Wood anatomy of Nepenthaceae[1]

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CARLQUIST, S. (Claremont Grad. Sch. and Pomona Coll., Claremont, CA 91711). Wood anatomy of Nepenthaceae. Bull. Torrey Bot. Club 108: 324-330. 1981.—Descriptions of the wood anatomy of Nepenthaceae, a monogeneric family, are offered for the first time. Data from three species show wide, short vessel elements characteristic of lianas, but also presence of fusiform vessel elements and of tracheids. Vestigial scalariform perforation plates with one or two bars occur on only a few vessel elements. Axial parenchyma is banded plus diffuse; rays are mostly uniseriate plus biseriate. Axial and ray parenchyma cells have bordered pits. Details of wood anatomy are consistent with a thealean relationship for the family.

Key words: *Nepenthes*; wood anatomy; lianas; Theales.

Secondary xylem of *Nepenthes*, sole genus of the Nepenthaceae, has not been studied previously. MacFarlane (1908) figures stems with a small amount of secondary growth, but does not discuss the histology of the xylem. Metcalfe and Chalk (1950), as well as other authors, do not discuss secondary growth; their comments are limited to the primary stems. This is understandable, because only a few, relatively old plants accumulate appreciable secondary xylem (see Materials and methods). The availability of stems with maximal amounts (for the genus) of secondary xylem especially collected for study of wood anatomy permitted this project.

Nepenthes consists of 72 currently recognized species (Kurata 1976; Schmid-Hollinger 1977). Presentation of data on wood anatomy on only three of these might at first glance be considered inadequate coverage. The results of the present study, however, suggest that wood anatomy in the genus may be relatively uniform, and therefore a survey of more numerous species might not yield much more information. Lack of work on wood anatomy of *Nepenthes* can be attributed not only to the limited amount of wood in plants of this genus, but also the tendency of wood

collectors and wood anatomists to neglect lianoid groups, just as families in which herbs predominate have been neglected. Wood anatomy of *Nepenthes* proves interesting not only because of special morphological features described below, but because it offers some evidence about the phylogenetic relationships of the family.

Materials and methods. Several years ago, a wood sample of *Nepenthes ampullaria* Jack collected on Gunung Lawit, Malaya, was kindly contributed by Dr. Christopher Davidson (his collection number 1313, RSA). The availability of this dried sample suggested the feasibility of studying secondary xylem in the family. During my 1978 expedition to Mt. Kinabalu, Sabah, I obtained stems with maximal wood accumulation of *N.* X *kinabaluensis* Kurata (= *N. rajah* Hook f. X *N. villosa* Hook f.), Carlquist 15517 (RSA) and *N. lowii* Hook f., Carlquist 15511 (RSA). Stems of these two species were preserved in a 50% ethyl alcohol solution. The dried stem of *N. ampullaria* is 18 mm in diameter, the secondary xylem cylinder (excluding pith and bark) about 4 mm in thickness. For the Kinabalu species, stems are about 22 mm in thickness, with the xylem cylinder about 6 mm in thickness. Sections of all the collections were prepared by means of a sliding microtome and stained with safranin; counterstaining of some sections with fast green permitted more accurate observation on pits and on primary walls. Macerations were prepared with Jef-

frey's fluid and stained with safranin. Observation of sections with polaroid discs failed to reveal any crystalline materials within the cells.

Anatomical observations. Vessel elements in *Nepenthes* are dimorphic. In transections (Fig. 1, 4, 5) the wider vessels appear conspicuously, almost invariably scattered in solitary fashion. One could, without further information, mistake these as the only vessel elements in the wood. However, macerations and longitudinal sections show that in addition to the wide vessels (Fig. 7) there are also narrow vessel elements which may be termed fusiform vessel elements (Fig. 8, 9). Of the conducting cells of the xylem, fusiform vessel elements comprise more than half. The term "fusiform" is used here merely in a topographic way to indicate shape, and to demonstrate a contrast with the wide, cylindrically-shaped vessel elements. In addition to wide and fusiform vessel elements, tracheids are present. These tracheids are not vascular tracheids: vascular tracheids could be distinguished, among other differences, by being the same length as vessel elements. Because of the markedly dimorphic nature of vessels in *Nepenthes*, the figure given for vessel diameter is based on the wide vessels only; no vessels per group figure could be reliably obtained. Vessel dimorphism is discussed further below.

Perforation plates of both wide and fusiform vessel elements are simple. In the latter vessel element type, perforation plates are occasionally double (Fig. 8, below) or triple (Fig. 14) and are often markedly subterminal rather than terminal (Fig. 13). Whether or not multiple perforation plates of this type represent vestiges of scalariform perforation plates is discussed below. Lateral wall pitting of vessels consists of circular bordered pits, alternate in arrangement (Fig. 13, 14). Vessel-ray pitting, however, may consist of elongate pits, running somewhat parallel to each other with each group of pits variously oriented (Fig. 10).

The imperforate tracheary elements in *Nepenthes* wood are all tracheids, bearing fully bordered circular pits. As figures below show, the tracheids are appreciably longer than the vessel elements, either wide or fusiform vessel elements. The ratio between the length of the tracheids and vessel elements is 1.75 in *N. ampullaria*, 1.43 in *N. X kinabaluensis*, and 1.21 in *N. lowii*. These ratios do not suggest markedly primitive wood, judging by comparisons made earlier (Carlquist 1975). Probably there is intrusive growth not merely of the tracheids as they mature from fusiform cambial initial derivatives, but of the fusiform vessel elements as well. Wall structure of the tracheids and fusiform vessel elements tends to be somewhat gelatinous, judging from the shrinkage patterns visible in transections (Fig. 3, 4).

The axial parenchyma of *Nepenthes* consists mostly of short uniseriate tangential bands, as shown between and below the two large vessels of Fig. 4, left. However, occasional diffuse axial parenchyma cells can be observed in all three species. Axial parenchyma cells mostly occur in strands of two, as illustrated in Fig. 9, right. Borders could be clearly observed on pits of the axial parenchyma cells (Fig. 11).

Vascular rays of the secondary xylem are mostly biseriate or uniseriate (Fig. 2, 6), the two types in about equal numbers. Multiseriate rays more than two cells wide are relatively scarce, although a few may be seen (Fig. 2, upper right). By study of transections one can see that wide pith rays of the primary stem are closed by conversion of primary rays to fascicular xylem soon after initiation of secondary growth. The reverse, conversion of a fascicular zone to ray cells, is much rarer but may occasionally be seen (Fig. 3). Rarity of multiseriate rays wider than two cells in secondary xylem of *Nepenthes* is interesting because many vines and lianas are characterized by retention of the primary rays as wide multiseriate rays in secondary xylem, little altered after commencement of cambial activity. Wide multiseriate rays give lianoid stems "cable-type" construction in which fascicular xylem areas are separated from each other by soft ray cells, which permit twisting of the fascicular segments as shifts in stem conformation and position occur.

However, *Nepenthes* does not form large lianas, so absence of the wide rays is not surprising. Ray cells as seen in radial section are erect or square predominantly. Only in the central portions of multiseriate rays are there a few procumbent cells. This seems less due to paedomorphosis (e.g., Carlquist 1962) than to the narrowness of multiseriate rays, which consist mostly of wing and sheathing cells, with few central body cells present. Central body cells in rays tend to be procumbent much more frequently than wing and sheath cells in dicotyledons at large.

Ray cells in *Nepenthes* are moderately thick and have mostly bordered pits (Fig. 12). Although bordered ray cell pits are often not reported in dicotyledons, they are more common than descriptions would indicate (e.g., Carlquist 1980). Bordered pits in ray cells often occur where ray cells are rather thick, in my experience. Borders may have been overlooked because they cannot, in ray cells, be seen readily in face view; rather, one must examine sections of ray cells, and radial sections most frequently reveal such sections of pits.

There are deposits of gummy materials in older portions of secondary xylem (Fig. 1, 3, 4). Elongate idioblasts with spirally-constructed walls but cap-like tips, mentioned and figured by such authors as Metcalfe and Chalk (1950), do occur in pith and bark of the three *Nepenthes* collections studied, but these idioblasts apparently do not occur in the secondary xylem.

Quantitative data on the woods studied are as follows:

N. ampullaria. Wide vessel elements average 332 μm long, 172 μm wide, 16 per sq. mm. of transection. Tracheids average 580 μm long, wall thickness 4.9 μm. Multiseriate rays fewer than uniseriate rays; uniseriates average 424 μm in height, multiseriates 852 μm.

N. X kinabaluensis. Wide vessel elements average 348 μm long, 83 μm in diameter, 49 per sq. mm. of transection. Tracheids average 496 μm long, wall thickness 4.4 μm. Uniseriate and multiseriate rays about equally numerous; uniseriates average 203 μm in height, multiseriates 394 μm.

N. lowii. Wide vessel elements average 335 μm long, 134 μm in diameter, 32 per sq. mm. of transection. Tracheids average 405 μm long, wall thickness 5.4 μm. Multiseriate rays more numerous than uniseriate rays; uniseriates average 277 μm in height, multiseriates 559 μm.

Discussion. Wide vessels in lianas seem adaptive because limited accumulation of secondary xylem (a limitation which permits flexibility, and rapid ascent to canopy levels without self-support) requires compensation by means of wider capillaries to supply a leafy crown of foliage. Wider vessels are also adaptive in lianas because positive pressures or mild tensions, never moderate to strong tensions, tend to occur in water columns of lianas (Carlquist 1975). Wide vessels might suffer deformation or collapse under moderate to high tensions. Numerous lianas conform to this plan, without occurrence of vessel dimorphism. However, one can hypothesize that in the course of rapid evolution from shrubby to lianoid habit, some vessels are widened, others narrowed, without elimination of the narrower vessels. In fact, vessel dimorphism of a more pronounced sort (wider vessels with simple perforation plates; narrower vessels with scalariform perforation plates and helical thickening) has been reported in a vining thealean family, Actinidiaceae (Metcalfe and Chalk 1950). Similar vessel dimorphism occurs in vining genera of another thealean family, Dilleniaceae (Vestal 1937).

Are the multiperforate perforation plates in some vessel elements of *Nepenthes* a relictual feature, or are they chance occurrences? If such plates were relictual, one would expect them to be more common in primary xylem, in accordance with the ideas of Bailey (1944) as confirmed by the extensive data of Bierhorst and Zamora (1965). In fact, this tends to be true in *Nepenthes*. To be sure, about 80% of the primary xylem vessels in *Nepenthes* macerations examined have simple perforation plates. However, the remainder have one or two bars across the perforation plate—sometimes partly traversing the plate as shown in Figure 15. The fact that
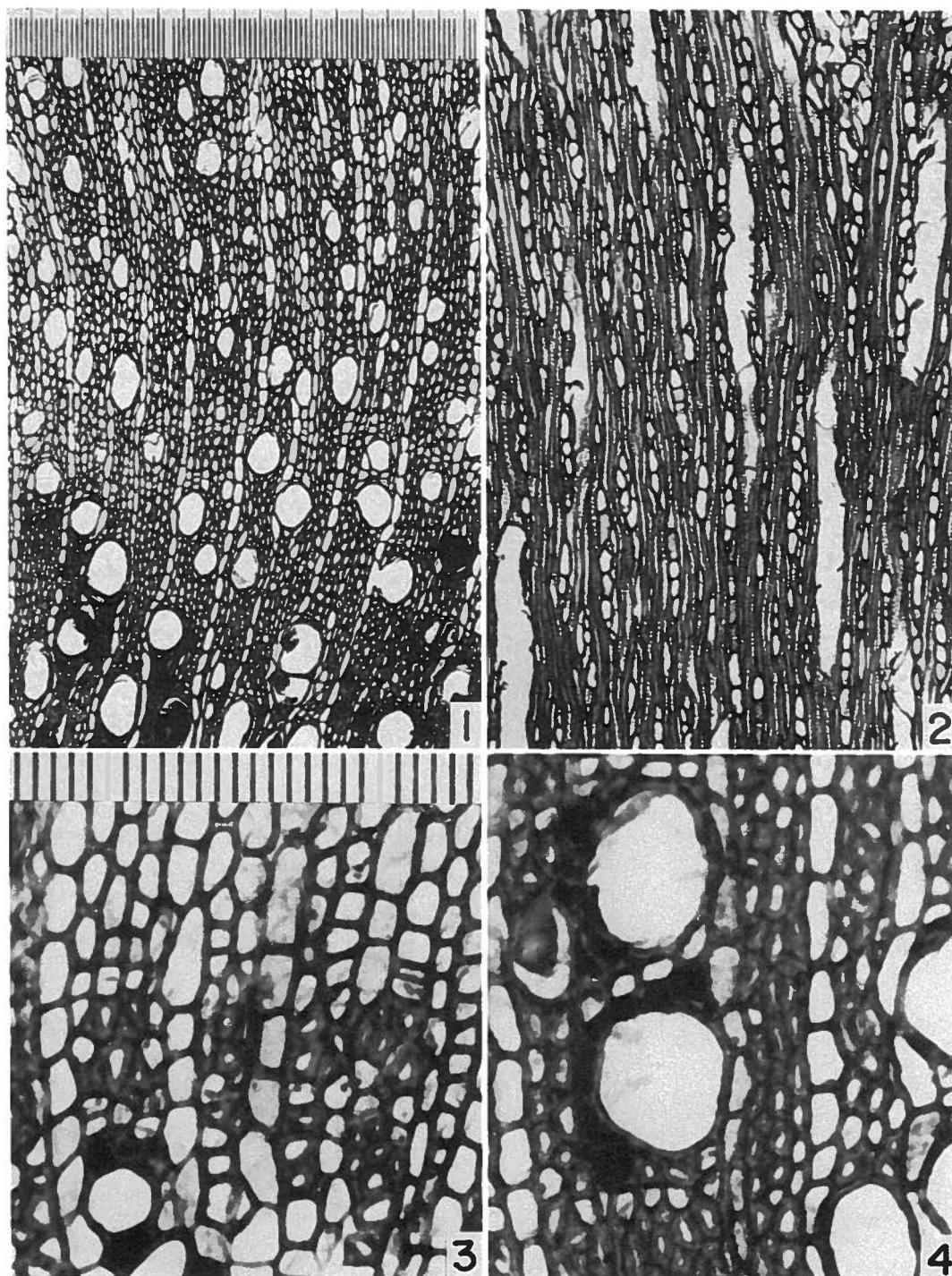
Figs. 1-4. Wood sections of *Nepenthes* X *kinabaluensis* Kurata, Carlquist 15517 (RSA). Fig. 1. Transection; vessels occluded by gummy materials (below). Fig. 2. Tangential section; wide multiseriate ray at upper right. Fig. 3. Portion of transection to show a wide multiseriate ray which begins as a zone of tracheids (below). Fig. 4. Portion of transection to show gelatinous walls of tracheary elements; axial parenchyma cells tend to be aggregated into tangential bands. Figs. 1, 2. magnification scale above Fig. 1 (divisions = 10 μm). Figs. 3, 4. scale above Fig. 3 (divisions = 10 μm).
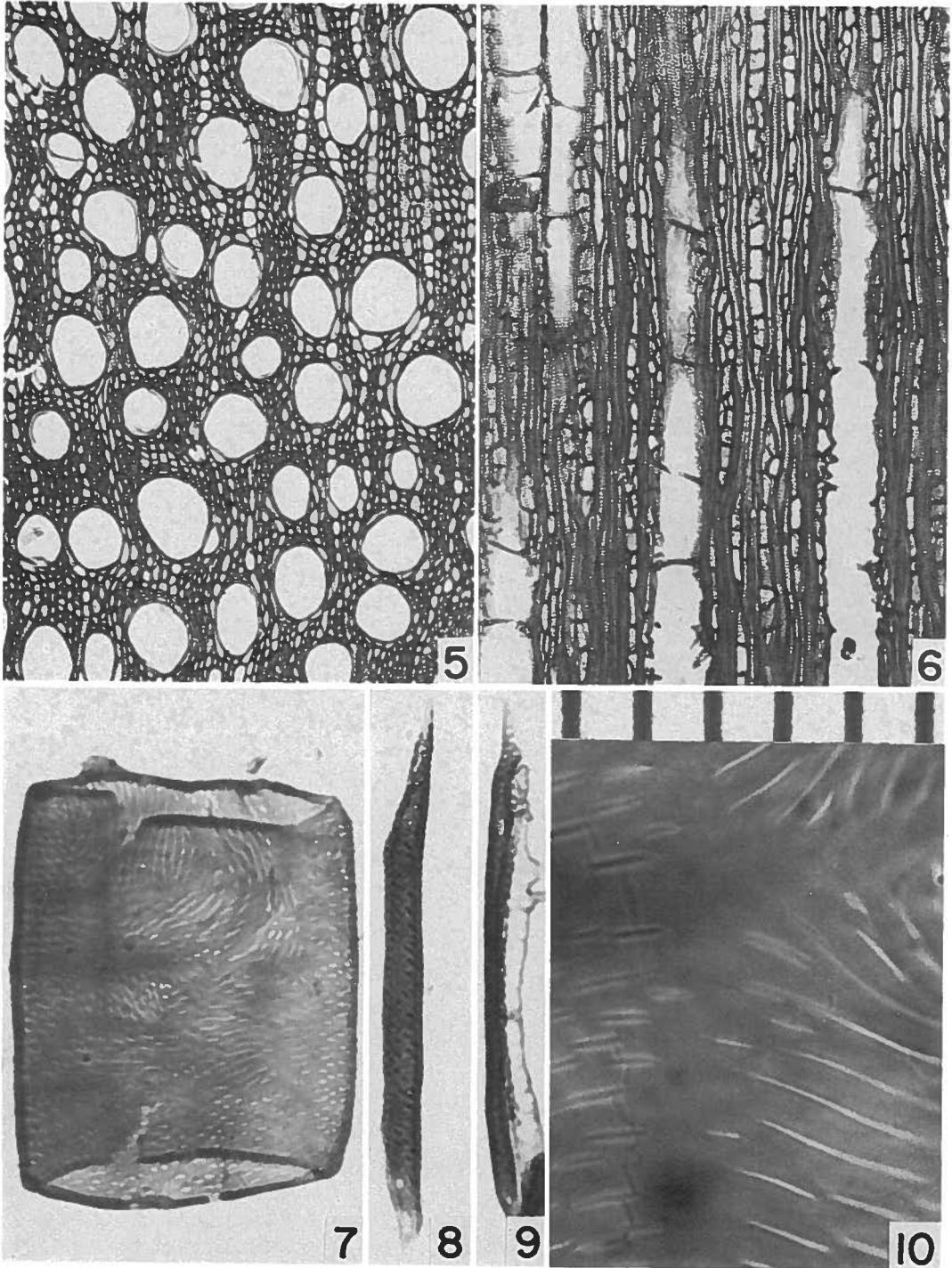
Figs. 5–10. Wood of *Nepenthes lowii* Hook. f., Carlquist 15511 (RSA). Fig. 5. Transection; large vessels rather uniform in diameter. Fig. 6. Tangential section. Most rays are uniseriate. Figs. 7–10. Vessel elements from maceration. Fig. 7. Typical wide vessel element. Fig. 8. Fusiform vessel element with two perforations at lower end. Fig. 9. Fusiform vessel element; pair of axial parenchyma cells at right. Fig. 10. Surface of vessel element of Fig. 7. showing elongate pits of vessel-ray pitting. Figs. 5, 6. scale above Fig. 1. Figs. 7–9. scale above Fig. 3. Fig. 10. scale above Fig. 10 (divisions = 10 μm).
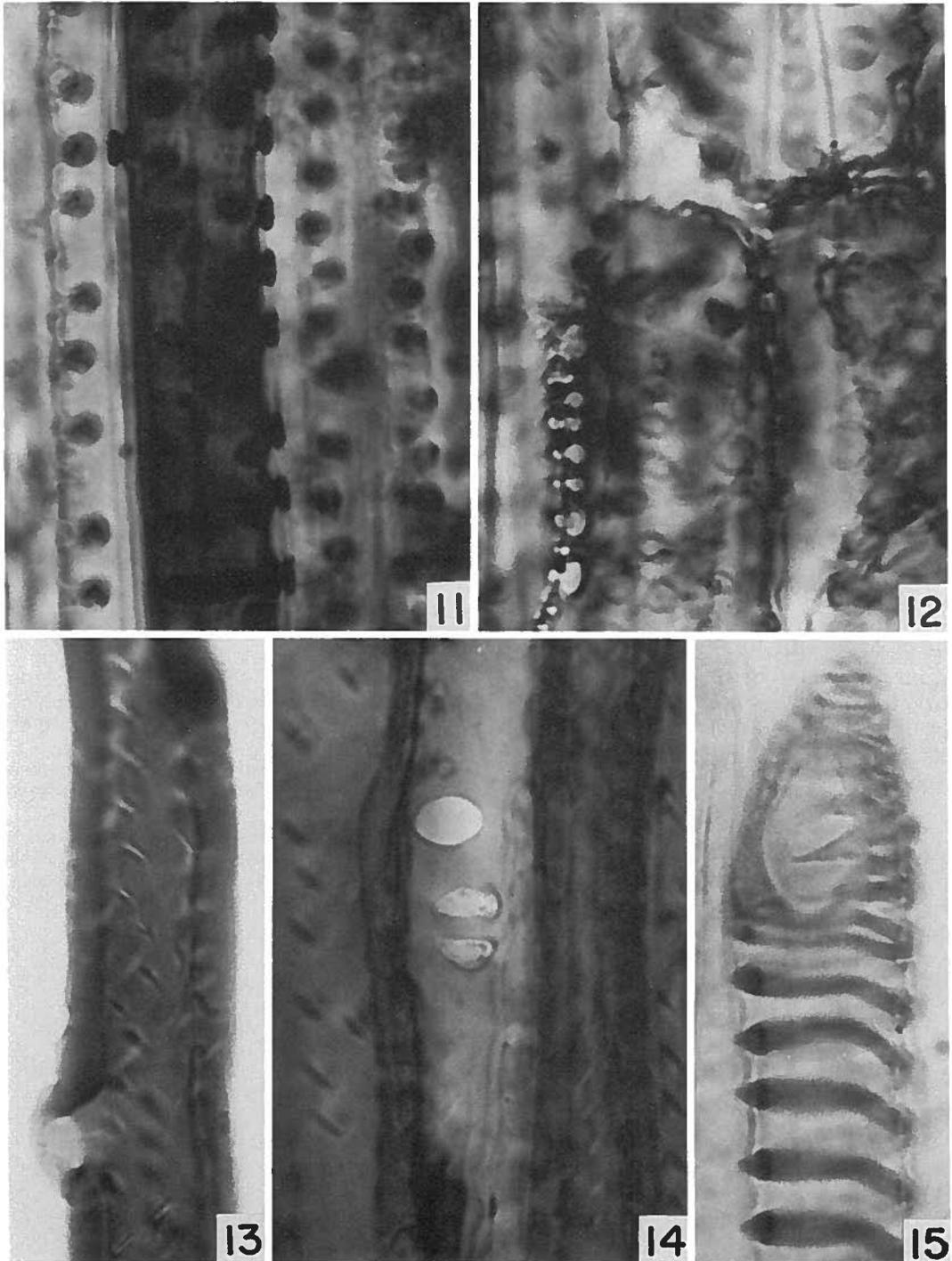
Figs. 11–15. Wood of *Nepenthes*. Fig. 11. *N. ampullaria* Jack, Davidson 1313 (RSA). Portion of radial section showing borders on pits of axial parenchyma cell (dark cell). Fig. 12. *N.* X *kinabaluensis*, portion of radial section to show pitting; borders clear on ray cell pits, lower left. Fig. 13. *N. lowii*, fusiform vessel element from maceration; perforation plate lower left. Fig. 14. *N. lowii*, fusiform vessel element from radial section, showing multiple perforation plate. Fig. 15. *N.* X *kinabaluensis*, primary xylem vessel element from maceration: two toothlike bars in the perforation plate. All figures, magnification scale above Fig. 10.

a small but constant proportion of plates with a few bars in primary and in secondary (Fig. 14) xylem may be found seems to indicate vestigial presence of a primitive feature, not random malformations. The presence of tracheids, rather than fibertracheids or libriform fibers, as the imperforate tracheary element type in *Nepenthes* seems clearly a primitive feature. Vining genera of thealean families such as the Actinidiaceae, Dilleniaceae, and Marcgraviaceae have features somewhat more primitive than Nepenthaceae, but not markedly so—merely a matter of their having more numerous bars on perforation plates of vessel elements.

Wood anatomy of Nepenthaceae does not yield any salient indications about the systematic position of the family. However, Nepenthaceae belongs to a thealean alliance according to the opinions of most phylogenists (e.g., Cronquist 1968; Dahlgren 1980; Melchior 1964; Thorne 1968). DeBuhr (1975), while stressing the thealean affinity of Sarraceniaceae in his study of woods of that family, does not rule out that Nepenthaceae may be allied to Theales. Nothing in wood anatomy of Nepenthaceae contradicts a thealean position for the family.

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