Vegetative anatomy and relationships of *Setchellanthus caeruleus (Setchellanthaceae)*

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Summary

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On account of its distinctive features, *Setchellanthus* cannot be included within any of the families of glucosinolate-producing plants. Features unknown in any of these families include abundant vasicentric tracheids, abaxial axial parenchyma, and only short uniseriate rays (composed of upright cells) in wood: and the presence of wide-helix tracheary elements in leaves. Wood offers the greatest number of phyletically significant features, and wood of *Capparaceae* offers many similarities, although the wood of *Helianthemum (Cisraceae)* is *even* more like that of *Setchellanthus.* Despite the fact that no myrosin cells were observed in *Setchellanthus,* it appears closest, on the basis of present information, to the glucosinolate-producing families.

Introduction

The relationships of *Setchellanthus* Brandegee are the focus of this paper and those that accompany it. Stress will be put on features that show similarities to other families, one concern being, however, the number of potentially related families one should consider, and how much original data should be developed in order to ensure that the comparisons are adequate. Assessing systematic relationships, one must reckon that some features are likely the result of adaptation to particular ecological factors. *Setchellanthus* occurs on dry limestone slopes in xeric areas, and a number of features in the vegetative anatomy of *Setchellanthus* can be viewed with relation to these ecological conditions.

On the label of the type specimen of *Setchellanthus caeruleus* Brandegee, the author wrote, "Gen. nov. Capparidacearum." A 1957 annotation by H. H. Iltis on this specimen reads, "should be placed in its own family; quite out of place in *Capparidaceae*". *Capparales* thus should be the primary group placed into comparison with *Setchellanthus.* The family content of *Capparales* has changed in recent years (e.g., Rodman, 1991a, b; Gadek & al., 1992; Rodman & al., 1993, 1994). These authors have shown that the glucosinolate-producing families (*Cupparales* s.1.) constitute a natural group. The following glucosinolate-producing families have been included here: *Akaniaceae, Bataceae, Brassicaceae, Bretschneideraceae, Capparaceae, Caricaceae, Gyrostemonaceae, Koeberliniaceae, Limnanthaceae, Moringaceae, Resedaceae, Salvadoraceae, Tovariaceae,* and *Tropaeolaceae.* In addition, *Cistaceae* are included in our comparisons with respect to wood anatomy: *Cistaceae* have recently been placed in *Malvales* in cladograms that show *Capparales* close to *Malvales* (Alverson & al., 1998; Nandi & al., 1998).

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Metcalfe & Chalk (1950) are a source of baseline data on vegetative anatomy for the families cited above. Additional data on wood anatomy of these families were available for *Akaniaceae* (Carlquist, 1996a). *Butaceae* (Carlquist, 1975), *Brassica-*ceae (Carlquist, 1971), *Bretschneidernceae* (Carlquist, 1996a), *Capparaceae* (Stern & al., 1963; Schmid & al., 1985; Fahn & al., 1986) *Caricaceae* (Carlquist, 1998) *Gyrostemonaceae* (Carlquist, 1978) *Koeberliniaceae* (Gibson, 1979). *Limnantha-ceae* (Carlquist, 1996b), *Resedaceae* (Carlquist, unpublished data), *Salvadoraceae* (Outer & Veenendal, 1981), Tovariaceae (Carlquist, 1985a), and *Tropaeolaceae* (Carlquist 1996b). Wood data on *Cistaceae* are derived from Metcalfe & Chalk (1950) as well as from slides in the possession of the first author.

One inevitably wishes more data than are available at any given time. However, in comparative work, depth of data may be of less importance than knowing the systematic distribution of characters of key importance. Consequently, attention will be focused on unusual features that may be indicative of relationship, such as Malpighian trichomes on leaves or occurrence in wood of exclusively uniseriate rays composed of upright cells.

Material and methods

Stems and leaves were available preserved in formalin-acetic-alcohol, from the collection *Iltis* & al. *31801* (WIS). These stems range from c. 1 mm in diameter, with little secondary growth, to 8 mm in diameter. In addition, a dried stem 1.4 mm in diameter was available from the Forest Products Laboratory wood collection *(MADw-25515),* vouchered by the specimen *Iltis & Lasseigne 100* (WIS). Details on collections are given by Iltis (1999).

From the latter sample, the second author prepared sliding microtome sections, some of which were stained with safranin; others were examined with scanning electron microscopy (SEM). The first author made preparations from the liquid-preserved samples of *Iltis & al. 31801*. Transections and paradermal sections of leaves were prepared by the usual paraffin techniques, and wood sections of the largest stems were made with a sliding microtome. Young stems (with leaves attached) were sectioned with a rotary microtome with the aid of a softening technique (Carlquist, 1982). All sections from *Iltis & al. 31801* were stained in a safranin-fastgreen combination, except for a few sections of the older stem, which were dried and examined with SEM. Wood macerations of both collections were prepared with Jeffrey's Solution and stained with safranin. Whole leaves and flower buds of the collection *Iltis & al. 31801* were air dried, using Hemo-De as an intermediate fluid, and viewed with SEM to obtain information on trichomes. The SEM photographs reproduced here as Fig 6-13 were prepared at the Forest Products Laboratory and are the property of the second author.

Number of vessels per group was determined as in earlier studies by the first author (viz., a solitary vessel = 1, a pair of vessels in contact = 2, etc.). Vessel diameter was measured as lumen diameter at widest point. Wood anatomical terms are in accord with the IAWA Committee on Nomenclature (Anonymous, 1964). except for "vasicentric tracheid", defined as in Carlquist (1985b, 1988).

The description of wood anatomy is based on the larger stem from *Iltis & al. 31801,* whose liquid preservation, with the staining employed, permitted accurate determination of axial parenchyma presence and demonstrated the nature of pitting in imperforate tracheary elements well.
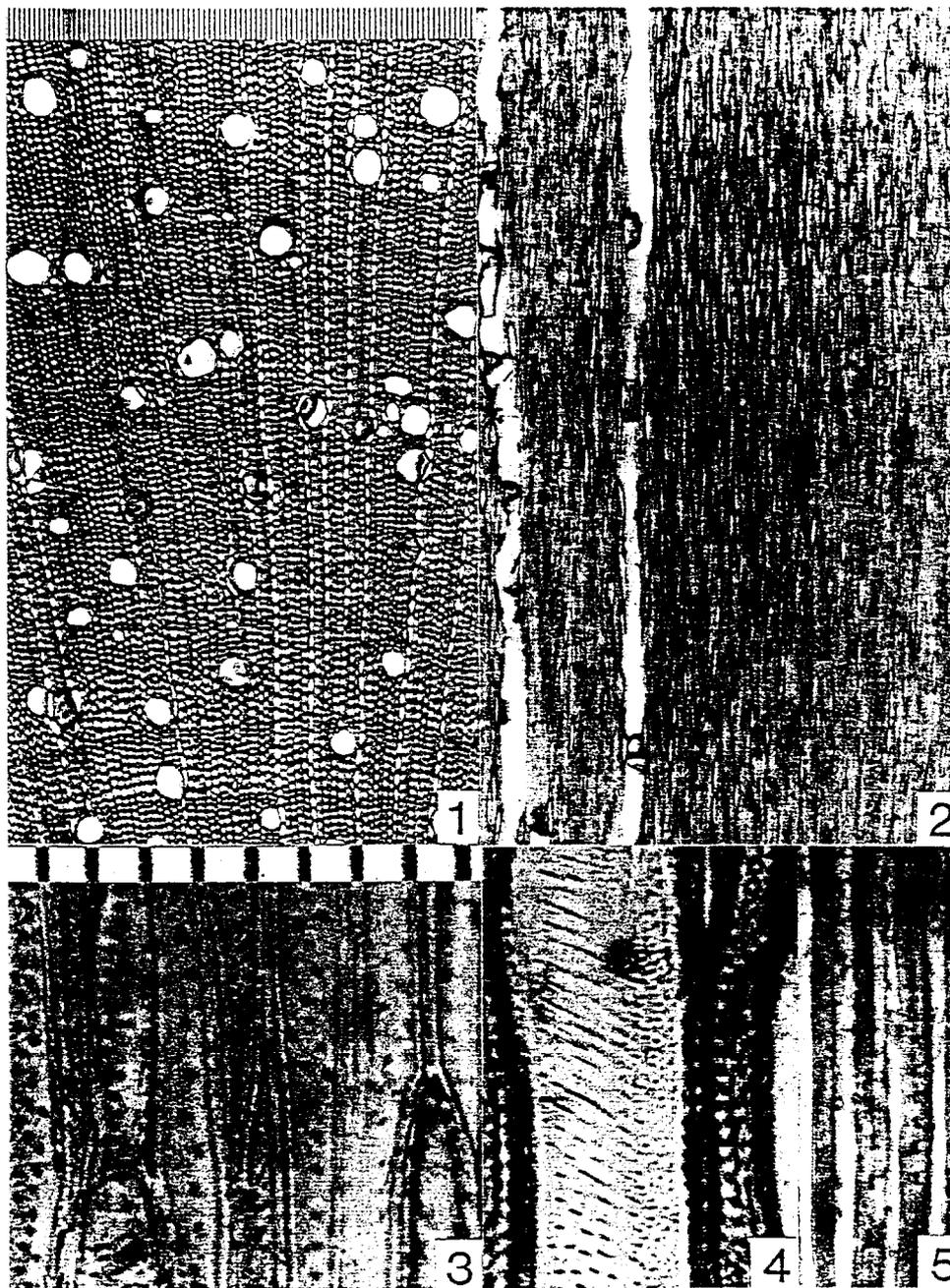
Fig. 1-5. Wood sections of *Setchellanthus caeruleus* (1-3, 5, *Iltis & al. 31801;* 4, *MADw-25515).* - 1, transection, showing solitary nature of vessels; 2, tangential section; rays mostly one cell high, appearing as inconspicuous ellipses; 3, portion of tangential section, to show densely placed small pits on vasicentric tracheids; 4, portion of tangential section; diagonally-oriented grooves interconnecting pit apertures occur on the vessel wall; 5. portion of radial section of vasicentic tracheids, showing the pits in sectional view. - Division of magnification scale = 10 µm (above Fig. 1 for 1-2 ; above Fig. 3 for 3-5).

Table 1. Wood features in *Setchellanthus caeruleus.* - VG = mean number of vessels per group; VD = mean vessel diameter (µm); VM = mean number of vessels (mm^{-2}); VL = mean vessel element length (µm); TL = mean imperforate tracheapl element length (µm).

Collection	stem portion diam.	VG	VD	VM	VL	TL
Iltis & al. 31801	1 mm	1.03	28	102	198	292
Iltis & al. 31801	8 mm	1.08	39	35	156	271
MADw-25515	14 mm	1.12	39	113	148	230

Wood anatomy

Growth rings not clearly evident, although some seasonal fluctuation *in vessel* diameter is present (Fig. 1). Vessels mostly solitary; more appreciable vessel grouping in the periphery of the wood sample, where grouping is mostly tangential. Vessels circular in transectional outline, wal1 thickness c. I µm. Vessel elements with simple perforation plates. Lateral wall pitting of vessels alternate (Fig. 4), pit diameter 2 µm. Vesturing on pits absent (Fig. 13) according to independent studies by both authors. Grooves interconnecting pit apertures ("coalescent pit apertures") present in some vessels (Fig. 4), but not in others. Helical thickening absent in vessels. Imperforate tracheary elements with minute bordered pits, pit cavity diameter c. 1.5 µm; pits denser on some elements (Fig. 3, 5), which qualify as vasicentric tracheids. About one third of the fibrous background of the wood composed of vasicentric tracheids; the remainder (more sparsely pitted elements) composed of fibre tracheids. Apertures of pits of imperforate tracheary elements elongate, some apertures extended as splits in the wall, possibly indicative of reaction wood. Mean diameter of imperforate tracheary elements 14 µm; mean wall thickness 2.3 µm. Axial parenchyma scanty and mainly paratracheal, primarily in abaxial distribution; some apotracheal parenchyma present as diffuse cells and diffuse-in-aggregate bands; some of the latter possibly marginal (in relation to growth ring termini) in distribution. Axial parenchyma as seen in longisection not subdivided into strands. Wall thickness of apotracheal parenchyma 0.8 µm. Rays all uniseriate (Fig. 2) mostly (86 %) one cell high, a few two cells (11 %) or three cells (3 %) high. All ray cells upright as seen in radial section, Paedomorphic Type III of Carlquist (1985). Wood non-storeyed. Crystals absent. Large amorphous deposits of an unidentified compound in some vessels (Fig. 1; Fig. 2, left).

The three wood portions analysed are arranged in Table 1 in order of increasing stem diameter. Number of vessels per group is about the same for all stem sizes, a figure rather low for a dicotyledonous wood. Vessels are much narrower in earlier formed-wood (Fig. 6) than in later-formed wood (Fig. 1), a common pattern in dicotyledons. Vessel density is lower in the large liquid-preserved samples (Fig. 8) than in the other portions. There is a pattern of progressive increase in length of vessel elements and imperforate tracheary elements with increase in stem diameter. Thus, *Setchellanthus* follows the paedomorphosis curve for length of tracheary elements (Carlquist, 1962) rather than the curve typical of strongly woody species.
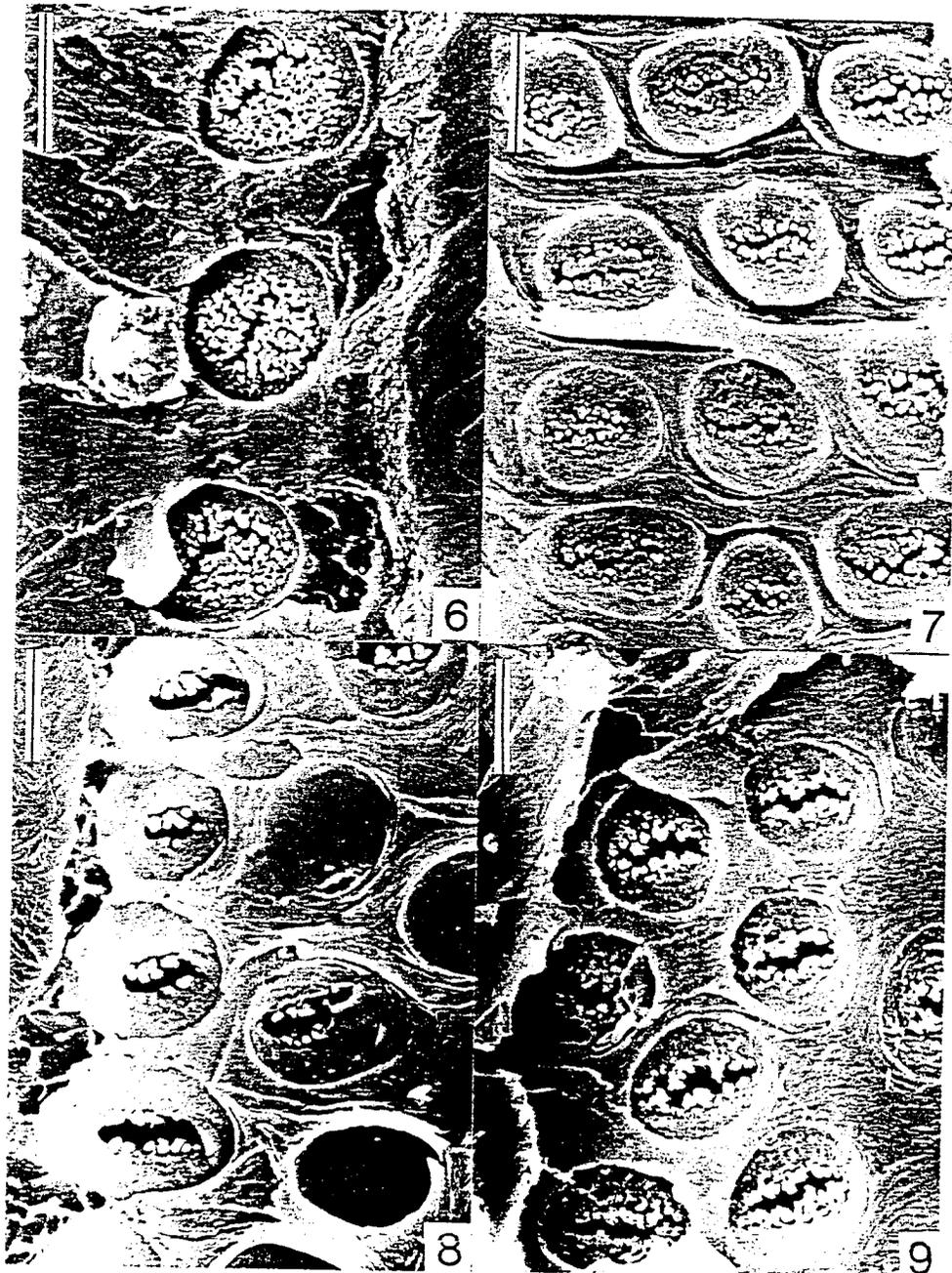
Fig. 6-9. SEM photographs of vestured pits on lateral walls of vessels, from longisections of woods of *Brassicaceae.* - 6, *Brassica oleracea (SJRw-37431);* 7, *Cakile maritima (SJRw-51486);* 8, *Descurainia sophia (SJRw-34179);* 9. *Lepidium fremontii (SJRw-23227).* - Scale bar = 5 µm (top left in each figure).

New data are presented on vesturing of pits in *Brassicaceae* and *Capparaceae* (Fig. 6-12) because current reports on this feature in the capparalean families are based on light microscopy only, and consequently are not definitive. For example, pits on vessels of *Capparaceae* are reported to be "obscurely vestured" by Stern & al. (1963) and "faintly vestured" by Fahn & al. (1986). The other references on wood anatomy of capparalean families cited above do not mention vesturing and thus may suggest absence of vestures.

In the *Brassicaceae, Brassica oleracea* L. (Fig. 6), *Cakile maritima* Scop. (Fig. 7), *Descurainia sophia* (L.) Prantl (Fig. 8), and *Lepidium fremontii* S. Watson (Fig. 9) all have vestured pits. Vesturing is comprised of minute warts; these are more widely distributed in *B. oleracea* (Fig. 6) and *C. maritima* (Fig. 7) than in the other two species, in which the vesturing tends to be more nearly restricted to the apertural region of the pit. In *Capparaceae,* a greater range of expressions was observed in the material studied. The species of *Capparis* L. shown (Fig. 10) has abundant vesturing, the warts tending to be coarser closer to the pit aperture than distal to the aperture. The two species of *Forchhammeria* Liebm. illustrated here represent two stages in presence of vesturing: *F. pallida* Liebm. (Fig. 11) definitely has a few wartlike vestures around the pit apertures, whereas *F. watsonii* Rose (Fig. 12) lacks vestures.

Primary stem, periderm, and bark

Cortex and pith (Fig. 14) are composed of spheroidal cells with primary walls. The vascular cylinder is a continuous one, doubtless related to the fact that rays are all uniseriate. The rays are evident as soon as secondary growth commences. Large parenchymatous gaps are present in the cylinder only associated with departure of leaf traces. Nodes are unilacunar; the leaf trace is a broad arc of vascular tissue that extends transversely away from the vascular cylinder. In the primary vascular cylinder, vessels are present in some portions, lacking in others; these differences persist into early secondary growth (Fig. 14: vessels present at left, absent at right), but disappear as secondary growth proceeds. There are no fibres in or adjacent to phloem, even when secondary growth is present (Fig. 14).

The epidermal origin of periderm is shown in the section of Fig. 14. Periderm originates much earlier in *Setchellanthus* than in most other dicotyledons. In older bark (attached to wood sections), occasional cortical cells are converted to thick-walled sclereids, and druses occur in cortical parenchyma. A few of the cortical cells in older stems contain numerous small rhomboidal crystals that are birefringent in polarised light.

Trichomes

Trichomes (Fig. 14-17) are present on stems, leaves, pedicels, and calyces. They are all of one type: one-celled Malpighian hairs ("T-shaped hairs") with elongate arms. The T-shaped cell has a thick lignified wall and is embedded in a multicellular base (Fig. 16-17). However, this base appears to be formed from an upwelling of epidetmal cells, usually in 5 but sometimes 4 or 8 series (Fig. 17). The 5 series begin as 5 cells in an upwelling of epidermal tissue, and each of the 5 cells divides periclinally (Fig. 15, above; Fig. 16). This upwelling happens very early, and mature cells forming the multicellular bases may be found on young leaf primordia (Fig. 8). On
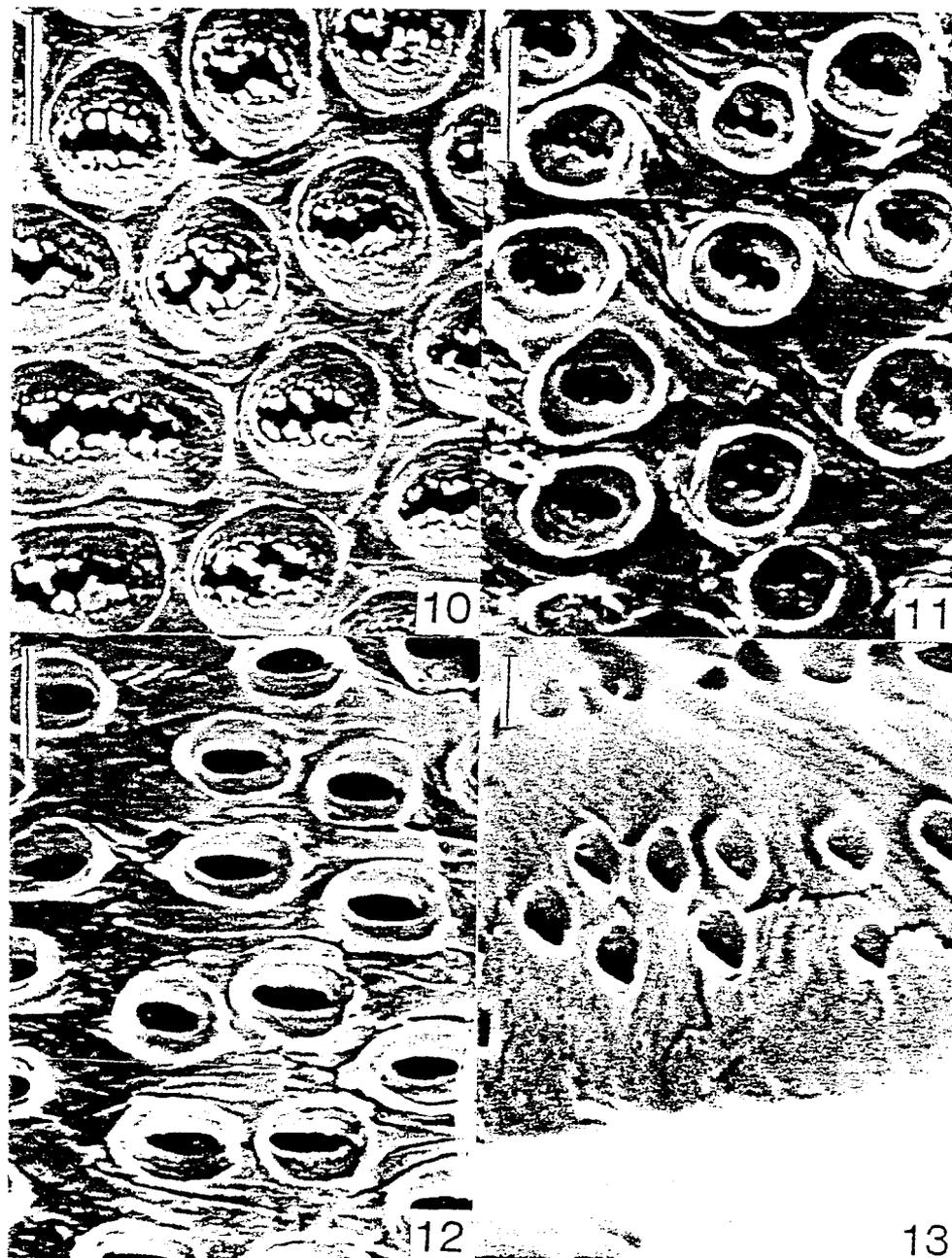
Fig. 10-13. SEM photographs of vestured (10, 11) and non-vestured (12, 13) pits on lateral walls of vessels, from longisections of woods of *Capparaceae* (10 - 12) and *Setchellanthaceae* (13). - 10, *Cappris* sp. *(MADw-40058);* 11, *Forchhammeria pallida (MADw-36160);* 12, *F. watsonii (MADw-36115);* 13. *Setchellanthus caeruleus (MADw-25515).* - Scale bar = 5 µm (top left in each figure).

the stem, upwelling extends to subepidermal cells as well as epidermal cells (Fig. 14, top). On young leaf primordia there are. in addition to mature Malpighian trichomes, immature trichomes with inflated terminal cells (Fig. 16, left). These trichomes do not mature. There is no way of telling whether they are abortive Malpighian hairs or a second trichome type that aborts early. As seen in gross aspect or with SEM, the Malpighian trichomes are oriented with the arms parallel to the long axis of a leaf, stem, or flower.

Leaf anatomy

The leaves of *Setchellanthus* are amphistomatal, with stomata about equally abundant on the two surfaces. The stomata are slightly sunken beneath the leaf surface (Fig. 15). Epidermal cells other than stomata tend to be larger in the abaxial than in the adaxial epidermis (Fig. 18). These cells have interlocking lobed outlines (Fig. 17, top). Guard cell pairs bear no constant orientation to surrounding cells, so that an anomocytic or rancunculaceous arrangement is present.

Four layers of palisade parenchyma are present facing the adaxial side of the leaf (Fig. 18); three layers of palisade parenchyma are present abaxially. The palisade cells on the adaxial face are more elongate than those on the abaxial side. Between adaxial and abaxial palisade layers, there are four layers of oval cells that may be called spongy cells, but are unlike typical spongy cells in that they are ovoid rather than irregular in shape, and interconnected by short arms (Fig. 20, bottom).

The larger leaf veins (Fig. 19) contain both xylem (above) and phloem, and the xylem is subdivided by plates of parenchyma. Smaller leaf bundles (Fig. 20) lack phloem and do not have parenchyma within xylem. Veins bear a bundle sheath composed of 1 (in some places 2) bundle sheath cell layers which, aside from their position, are not notably differentiated in any way.

In larger bundles, protoxylem tracheary elements are not unusual: they have ordinary annular or helical bands of secondary wall material (Fig. 19). Metaxylem tracheary elements of larger veins as well as most tracheary elements of smaller veins (Fig. 19-20) have wide helices. The term "wide-helix tracheid" was devised earlier (Carlquist, 1960) for cells with such bands. As seen in transection, these wide-helix tracheary elements look like thick-walled fibres, but longisections of veins (in paradermal sections) demonstrate that all of the metaxylem elements are wide-helix tracheary elements, and no fibres whatsoever are present (Fig. 21).

Vegetative anatomy and relationships of Setchellanthus

Among the families under consideration, minute alternate pits, as found in vessels of *Setchellanthus,* are characteristic of *Capparaceae* and *Cistaceae.* Data on vesturing of vessel pits are given above for *Brassicaceae* and *Capparaceae.* Among other capparalean families, vesturing is also reported in lateral wall pits of *Koeberlinia* Zucc. by Gibson (1979). Fahn & al. (1986) report "weakly vestured" pits in *Cistus (Cisradae).* The absence of vesturing in vessel pits of *Setchellanthus* is a noteworthy feature, but as shown for *Forchhammeria,* vesturing can be present or absent within a single genus of *Capparaceae.* Thus, vesturing cannot be counted a highly reliable systematic criterion for claiming relationships within these families.

Imperforate tracheary elements of *Setchellanthus* are fibre tracheids and vasicentric tracheids with relatively minute bordered pits. *Capparaceae* were reported by

Fig. 14-17. Setchellanthus caeruleus, sections of young stem and leaves (*Iltis & al. 31801). -* 14, young stem transection, epidermis with trichomes at top, some secondary xylem is present; 15, guard cell pair in sectional view, from transection of abaxial surface of mature leaf; 16. Maipighian trichome in sectional view, from transection of leaf primordium; 17, characteristic shape of cells from abaxial epidermis and. below, epidermal cells that form trichome stalk in transectional view. - Divisions of magnification scale = 10 µm (above Fig. 14); Fig. 15-17. same scale as Fig. 3.

Metcalfe & Chalk (1950) to have "simple or faintly bordered" pits on imperforate tracheary elements, but only simple pits are reported in the species studied by Fahn & al. (1986), whereas those studied by Stem & al. (1963) are claimed to have minutely bordered pits. The first author, studying Stern's slides, could not confirm the presence of borders. In *Brassicaceae,* Metcalfe & Chalk (1950) report minute bordered pits in imperforate tracheary elements, whereas only simple pits are reported in *Brassicaceae* studied by Carlquist (1971) and Fahn & al. (1986). Simple pits are reported in *Brerschneideraceae* (Carlquist, 1996a). *Moringaceae* (Metcalfe & Chalk, 1950; Carlquist, 1998). *Sulvadoraceae* (Outer & Veenendal, 1981), *Tovariaceae* (Carlquist, 1985a). and *Tropaeolaceae* (Carlquist, 1996b), whereas imperforate tracheary elements have clearly bordered pits in *Akaniaceae* (Carlquist 1996a), *Bataceae* (Carlquist, 1978). *Gyrostemonaceae* (Carlquist, 1978), and *Koeberliniaceae* (Gibson, 1979). *Cistaceae* have tracheids with rather large bordered pits, so that the imperforate tracheary elements qualify as tracheids, as they do in *Gyrostemonaceae* and *Koeberliniaceae* (Fahn & al., 1986; Carlquist, unpublished data). The difference between a minutely bordered pit and a simple pit in imperforate tracheary elements is of minor import, although the more fully bordered pits are considered more primitive (e.g., Metcalfe & Chalk, 1950: xlv). If that interpretation is correct, *Setchellanthus* is plesiomorphic in this character state as compared to *Brassicaceae, Capparaceae,* and *Tovariaceae.*

Setchellanthus stands out among the capparalean families in having both fibre tracheids and vasicentric tracheids. Among genera referred to *Capparaceae,* vasicentric tracheids transitional to vascular tracheids (with the latter much more abundant) occur in *Isomeris* Nutt. and *Oceanopapaver* Guillaumin (Carlquist, 1985b). but these differ from *Setchellanthus,* in which vasicentric tracheids are abundant, and equally abundant throughout a growth ring. The abundance of vasicentric tracheids in *Setchellanthus* is doubtless related to lack of vessel grouping in that genus, just as the true tracheids of *Cistus* and *Koeberlinia* are correlated with solitary vessels (Carlquist, 1984).

Axial parenchyma is essentially paratracheal in the capparalean families, mostly scanty vasicentric *(Akaniaceae, Bataceae, Brassicaceae, Bretschneideraceae, Capparaceae, Gyrostemonaceae, Tovariaceae, Tropaeolaceae),* less commonly abundant vasicentric *(Moringaceae* and a few *Capparaceae). Setchellanthus* has 3 form of paratracheal parenchyma (abaxial) not reported in the glucosinolate-producing families, but it also has apotracheal parenchyma and occasional diffuse-in-aggregates and sometimes marginal parenchyma. With respect to axial parenchyma, its closest resemblances are with *Koeberliniaceae* and *Cistaceae,* in both of which scanty vasicentric parenchyma is combined with diffuse and diffuse-in-aggregates: some of the latter are marginal in *Cistaceae* (Gibson, 1979; Fahn & al., 1986). Axial parenchyma ceils are not subdivided in *Setchellanthus;* this is an unusual condition in dicotyledons at large, but also occurs in *Bataceae, Brassicaceae, Gyrostemonaceae,* and *Tovariaceae.* Axial parenchyma in *Koeberlinia* is always in strands of 24 cells (Carlquist, unpublished data), whereas in *Cistaceae* and *Moringaceae,* axial parenchyma may be either undivided or in strands of 2-4 cells. There is 3 possibility that apotracheal bands of undivided axial parenchyma may have originated by fibre dimorphism rather than reconfiguration of pre-existing axial parenchyma in *Brassicaceae* (Carlquist, 1971). *Capparaceae,* or *Gyrostemonaceae* (Carlquist, 1978). but this phenomenon is absent in *Setchellanthus.*
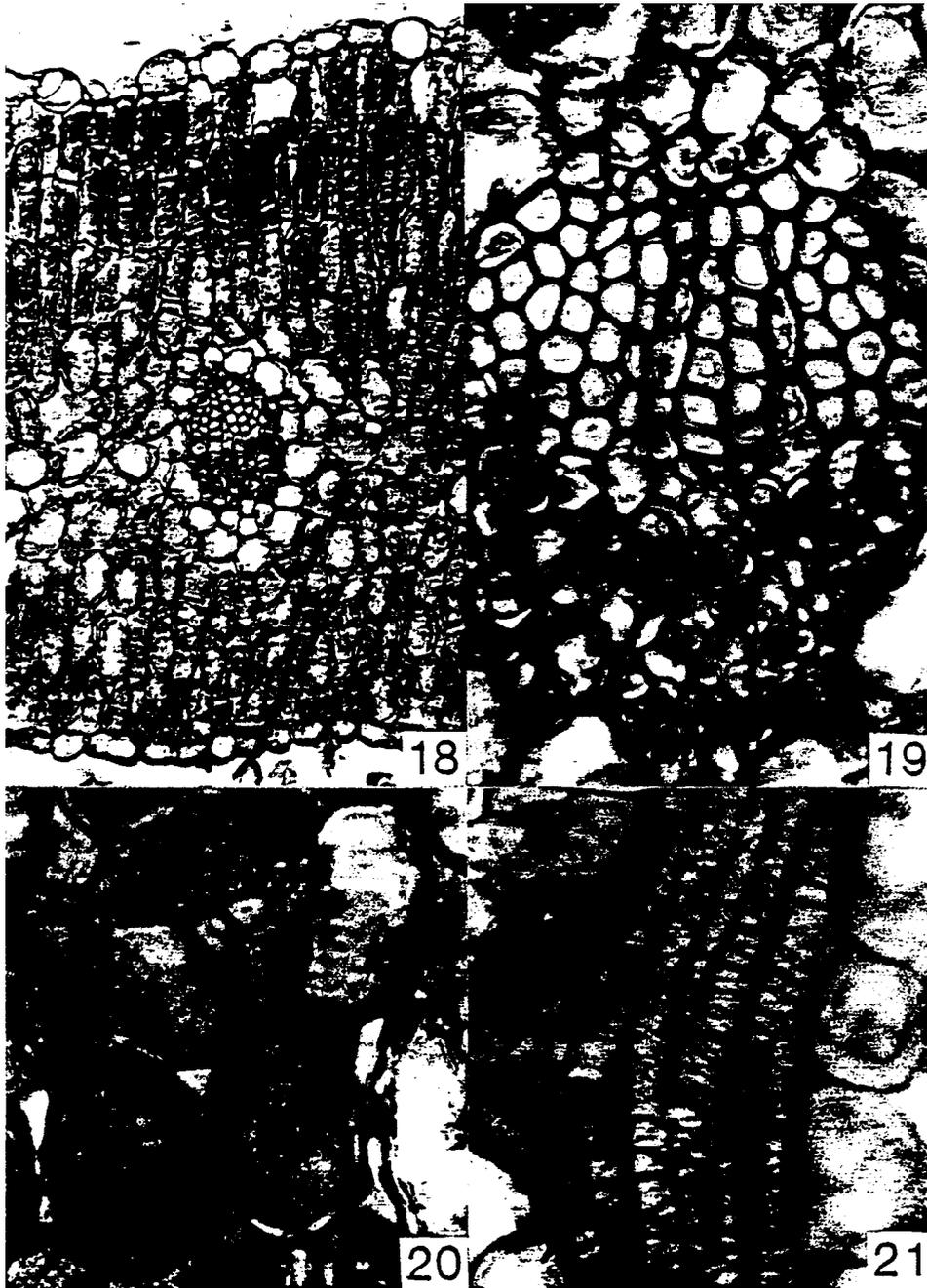
Fig. 18-21. *Setchellanthus caeruleus,* sections of leaf *(Iltis & al. 31801).* - 18, transection of leaf, abaxial face above, to show isolateral palisade condition; 19, larger vein in transection, phloem below; two bands of parenchyma traverse xylem: SO, smaller vein in transection and adjacent mesophyll cells: phloem is lacking in the vein: 21, longitudinal section of venation from paradermal section of leaf, all tracheaty elements contain wide-banded helices, fibres are absent. - Fig. 18, same scale as Fig. 14; Fig. 19-21. same scale as Fig. 3.

The rays of *Setchellanthus* are unusual in dicotyledons in three respects: they are exclusively uniseriate; they are mostly only a single cell tall as seen in tangential section; and the ray cells are entirely upright as seen in radial sections. Predominantly or exclusively upright ray cells may relate to life form; such rays are indicative of herbaceous or minimally woody habit in *Brassicaceae, Resedaceae, or Tovariaceae* (all of which have both multiseriate and uniseriate rays, however). Ray cells that are upright or nearly so is characteristic of paedomotphosis in woods (Carlquist, 1962), and paedomorphosis, in turn, is related to relatively non-woody habits. *Capparaceae* mostly have both multiseriate and uniseriate rays, but the rays are composed of procumbent cells predominantly (Stem & al., 1963; Fahn & al., 1986). There are a few *Capparaceae* in which uniseriate rays predominate, as in *Capparis cynophollophora* L. (Stem & al., 1963). *Cistaeae* are pertinent in this regard, because in *Cisrus* uniseriate and narrow multiseriate rays are present, and procumbent cells occur only in the central portions of biseriate and pluriseriate rays (Metcalfe & Chalk, 1950). However, in *Helianthemum* Mill. of the *Cistaceae rays* are almost identical to those of *Setchellanthus* and agree with them in the three respects cited (Carlquist, unpublished data). Uniseriate rays composed of upright cells exclusively have been termed Paedomorphic Type III (Carlquist, 1988), and characterise small shrubs.

Storeyed structure occurs in woods of some *Brassicaceae, Caparaceae, Caricaceae, Gyrostemonaceae,* Moringaceae, and *Salvadoraceae;* it is present to a lesser extent in *Bataceae* (see wood references cited above). Storeyed structure is absent in *Setchellanthus,* as it also is in *Akaniaceae, Bretschneideraceae, Cistaceae, Koeberliniaceae, Resedaceae, Tovariaceae,* and *Tropaeolaceae.* To be sure, storeying tends to be more common in woody species than in herbs; storeying is not revealed until divisions increasing the circumference of the cambium have occurred in appreciable numbers. The amount of wood in the larger wood samples *of Setchellanthus,* however, would easily be enough to reveal presence of storeying, so its absence in that genus is significant.

Epidermal origin of periderm occurs in *Setchellanthus;* it has been reported by Metcalfe & Chalk (1950) for *Cistaceae* but only one genus of *Capparaceae (Crataeva* L.). Because the site of periderm origin is often not reported in dicotyledons. data are lacking for most of the families considered in the present study.

The distinctive Malpighian trichomes of *Setchellanthus* likely will prove of phyletic significance in assessing its relationships when trichomes have been described for a larger number of genera in the families considered here. At present, Malpighian ("T-shaped") trichomes have been reported in *Brassicaceae* for *Arabidopsis* Schur, *Draba* L., *Erysimum* L. (including *Cheiranthus* L.), *Farsetia* Tuna, and *Lobularia* Desv.; and in *Cuppuraceae* for *Capparis quiniflora* DC. and *C. zeyheri* Turcz. (Metcalfe & Chalk, 1950).

Brassicaceae are often cited as exemplifying anisocytic ("cruciferous") stomata, but anomocytic ("ranunculaceous") stomata are more widespread in the family; they also occur in *Bataceae, Cistaceae, Gyrostemonaceae, Moringaceae,* and *Tovariaceae. Setchellanthus* thus agrees in this respect with the majority of the families considered.

Amphistomatal leaves are primarily of ecological significance: they occur in plants of sunny habitats, and can be suspected in species in which leaves are displayed at an angle other than horizontal. In addition to the occurrence of this leaf

structure in *Setchellanthus,* one can find it in *Bataceae* and *Gyrostemonaceae* (Carl-quist, unpublished data), as well as in *Cakile* Mill. *(Brassicaceae)* and several *Cupparaceae* (Metcalfe & Chalk, 1950).

The wide-helix tracheary elements in leaf veins of *Setchellanthus* are an unusual feature, but they are likely not indicative of wider phyletic relationships. Wide-helix vascular or vasicentric tracheids are common in globular cereoid cacti (Gibson, 1973); they have been particularly well figured in Gibson (1978). Wide-helix tracheids were first reported in veins of leaf tips of *Abolboda* Humb. & Bonpl. of the *Aboibodaceae* (Carlquist, 1960). and are similar to the "wide-helix tracheoidal idioblasts" that occur in veins of leaves of the fern *Botrychium* L. (Amott, 1960). Wide-helix tracheary elements are likely of functional significance because of their ability to expand and contract with changes in water content of a plant organ. The width of the helices likely conveys maximal strength to this cell, so that its linear conformation can be retained despite contraction and expansion with changes in water content of the tracheary element.

Druses and spherocrystals (the latter with more numerous component crystals and a smoother surface outline than druses) are so widespread in dicotyledons that their presence or absence is not phyletically significant - they are obviously homoplasious. Druses have been reported in *Capparaceae* and *Cistaceae* (Metcalfe & Chalk, 1950). but they are absent in *Koeberliniaceae* (Gibson, *1979)* and *Salvadoraceae* (Outer & Veenendal, 1981).

In sum, the families of *Capparales* s.1. share a large number of character state expressions with *Setchellanthus.* Numerous resemblances to *Cistaceae* also occur, most notably in wood structure *(Helianthemum* is noteworthy in this regard). Cisraceae probably belong to *Malvales* and are closely related to *Capparales* (Alverson & al., 1998: Nandi & al., 1998). but various anatomical features shared by particular genera of the two orders may be homoplasies. The occurrence of Malpighian trichomes both in *Setchellanthus* and in a few species of *Brassicaceae* and *Capparaceae* is also worthy of mention in this connection. In comparative studies, one is likely to find more numerous similarities when comparing a given genus to a family with numerous species rather than to a family with only one or two species. *Setchellanthus* likely derives from a less woody ancestor. The presence of clear borders on imperforate tracheary elements in *Setchellanthus* is likely a more primitive condition than is the absence or minimal presence of borders, just as the gynoecial condition in *Setchellanthus* (three carpels, "axile" placentation) appears plesiomorphic in comparison to gynoecial configurations of most other *Capparales.*

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