Figure III/21A+B; Figure IV/1+2) support Hammond's interpretation.

Stipules in Podostemoideae. In many Podostemoideae the leaf sheaths are stipular because they have one or two lobes or teeth that extend beyond the leaf insertion area. Prominent stipular sheaths (two per double-sheathed leaf) are found in various American Podostemoideae such as *Apinagia* and *Marathrum* (Rutishauser et al. 1999). The structural diversity of stipules (including stipular sheaths) is extraordinary in Podostemoideae, especially within the genus *Podostemum* and its sister genus *Crenias* (Ancibor 1990; Cook and Rutishauser 2001; Hammond 1936, 1937; Moline 2001; Novelo and Philbrick 1997; Philbrick and Novelo, in prep.; Tur 1997, 1999). Interpreting exactly what a stipule is in *Podostemum* can be difficult. In some species (e.g., *P. ceratophyllum*) the stipule is an entire boat-like extension of the

sheathing leaf base. Sometimes the boat-shaped extension is divided into stipular teeth [e.g., *P. distichum* (Cham.) Wedd., *P. rutifolium* Warm.]. In other species (e.g., *Crenias* spp., *P. muelleri*) the stipule is a single asymmetrically placed lobe on the base of the leaf, which was interpreted by Jäger-Zürn (2002) as a "stipella" rather than a stipule. In still other taxa (e.g., *Cladopus, Diamantina*) the digitate segments of the leaf seem to intergrade with "stipules" (i.e., the outer most leaf segments; Philbrick et al. 2004; Rutishauser and Pfeifer 2002). In these latter cases, it is difficult to distinguish morphologically between leaf segments and stipules. *Podostemum irgangii* C. T. Philbrick & Novelo (Philbrick and Novelo 2001) has two types of stipules, one of which is finger-like. The finger-like stipules arise directly from the base of the petiole (in the median area); when mature they seem to arise from the stem, not the petiole itself. A second type of stipule occurs next to the leaf. This latter type is ear-shaped and occurs laterally to the petiole base (Philbrick and Novelo 2001; their Figure 1B, C).

Non-axillary branching and stem bifurcation of *Podostemum ceratophyllum* as compared to other New World Podostemoideae. In most angiosperms, axillary branching entails the production of a lateral shoot bud in the distal axil of a subtending, single-sheathed leaf. Such "typical" axillary branching does not occur in *P. ceratophyllum* and is uncommon in Podostemaceae (Rutishauser 1997). There are only a few documented cases in the family where axillary branching seemingly occurs (Ameka et al. 2002; see below).

In contrast to most other flowering plants, many Podostemoideae are characterized by leaves with two sheaths that are inserted laterally and exactly opposite (many Podostemoideae) or obliquely opposite (i.e., adjacent to) each other (*Podostemum ceratophyllum*). Such leaves have been called double-sheathed or "dithecous" by Warming (1881) and others, whereas the one-sheathed leaves (as typical in angiosperms) have been referred to as single-sheathed or "monothecous" (Jäger-Zürn 2000c, 2002; Rutishauser and Grubert 1999, 2000; Rutishauser et al. 1999). The occurrence of double-sheathed leaves allows the stem to branch by a peculiar process that, due to the absence of a more appropriate term, we refer to as "bifurcation." This phenomenon has also been called dichotomy (Engler 1928) or dichotomous branching (Rutishauser 1997). Bifurcation is a process analogous to typical branching in other angiosperms. Three hypotheses have been proposed to explain bifurcation, non-axillary branching, and the presence of double-sheathed leaves in Podostemoideae:

1. Warming (1881) proposed that stems of *Podostemum cerato-phyllum* were monopodial in spite of the presence of double-sheathed leaves. According to Warming the bud in the internal ("notoscopic") sheath is a direct continuation of the main stem (mother shoot) whereas the bud in the external ("basiscopic") sheath gives rise to a lateral shoot.

2. Troll (1941) and Jäger-Zürn (1994, 2002) proposed that the position of the axillary bud relative to the leaf was shifted relative to typical axillary branching. Jäger-Zürn (2002) wrote about the unusual branching in Podostemoideae having double-sheathed leaves: "The branching pattern ... represents a kind of recaulescence that occurs on the 'wrong' (reverse) side of the leaf ... This phenomenon and the evolutionary process of the (deviating) subfoliar branch position remain enigmatic."

3. An alternative explanation is that the bifurcation observable in *Podostemum ceratophyllum* is non-axillary (i.e., not derived from an axillary branching precursor). Rather, this situation is a consequence of the presence of double-sheathed leaves which are unique among flowering plants. Such a view was presented by Engler (1928: 11) who wrote about branching of various podostemoid members: "Depending on the strength of the lateral shoot the whole shoot system expresses a monopodial, di-chotomous or sympodial branching pattern. Where dichotomy occurs, the double-sheathed leaf is situated in the middle of the dichotomy, with 1 sheath on each side." [Original German version: "Je nach Stärke des Seitensprosses wird das Sprosssys-tems monopodial oder dichotomisch oder sympodial. Wo Dichotomie zustande kommt, steht das dithecische Blatt mitten in der Dichotomie, mit 1 Scheide an jeder Seite."]

As a working hypothesis, we prefer the third interpretation. Double-sheathed leaves are interpreted as an evolutionary novelty (key innovation, synapomorphy) of the subfamily Podostemoideae and occur in what seem to be basal genera such as *Apinagia, Marathrum,* and *Mourera* (Kita and Kato 2001; Rutishauser and Grubert 1999, 2000; Rutishauser et al. 1999). Jäger-Zürn (2000c) found double-sheathed leaves as parts of branched floral shoots in *Endocaulos, Sphaerothylax,* and *Thelethylax* from Africa (including Madagascar). More elaborate podostemoid taxa, including some African and most Asian members, seem to have lost double-sheathed leaves. They show non-axillary shoot branching without the presence of a double-sheathed leaf, or lack shoot

branching completely (Rutishauser 1997; Rutishauser and Pfeifer 2002). There are a few podostemoid members [e.g., *Saxicolella submersa* (J. B. Hall) C. D. K. Cook & Rutish., syn. *Polypleurum submersum* J. B. Hall] that seem to have reverted back to the axillary branching that is usual for most angiosperms (Ameka et al. 2002).

Infraspecific variability. The production of truncated shoot systems, and resulting "bushy" growth forms, have been associated with the recognition of subspecific taxa of *Podostemum ceratophyllum*. Four taxonomic varieties have been recognized in *P. ceratophyllum*: var. *ceratophyllum*, var. *circumvallatum* P. Royen, var. *abrotanoides* (Nutt.) Wedd., var. *chondroides* Fassett. Royen (1954, p. 229) did not formally recognize the latter two varieties, stating that they belonged to the typical *P. ceratophyllum* variety "as they are merely extreme variants connected with the ordinary form by a series of intermediate stages." Although Royen (1954) accepted var. *circumvallatum* as distinct, Philbrick and Novelo (in prep.) will not. These later authors interpret plants that have been called var. *circumvallatum* as representing an extreme form of the typical *P. ceratophyllum*. It remains to be seen what factors influence the production of the growth forms of the species.

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