

The genus *Amphiroa* (Lithophylloideae, Corallinaceae, Rhodophyta) from the temperate coasts of the Australian continent, including the newly described *A. klochkovana*

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Studies of *Amphiroa* (Lithophylloideae, Corallinaceae, Rhodophyta) from the temperate coasts of Australia provide new evidence that differences in tetrasporangial conceptacle pore canal anatomy are diagnostically significant in delimiting species within the genus. Differences in overall morphology and genicular anatomy are also reliable for delimiting species. These data are supported by examination of relevant type specimens. Four species occur in temperate Australian waters. Three (*Amphiroa anceps*, *Amphiroa beauvoisii*, and the newly described *Amphiroa klochkovana*) occur in southeastern Australia, and three (*A. anceps*, *A. beauvoisii*, and *Amphiroa gracilis*) occur in southern and southwestern Australia. Comparisons of *A. beauvoisii* and *A. anceps* have shown that they cannot be separated at species level morphologically but clearly differ in tetrasporangial conceptacle pore canal anatomy. This has important flow-on implications concerning specimen identification, reported geogeographic distribution and putative heterotypic synonymy of the two species. Relevant historical data, a species key and a synoptic description of *Amphiroa* also are included.

INTRODUCTION

Amphiroa, one of six currently recognized genera in the Corallinaceae, subfamily Lithophylloideae, is widespread in tropical and warm temperate waters, also occurs in cool temperate waters, and is known from the fossil record. Woelkerling *et al.* (2002, p. 370, table 2; p. 372, table 3) summarized the diagnostic characters of and provided a dichotomous key to the six known genera of Lithophylloideae with living species [*Amphiroa*, *Ezo*, *Lithophyllum* (including *Titanoderma*), *Lithothrix*, *Paulsilvella* and *Tenarea*].

This account contains a new taxonomic treatment of species of *Amphiroa* (Corallinaceae, Corallinales, Rhodophyta) confirmed to occur in temperate Australia and provides new evidence that differences in tetrasporangial conceptacle pore canal anatomy are diagnostically significant in separating species within the genus. Our study of new and historical collections, including types, has led to the conclusion that four species occur in temperate Australian waters. Three (*Amphiroa anceps*, *Amphiroa beauvoisii*, and the newly described *Amphiroa klochkovana*) occur in southeastern Australia and three (*A. anceps*, *A. beauvoisii*, and *Amphiroa gracilis*) occur in southern and southwestern Australia. We also have concluded that the status of 21 taxa previously considered synonyms of *A. anceps* or *A. beauvoisii* requires reassessment.

In the context of this study, temperate Australia encompasses two biogeographic provinces. The southeastern coastal area from the Queensland–New South Wales border south to

Gabo Island, Victoria roughly comprises the Peronian province (Womersley 1990, Millar 2007). Lord Howe Island (see Millar & Kraft 1993) and Norfolk Island (see Millar 1999), although politically part of New South Wales, were not included because they are 600 and 1400 km respectively from the Australian mainland and show only partial biogeographic links to the Peronian province (Millar 2007). The southern coast of Australia, including Tasmania, constitutes the Flindersian province, which is said to diffuse northward along the west coast to somewhere between Cape Leeuwin and Geraldton (Huisman 2007; Millar 2007). Following Womersley (1984, p. 13), warmer-water species that occur along the southwestern coast of Australia but are not also definitely known from the south coast are not dealt with.

In addition to the species accounts and new data on relevant types, the taxonomic implications of the results are considered in relation to the diagnostic value at species level of differences in tetrasporangial conceptacle pore canal anatomy and differences in genicular anatomy, and in relation to species biogeography. Relevant historical data, a species key, and a synoptic description of *Amphiroa* also are included.

MATERIAL AND METHODS

Data are based on type material, newly collected material and herbarium collections from Université de Caen, Caen, France (CN), Laboratoire de Cryptogamie, Muséum national d'Histoire naturelle, Paris, France (PC), Department of Botany, La Trobe University, Victoria, Australia (LTB), National Herbarium of Victoria, Royal Botanic

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Gardens, South Yarra, Victoria, Australia (MEL) and National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, New South Wales, Australia (NSW). Specimens originally in LTB and transferred to MEL have both LTB and MEL numbers cited. Herbarium abbreviations follow the *Index Herbariorum*, formerly in print (Holmgren *et al.* 1990), now online electronically (Holmgren and Holmgren 1998). The International Code of Botanical Nomenclature (ICBN) cited is the Vienna edition (McNeill *et al.* 2006).

Field procedures, species identification and microtechnique are detailed in Harvey *et al.* (2006). Morphological and anatomical terminology follows Woelkerling (1988). Synoptic descriptions contain information on all diagnostic characters and other significant features, including those useful for specimen identification.

HISTORICAL BACKGROUND

Published records of species *Amphiroa* from temperate Australia begin with Lamarck (1815: 238), who described *A. anceps* as a species of *Corallina* on the basis of specimens from ‘...les mers Australes ou de la Nouvelle-Hollande’ collected by F. Peron & C.A. Lesueur during the French expedition of 1800–1804 under the command of T.N. Baudin. (Ducker 1979b).

Since then, at least six additional species [*A. beauvoisii* Lamouroux, *Amphiroa dilatata* Lamouroux; *Amphiroa ephedraea* (Lamarck) Decaisne; *Amphiroa galaxauroides* Sonder; *A. gracilis* W.H. Harvey; *Amphiroa nobilis* Kützing] have been reported from the region; published records are summarized by Womersley & Johansen (1996) for southern and southwestern Australia and by Millar & Kraft (1993) for southeastern Australia.

In conjunction with a detailed study of species of *Amphiroa* collected during the Siboga Expedition (see Weber 1902 for details), Weber-van Bosse (1904, p. 93) concluded that *A. dilatata*, *A. galaxauroides*, and *A. nobilis* were conspecific with *A. anceps*, and that a W.H. Harvey specimen of *A. ephedraea* from New South Wales (explicit locality not indicated) numbered 458 was a misidentified specimen of *A. anceps*.

More recently, Womersley & Johansen (1996) concluded from a detailed floristic study that only two species (*A. anceps* and *A. gracilis*) occurred in southern and southwestern Australia, and they accepted the synonymies proposed by Weber-van Bosse (1904) and suggested (Womersley & Johansen 1996, p. 286) that records of *A. beauvoisii* and *A. ephedraea* from the region probably involved misidentified specimens of *A. anceps*. No similar detailed study of species occurring in southeastern Australia has been published.

TAXONOMIC ACCOUNTS

Amphiroa J.V.F. Lamouroux (1812, p. 186)

SYNOPTIC DESCRIPTION: Plants consisting of a calcified crustose base (often inconspicuous) or a peglike largely

endophytic base or lacking a recognizable base or with multiple attachment points apparently formed secondarily and erect to recumbent axes composed of calcified segments (intergenicula) and secondarily decalcified segments (genicula); branching of axes variously dichotomous, alternate pinnate, irregular, trichotomous or clustered, with mixtures and with adventitious branches occurring in some species; branch segments flattened to compressed to cylindrical.

Thallus construction in upright axes monomerous, consisting of a single system of branched, laterally coherent filaments organized into alternating intergenicula and genicula.

Intergenicula (as seen in median longitudinal section) composed of a central core (medullary) region in which thin-walled, calcified, elongate cells of adjacent filaments become more or less aligned to form longer tiers of arching cells interspersed by shorter tiers, and a peripheral (cortical) region where distal portions of calcified core filaments or their derivatives bend outward and terminate at the thallus surface in epithallial cells with rounded or flattened outer walls; branch apices usually composed only of core filaments that terminate in meristematic initials. Cells of adjacent intergenicular filaments linked by secondary pit connections; cell fusions absent.

Genicula arising secondarily behind branch apices; composed (as seen in median longitudinal section) of one or usually more arching tiers of transformed, thick-walled, decalcified core-region cells, and in some species also consisting of associated decalcified peripheral-region cells. Transition from decalcified genicula to calcified intergenicula occurring within single tiers of cells or between adjacent tiers of cells.

Life history, where known, triphasic with haploid gametangial plants, diploid carposporophytes and diploid tetrasporangial plants. Bisporangial plants of unknown ploidy level also found in some species. Gametangial plants, tetrasporangial plants and bisporangial plants all isomorphic; carposporophytes developing within old female conceptacles after presumed karyogamy.

Male and female gametangia, tetrasporangia and bisporangia formed in separate uniporate conceptacles; male and female conceptacles occurring on the same, or in most species, on different plants. All mature conceptacles situated on the surfaces of intergenicula, formed laterally in peripheral (cortical) regions of intergenicula and more or less flush with or protruding somewhat above the surrounding intergenicular surface.

Carpogonia, where known, terminating two-celled filaments arising from the floor of female conceptacle chambers. Spermatangial filaments, where known, unbranched, arising from the floor of male conceptacle chambers.

Carposporophytes, where known, developing within female conceptacle chambers after presumed karyogamy; mature carposporophytes usually composed of a central fusion cell and peripheral carposporangial filaments bearing terminal carposporangia.

Tetrasporangia/bisporangia arising from the conceptacle floor peripheral to or interspersed among sterile, often degenerate filaments that originally contributed to conceptacle roof formation or form a central columella; sporangia with zonately arranged spores.

Table 1. Diagnostic characters of *Amphiroa* and of the subfamily, family and order of Corallinophycidae (Florideophyceae, Rhodophyta) to which it belongs. Each taxon possesses the diagnostic characters listed for its own rank and the diagnostic characters of higher ranks in the classification hierarchy. Chemical and ultrastructural characters considered diagnostic of the Corallinophycidae and the Rhodophyta are presumed to occur in the species studied but have not been so confirmed during the present study.

Sources of data	Woelkerling <i>et al.</i> (2002, 2008); Harvey <i>et al.</i> (2003); Saunders & Hommersand (2004); Yoon <i>et al.</i> (2006); Le Gall & Saunders (2007); <i>AlgaeBase</i> (http://www.algaebase.org).
Classification	Phylum Rhodophyta, Class Florideophyceae, Subclass Corallinophycidae, Order Corallinales, Family Corallinaceae, Subfamily Lithophylloideae, Genus <i>Amphiroa</i>
Phylum	Rhodophyta Wettstein (1901, p. 46). Eukaryotic; chlorophyll <i>b</i> and chlorophyll <i>c</i> absent; allophycocyanin, phycocyanin, and phycoerythrin present in the form of phycobilisomes on unstacked thylakoids; flagella absent; centrioles absent; plastid bound by two membranes and producing floridean starch that is deposited in the cytoplasm.
Class	Florideophyceae Cronquist (1960, p. 438). Growth by means of apical cells and lateral initials forming branched filaments in which the cells are linked throughout by primary pit connections.
Subclass	Corallinophycidae Le Gall & Saunders (2007, p. 1129). Calcification in the form of calcite; pit plugs with two cap layers at cytoplasmic faces; outer pit-plug cap layer dome shaped; pit-plug membrane absent.
Order	Corallinales Silva & Johansen (1986, p. 250). Gametangia produced in conceptacles.
Family	Corallinaceae Lamouroux (1812, p. 185). Tetrasporangia produced in uniporate conceptacles; tetrasporangia without apical plugs; tetrasporangia with zonately arranged spores.
Subfamily	Lithophylloideae Setchell (1943, p. 134). Cells of contiguous vegetative filaments linked by secondary pit connections.
Genus	<i>Amphiroa</i> Lamouroux (1812, p. 186). Genicula present; genicula without dimerous flangelike branches that grow downward and cover intergenicula.

ETYMOLOGY: According to De Toni (1905, p. 1805), *Amphiroa* is based on ‘... *amphi* circum et *roa* malus Punica’.

LECTOTYPE SPECIES: *Amphiroa tribulus* (Ellis & Solander) Lamouroux; designated by Hamel & Lemoine (1953, p. 40).

BASIONYM: *Corallina tribulus* Ellis & Solander (1786, p. 124). Lamouroux (1812, p. 186) explicitly included two species in the original presentation of *Amphiroa* [*A. tribulus* and *Amphiroa cuspidata* (Ellis & Solander) Lamouroux] but did not designate a type species. Schmitz (1889, p. 455) choice of *Amphiroa rigida* Lamouroux (1816, p. 297) as type species is untenable because Lamouroux (1812) did not explicitly cite it in the original presentation of the genus.

REMARKS: The diagnostic characters that separate *Amphiroa* from other genera of Lithophylloideae are listed in Table 1. All species of *Amphiroa* also possess those features considered diagnostic of the subfamily Lithophylloideae, the family Corallinaceae, the order Corallinales, the subclass Corallinophycidae, the class Florideophycidae, and the phylum Rhodophyta (see Table 1).

Over 200 species and infraspecific taxa have been ascribed to *Amphiroa*. Continuously updated lists of names are presently provided online within the *Index Nominum Algarum* (<http://ucjeps.berkeley.edu/INA.html>) and within *AlgaeBase* (<http://www.algaebase.org>). No world monograph of *Amphiroa* has been published, and the status and delimitation of many species requires reassessment in a modern context (e.g. see comments in Norris and Johansen 1981, p. 13 under *Amphiroa brevianiceps*; Millar 1990, p. 315 under genus name; Abbott 1999, p. 178 under *Amphiroa foliacea*). Where reassessments have occurred, synonymies have been proposed. Norris and Johansen (1981, pp 6–12), for example, identified five putative heterotypic synonyms of *A. beauvoisii* from a comparative study of types. According to Riosmena-Rodriguez and Siqueiros-Beltrones (1996, p. 135), the true number of species is still controversial, with estimates ranging from 20 to 90. If

Riosmena-Rodriguez and Siqueiros-Beltrones (1996) are correct, *Amphiroa* is the second most biodiverse genus in the Lithophylloideae, after *Lithophyllum*.

As noted by Norris and Johansen (1981, pp. 4–5) and Riosmena-Rodriguez and Siqueiros-Beltrones (1996, pp 135–136), species delimitation in *Amphiroa* has been based overwhelmingly on vegetative features and on thallus size and growth habit. Johansen (1969, 1981, pp. 68–72) described two distinct patterns of genicular development in species of *Amphiroa*; whereas, Cabioch (1969, 1972, pp. 206–208) studied early thallus development, and Dolan (2001) examined the taxonomic value of characters associated with core cell tiers in intergenicula and genicula. Examples of characters and character states used to delimit species occur in identification keys in Taylor (1945, pp. 185–186, 1960, p. 403), Dawson (1953, pp. 134–135), Norris and Johansen (1981, pp. 5–6), Womersley and Johansen (1996, p. 285), Stegenga *et al.* (1997, p. 576), Desikachary *et al.* (1998, pp 58–59), Yoshida and Baba (1998, p. 531), Johansen (in Abbott 1999, p. 177), Littler and Littler (2000, p. 20), John *et al.* (2003, p. 71), Moura & Guimarães (2005, p. 10), and Oliveira *et al.* (2005, p. 74). The diagnostic value of many of these characters, however, needs to be reassessed in a modern context to determine the extent to which they vary within and across populations of individuals.

Except for the study of Riosmena-Rodriguez and Siqueiros-Beltrones (1996; especially see p. 138, table 3), the diagnostic value of characters associated with conceptacles at species level has remained largely unexplored (also see comments in Riosmena-Rodriguez and Siqueiros-Beltrones 1996, pp. 135–136). Reproductive features rarely are mentioned in previously published species keys, and then only in terms of conceptacle diameter and tetrasporangium size. During the present study, however, it became clear that differences in tetrasporangial conceptacle pore canal anatomy are diagnostically significant at species level and can be used to separate species and identify specimens. Further details appear below and in the Discussion.

Table 2. Diagnostic characters of species of *Amphiroa* confirmed to occur in temperate Australia

Species	Intergenicula	Genicula	Branching	Tetrasporangial conceptacle pore canals
<i>Amphiroa anceps</i> (Lamarck) Decaisne	Most or all intergenicula compressed to flattened (Fig. 7)	Composed only of decalcified core-region cells (Fig. 12)	Plants lacking fascicles of five or more branches arising from a single geniculum (Fig. 8)	Rings of large block-shaped cells absent (Figs 14, 15)
<i>Amphiroa beauvoisii</i> Lamouroux	Most or all intergenicula compressed to flattened (Fig. 24)	Composed only of decalcified core-region cells (Fig. 31)	Plants lacking fascicles of five or more branches arising from a single geniculum (Fig. 25)	Top of canal surrounded by a ring of large block-shaped cells (Fig. 37)
<i>Amphiroa gracilis</i> W.H. Harvey	Intergenicula terete (cylindrical) (Fig. 45)	Composed both of decalcified core-region cells and decalcified peripheral region cells (Fig. 48)	Plants with at least some fascicles (compact cluster or bundle) of five or more branches arising from a single geniculum (Figs 46, 49)	Rings of large block-shaped cells absent (Figs 52, 53)
<i>Amphiroa klochkovana</i> Harvey, Woelkerling & Millar	Most lower intergenicula compressed to flattened; most upper intergenicula terete (cylindrical) (Fig. 54)	Composed both of decalcified core-region cells and decalcified peripheral-region cells (Fig. 58)	Plants with at least some fascicles (compact cluster or bundle) of five or more branches arising from a single geniculum (Figs 54, 55)	Rings of large block-shaped cells absent (Figs 62, 63)

Data taken from present study.

KEY TO SPECIES OF *AMPHIROA* IN TEMPERATE AUSTRALIA

1. All upper intergenicula compressed to flat (Figs 7, 24), never terete (cylindrical); genicula composed only of decalcified core region cells (Figs 12, 31); plants lacking fascicles of five or more branches arising from a single geniculum 2
1. Most or all upper intergenicula terete (Figs 45, 54); genicula composed both of decalcified core-region cells and decalcified peripheral-region cells (Figs 48, 58); plants with at least some fascicles (compact cluster or bundle) of five or more branches arising from a single geniculum (Figs 49, 54) 3
2. Tetrasporangial conceptacle pore canals flanked by filaments that grow parallel to the pore canal as well as basal filaments that project laterally toward the canal; top of canal surrounded by a ring of large block-shaped cells (Figs 35, 36) that may eventually degenerate to form a depression above the pore (Fig. 38) *Amphiroa beauvoisii*
2. Tetrasporangial conceptacle pore canals flanked only by filaments that project laterally toward the canal; rings of large block-shaped cells absent (Figs 14–17). *Amphiroa anceps*
3. Plants consisting of both compressed/flattened and terete intergenicula (Fig. 61); most upper intergenicula compressed/flattened; most lower intergenicula terete (Figs 54, 55) *Amphiroa klochkovana*
3. Plants consisting of terete intergenicula throughout (Fig. 45); compressed to flattened intergenicula not present *Amphiroa gracilis*

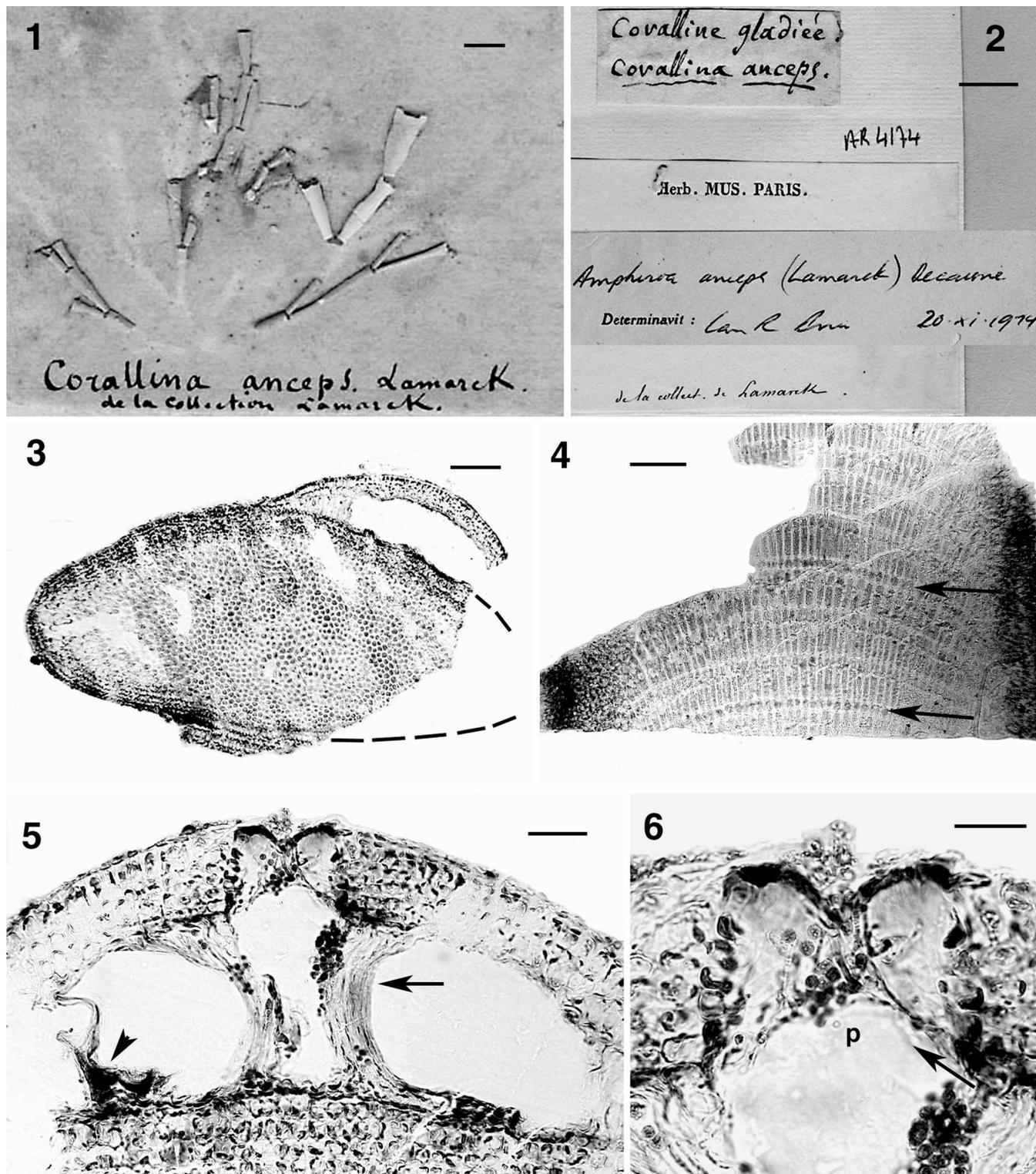
Species accounts are presented alphabetically by specific epithet. Table 2 lists the diagnostic characters of the four species of *Amphiroa* now confirmed to occur in temperate Australia.

Amphiroa anceps (Lamarck) Decaisne (1842b, p. 125)

Figs 1–17

SYNOPTIC DESCRIPTION: Temperate Australian plants epilithic; attached ventrally to substrate by a calcified, crustose, nongeniculate base and producing branched erect axes up to 150 mm long that consist of alternating calcified segments (intergenicula) and secondarily decalcified segments (genicula). Branching generally complanate (in one plane) (Fig. 8) and dichotomous, sometimes with occasional trichotomies (Fig. 8); branches usually arising from most but not all intergenicula; intergenicula compressed to flat (Fig. 11) (occasionally more terete near the base); mostly of similar width throughout plant although sometimes broader distally at points of branching (Fig. 9), 3.0–10 mm long, 0.6–2.0 (–3.0) mm wide, and 300–600 µm thick.

Erect axes monomerous, consisting throughout of a single continuous system of branched, laterally coherent filaments; in median longitudinal section (Fig. 12); axes of intergenicula and genicula with a broad uninterrupted central core (medullary) region in which filaments are oriented more or less parallel to the branch surface, passing in intergenicula into a narrower peripheral (cortical) region in which portions of core filaments or their derivatives bend outward to become more or less diagonally or perpendicularly oriented to the branch surface; peripheral region usually lost in mature genicula. Cells of adjacent filaments in core region mostly 8–15 µm in diameter, aligned in one to five arching tiers of longer cells (40–85 µm long) followed by a single arching tier of shorter cells (6–40 µm long). Cells of adjacent filaments in peripheral region not aligned in arching tiers, mostly 7–13 µm in diameter and 10–19 µm long; peripheral portions of filaments terminating at the thallus surface in epithallial cells 5–10 µm in diameter and 4–5 µm long and with rounded or flattened outer walls (Fig. 10). Peripheral region and epithallial cells secondarily lost in genicula (Fig. 12). Cells of adjacent



Figs 1–6. *Amphiroa anceps*. Lectotype (PC 00228677).
Fig. 1. Remaining portion of lectotype specimen. Scale bar = 5 mm.
Fig. 2. Labels accompanying the lectotype. Uppermost label written by Lamarck. Determinavit slip written by Ian Price. Bottom label written by J. Decaisne. AR4174 is an older herbarium specimen number for the lectotype. Scale bar = 10 mm.
Fig. 3. Transverse section through a fragmentary intergeniculum showing core-region filaments in cross-sectional view. Arching tiers of cells not observable in this view. Dotted lines indicate position of missing part of section. Scale bar = 100 μ m.
Fig. 4. Longitudinal section through part of a fragmentary intergeniculum. Note single tier of shorter cells (arrows) separated by tiers of longer cells. Scale bar = 100 μ m.

filaments linked by secondary pit connections (Fig. 10); cell fusions absent.

Genicula formed behind branch apices as a consequence of secondary decalcification of short segments of adjacent core filaments (Fig. 12); associated peripheral-region filaments remaining calcified; calcified portions subsequently cracking apart and usually sloughing off, sometimes leaving calcified spurlike extensions flanking the genicula (Figs 9, 12, 13). Mature genicula (as seen in median longitudinal section) composed of five or more successive arching tiers of transformed, thicker-walled (and more darkly staining) core-region cells (Fig. 12); transitions from calcified intergenicula to decalcified genicula occurring within single core-region cells or between successive cells of tiers; core cells in genicula similar in size to core cells in intergenicula, aligned in one to five arching tiers of longer cells followed by a single arching tier of shorter cells.

Tetrasporangial conceptacles uniporate, formed in peripheral regions of intergenicula; scattered over the surface of intergenicula (Fig. 13) and protruding above surrounding thallus surface (Fig. 11). Conceptacle pore canals flanked by filaments that project laterally toward the canal (Figs 6, 15, 17); rings of large block-shaped cells absent. Mature roof filaments above chamber mostly four to six cells long (including epithallial cells).

Tetrasporangia formed peripherally; central columella of sterile, elongate more or less degenerate cells sometimes present; conceptacle chamber floor more or less flat or sometimes with a central hump (Figs 14, 16). Each mature sporangium 20–55 µm in diameter and 70–85 µm long, containing four zonately arranged tetraspores. Bisporangia not seen but reported by Womersley & Johansen (1996, p. 286). Mature conceptacle chambers 230–450 µm in diameter and 85–140 µm high.

Gametangial and carposporangial plants not recorded in temperate Australian material.

PROTOLOGUE: Lamarck 1815, p. 238 (as *Corallina anceps* Lamarck).

ETYMOLOGY: *anceps*, from the Latin, meaning two-edged; probably referring to the flattened intergenicula. Lamarck (1815) did not explain the etymology.

SYNONYMS: *Amphiroa anceps* (Lamarck) Decaisne is the only known homotypic synonym. Putative heterotypic synonyms, listed in Table 3, require reassessment. Further comments appear in the Discussion.

MISAPPLIED NAME:

‘*Amphiroa ephedraea*’ auct. non (Lamarck) Decaisne

The W.H. Harvey specimen (NSW 774014) from Kiama, New South Wales (listed below) was incorrectly identified by W.H. Harvey as *A. ephedraea* and distributed in 1857 as

number 458N in set 49 of Harvey’s exsiccata *Duplicate Australian Algae*. Further comments on this exsiccata occur in the account of *A. gracilis* below. On the basis of conceptacle anatomy, however, NSW 774014 belongs to *A. anceps*.

W.H. Harvey (1863, p. xxix) subsequently incorrectly reported *A. ephedraea* from New South Wales, partly on the basis of his specimen 458N from Kiama and partly on another specimen (458M) from Newcastle, also labelled *A. ephedraea* by Harvey. The Newcastle specimen, however, belongs to *A. beauvoisii* (as noted in the account of that species below).

Amphiroa ephedraea, studied in detail by Johansen (1968, 1969), has not been confirmed to occur in southeastern or southern Australia. With one other exception (discussed above), we have not been able to determine whether previous records of *A. ephedraea* from this region, summarized in the synonymy of *A. anceps* by Millar & Kraft (1993, p. 12) and by Womersley & Johansen (1996, p. 285), might pertain to *A. beauvoisii* or *A. anceps* or some other species.

LECTOTYPE: PC, General Herbarium, PC0028677, designated here by W. Woelkerling & B. de Reviers. Dr Bruno de Reviers is based at the Département Systématique et évolution, Muséum national d’histoire naturelle, Paris. Type locality: ‘...les mers Australes ou de la Nouvelle-Hollande. Péron et Lesueur.’ (Lamarck 1815, p. 239). The lectotype is depicted here in Figs 1–6.

ADDITIONAL SPECIMENS EXAMINED: **Queensland:** Rockhampton (1809?, MEL 664926) (Herbarium of Sonder). **NSW:** Catherine Hill Bay (*Taylor*, 2.v.2004, NSW 774014). Kiama (*Harvey*, June 1855, NSW 712048/Harvey 458N) (This specimen from W.H. Harvey’s Australian Algal Exsiccatae Set no 49 sold to W. Stewart Esq.). Jervis Bay (*Lucas*, ?vii.1899, NSW 766708). **South Australia:** Port Willunga (*Woelkerling*, 9.iv.1967, LTB 884/MEL 2063173). **Western Australia:** Eyre, Twilight Cove (*Woelkerling, Platt & Jones*, 2.ii.1984, LTB 14054). Rottneest Island, East Strickland Bay (*Woelkerling*, 12.ii.1978, LTB 11042/MEL 2063212). Kalbarri (*Johansen*, 7.xii.1981, MEL 2063210).

Specimens at MELU from Coffs Harbour and other localities cited by Millar (1990, p. 316) under the name *A. anceps* were severely damaged in a flood at MELU and have not been re-examined during this study.

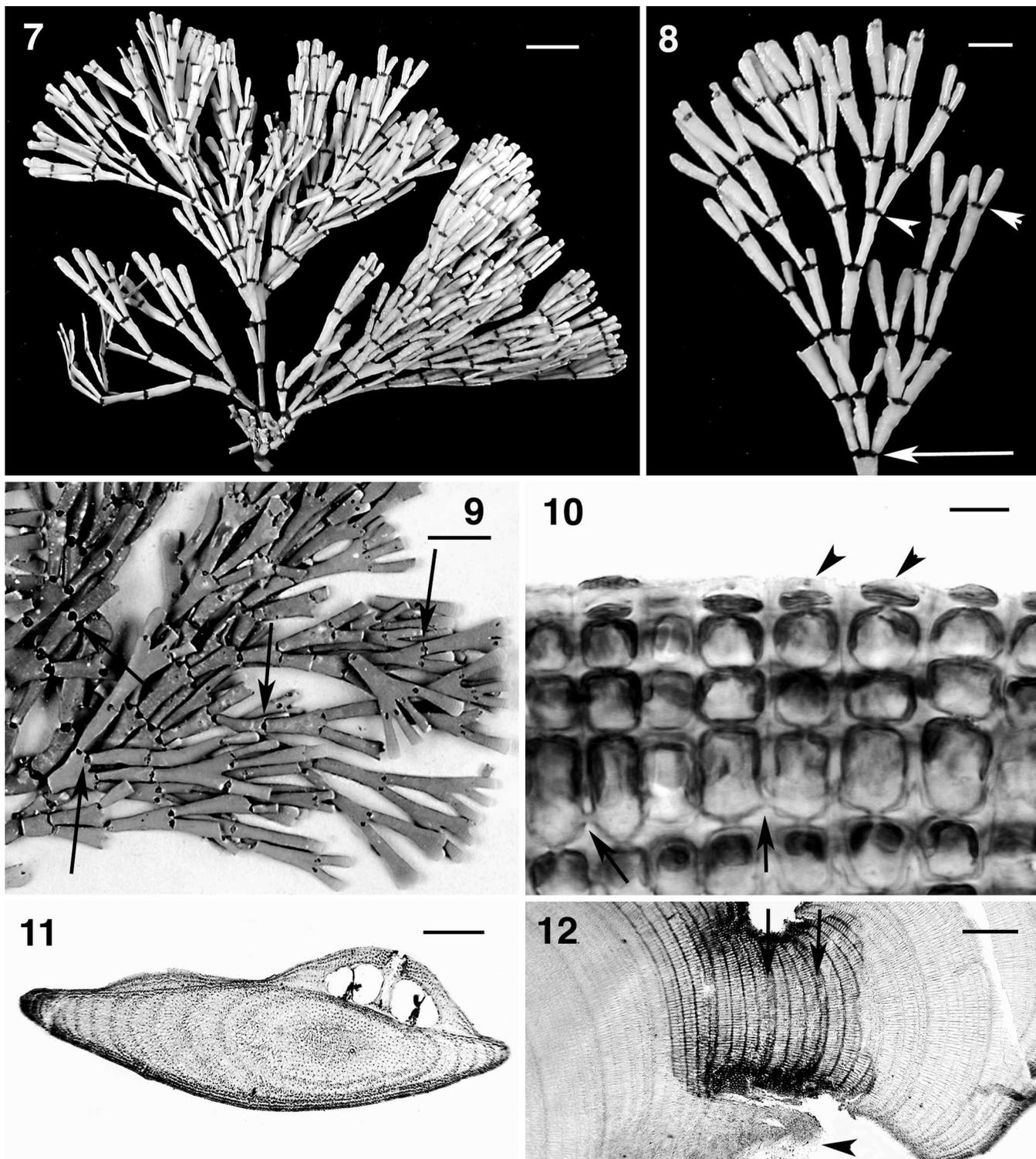
LECTOTYPE MORPHOLOGY AND ANATOMY: All features evident in the lectotype of *Amphiroa anceps* (Figs 1–6) are concordant with those in specimens from southern Australia (Figs 7–17).

The lectotype specimen (Figs 1, 2) is extremely fragmentary, consisting of a few compressed intergenicula from what originally was part of a single branched erect axis, as evidenced by the shadowy impressions on the lectotype herbarium sheet (Fig. 1). A single partial intergeniculum containing a single conceptacle was examined anatomically.

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Fig. 5. Section through a presumed tetrasporangial conceptacle showing remains of filaments that contributed to roof formation (arrow). Possible remnants of several sporangia are on left side of conceptacle chamber floor (arrowhead). Scale bar = 35 µm.

Fig. 6. Closer view of pore canal (p). Note the absence of block-shaped cells like those found in *A. beauvoisii* (Fig. 36) and flanking filaments projecting laterally toward the canal (arrow). Scale bar = 20 µm.



Figs 7–12. *Amphiroa anceps*.

Fig. 7. Plant with several erect axes arising from a common base. Note flattened intergenicula that are more or less of equal width throughout the branches. Plant from Rottnest Island WA (southern Australia) (MEL 2063212). Scale bar = 10 mm.

Fig. 8. Part of a branch axis showing mostly dichotomous (arrowheads) and occasional trichotomous (arrow), complanate branching. (MEL 2063212). Scale bar = 5 mm.

Fig. 9. Part of W.H. Harvey’s original collection 458N from Kiama New South Wales. Note spurlike extensions in surface view evident at the distal ends of some intergenicula (arrows) (NSW 712048). Scale bar = 10 mm.

Fig. 10. Transverse section through intergeniculum showing secondary pit connections (arrows) between cells of adjacent peripheral-region filaments and epithallial cells (arrowheads) (MEL 2063173). Scale bar = 10 μ m.

To avoid further destruction of what remains of the lectotype, no segments containing genicula were examined anatomically.

The vegetative anatomy of the single partial lectotype intergeniculum (Figs 3, 4) compared favourably with that in more modern material (Figs 11, 12). In median longitudinal section, cells of adjacent core-region filaments of the lectotype fragment were arranged in three to four arching tiers of longer cells followed by a single arching tier of shorter cells (Fig. 4). This arrangement is not evident in transverse section (Fig. 3). A narrow peripheral region flanks a broad core region.

The single lectotype conceptacle sectioned (Figs 5, 6) is devoid of contents, but the occurrence in the chamber of degenerate filaments that arose from the chamber floor and contributed to roof formation provides evidence that the conceptacle was tetrasporangial or bisporangial; such filaments occur in tetrasporangial/bisporangial conceptacles in other species of *Amphiroa* but are unknown in gametangial conceptacles, where the floor is largely occupied by spermatangia, carpogonia or the fusion cell of a carposporophyte. What may be a remnant of a sporangium occurs on the left side of the conceptacle chamber (Fig. 5).

The conceptacle roof consists mostly of four to six layers of cells (Fig. 5). The pore canal is poorly preserved (Fig. 6) but all flanking filaments that are visible project laterally toward the canal. No ring of large block-shaped cells occurs, but the canal appears to be occluded by mucilage. The chamber measured 370 µm in diameter and 110 µm high; no columella was evident.

OBSERVATIONS ON OTHER SPECIMENS: The morphology and anatomy of more recently collected material are illustrated in Figs 7–17. Branching of axes is mostly complanate and dichotomous with occasional trichotomies (Figs 7–9). Intergenicula are compressed to flattened (Fig. 11); genicula (Fig. 12) are composed of five or more arching tiers of thicker-walled decalcified cells of adjacent core filaments. During genicular formation, associated peripheral portions of filaments remain calcified and subsequently crack apart and slough off, sometimes leaving spurlike extensions flanking the genicula (Figs 9, 12, 13).

Tetrasporangial conceptacles are scattered over both surfaces of the compressed to flattened intergenicula and protrude somewhat above the surrounding thallus surface (Fig. 13). Within conceptacle chambers, tetrasporangia occur peripherally (Figs 14, 16); degenerate filaments that contributed to roof formation sometimes persist more centrally (Figs 14, 16), and one conceptacle illustrated in Womersley & Johansen (1996, p. 284, fig. 130E) shows a distinct central hump and columella.

Tetrasporangial conceptacle roofs (Figs 14–17) are mostly three to seven cells thick above the chamber, and the pore canals are flanked only by filaments that project laterally toward the canal; rings of large block-shaped cells do not occur. Variation in roof thickness does not appear to be taxonomically significant.

Gametangial plants and carposporophytes were not encountered during the present study, but Ganesan (1968, pp. 8–14, text figs 1, 2, 5–7, 12–20, pl. 1, figs 3, 4) provided a detailed account on the basis of Indian specimens identified as *A. anceps*. Ganesan's (1968, p. 13, text fig. 13) line drawing of a tetrasporangial conceptacle with a pore canal region is unusual in that the roof on one side of the pore is thicker than that on the other side, something not seen during this study or mentioned by Womersley & Johansen (1996). Further studies of Indian specimens are needed.

HABITAT AND DISTRIBUTION: During the current study, *A. anceps* was confirmed to occur in southeastern, southern and southwestern Australia. In southeastern Australia *A. anceps* was found from Rockhampton, Queensland southward to Jervis Bay, NSW. It also occurs from Port Willunga, South Australia (on the southern Australian coast) westward and northward to Kalbarri, Western Australia (on the southwestern Australian coast). Specimens were found on rock in intertidal pools and to depths of 3 m. All plants were epilithic, and only tetrasporangial plants were found. The full geographic range in Australia, however, has not been determined.

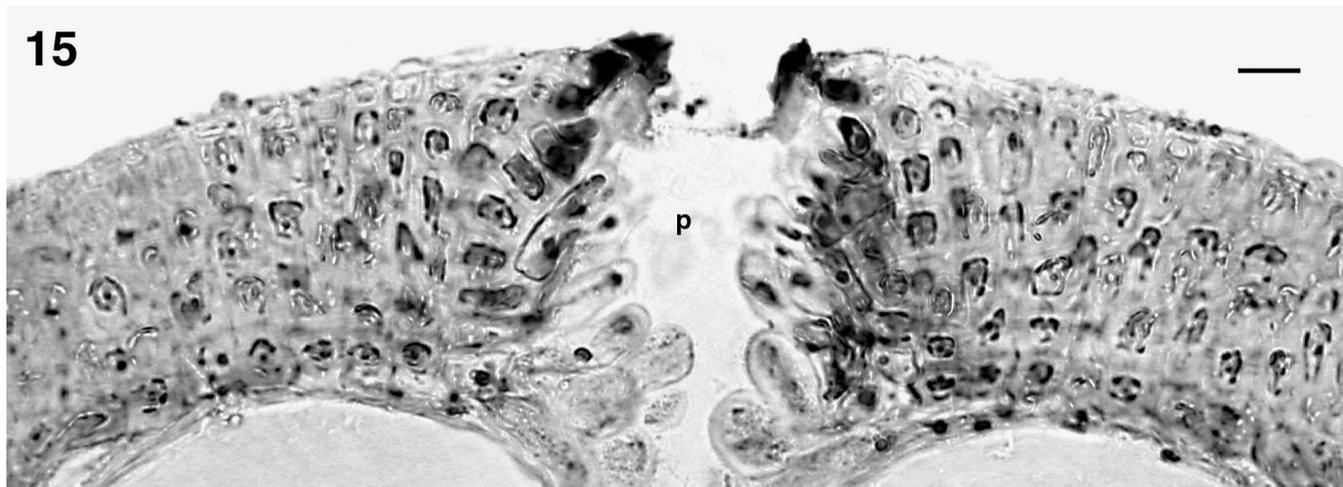
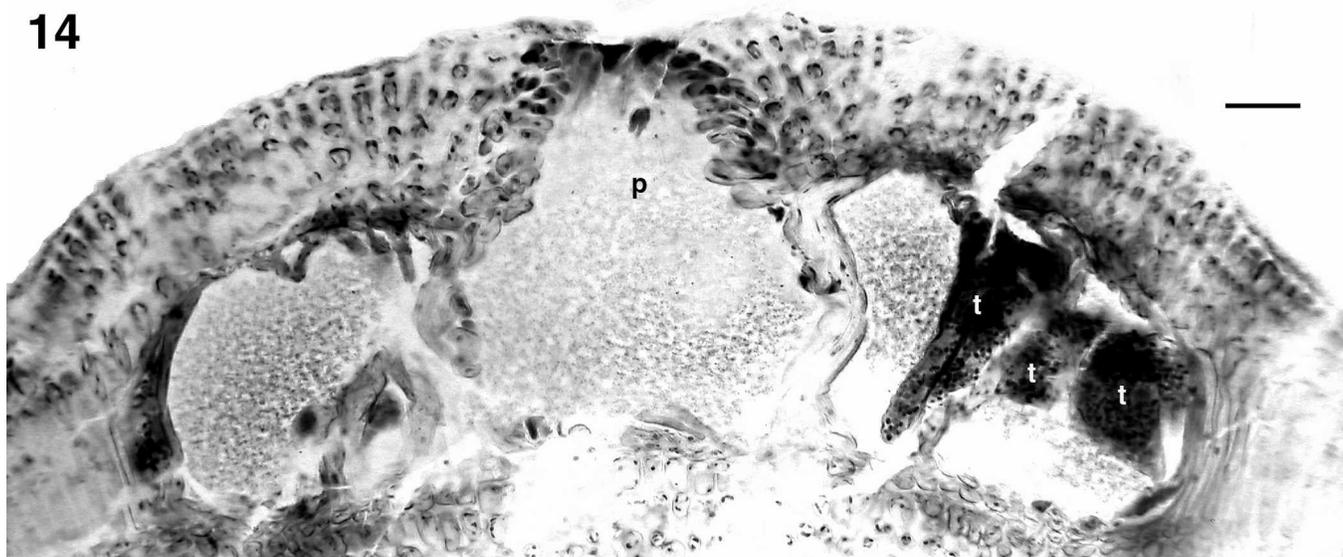
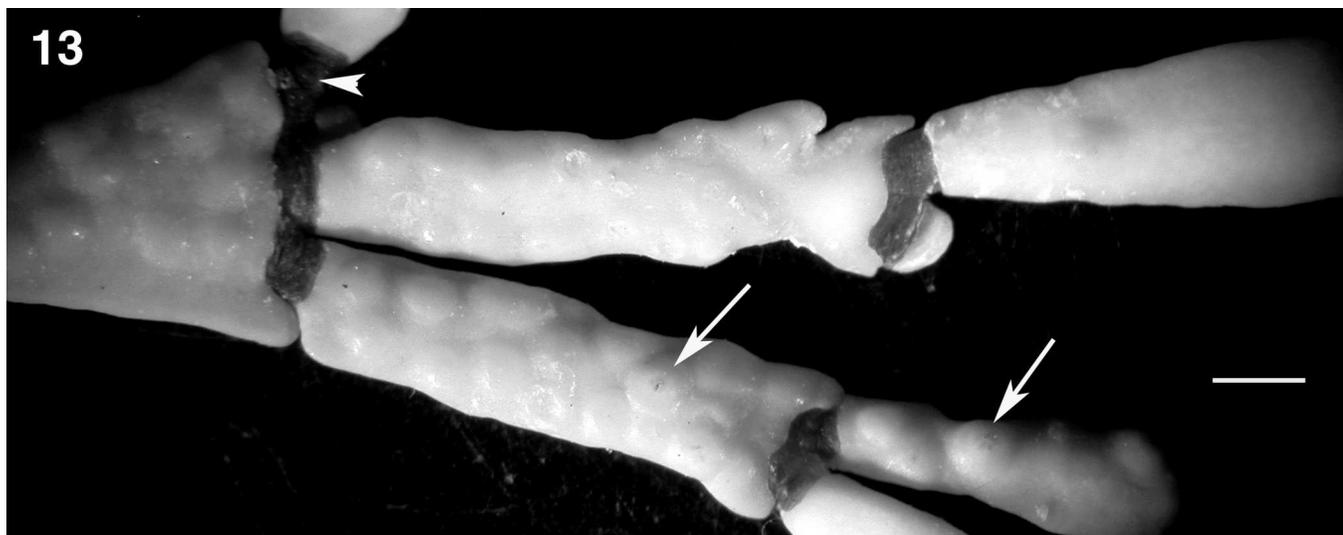
According to Womersley & Johansen (1996, p. 286), *A. anceps* grows in intertidal pools and to depths of at least 22 m in southern Australia, and is found all around Australia except for Tasmania. Womersley & Johansen (1996, p. 286) also report that *A. anceps* is widespread in the Indo-Pacific, whereas Womersley & Bailey (1970, p. 313) and Huisman & Walker (1990, p. 411) state that the species is widespread in tropical and subtropical (and warm temperate) seas. These Australian and worldwide reported distributions, however, require re-evaluation to confirm that the records are based on specimens that have the same tetrasporangial pore canal anatomy as occurs in the type and in southeastern and southern Australian specimens. Further comments occur below in the Discussion.

RELATIONSHIPS TO OTHER SPECIES: The relationships of *A. anceps* to other species found in temperate Australia are considered in the Discussion. Comparisons of *A. anceps* with other species (including the putative heterotypic synonyms listed in Table 3) are difficult to make at present, because of the lack of modern data on type specimens (particularly on conceptacle anatomy) and the consequent uncertainty that published identifications of specimens are correct.

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Fig. 11. Transverse section through a compressed intergeniculum showing core-region filaments in cross-sectional view and peripheral-region filaments in tangential to surface view. Note edge of one conceptacle at upper left and section through pore canal of second conceptacle at upper right. (LTB 14054). Scale bar = 200 µm.

Fig. 12. Longitudinal section through a mature geniculum (dark staining area) and parts of flanking intergenicula (lighter area) (compare with surface view in Fig. 13). Note single tiers of shorter cells (arrows) separated by tiers of longer cells both in intergeniculum and flanking intergenicula. Also note that margins of geniculum do not necessarily correspond to ends of cell tiers, and note remnants of associated calcified peripheral filaments, some of which have formed a spurlike extension (arrowhead). (LTB 14054). Scale bar = 200 µm.



Figs 13–15. *Amphiroa anceps*.

Fig. 13. Surface view of intergenicula with scattered, uniporate conceptacles (arrows). Conceptacles occur on both faces of intergenicula. Note both trichotomous and dichotomous branching and spurlike extensions at distal ends of some intergenicula where surrounding calcified peripheral-region filaments have partly or completely (arrowhead) disappeared after rupturing during geniculum formation. (MEL 2063212). Scale bar = 12 mm.

***Amphiroa beauvoisii* Lamouroux (1816, p. 299)**

Figs 1–38

SYNOPTIC DESCRIPTION: Temperate Australian plants epilithic; attached ventrally to substrate by a calcified, crustose, nongeniculate base and producing branched erect axes up to 85 mm long that consist of alternating calcified segments (intergenicula) and secondarily decalcified segments (genicula). Branching generally complanate (in one plane) (Fig. 25) and dichotomous, sometimes with occasional trichotomies (Fig. 29) or quadrachotomies (Fig. 27); branches arising from some or most intergenicula; intergenicula compressed to flat (Figs 20, 30) (occasionally more terete near the base); mostly of similar width throughout plant although sometimes broader distally at points of branching (Figs 18, 28), mostly 3.0–6.5 mm long, 1.0–3.5 mm wide (Figs 24–27), and 300–400 μm thick.

Erect axes monomerous, consisting throughout of a single continuous system of branched, laterally coherent filaments; in median longitudinal section (Figs 21, 31); axes of intergenicula and genicula with a broad uninterrupted central core (medullary) region in which filaments are oriented more or less parallel to the branch surface, passing in intergenicula into a narrower peripheral (cortical) region in which portions of core filaments or their derivatives bend outward to become more or less diagonally or perpendicularly oriented to the branch surface; peripheral region usually lost in mature genicula. Cells of adjacent filaments in core region mostly 8–13 μm in diameter, aligned in one to three arching tiers of longer cells (45–85 μm long) followed by a single arching tier of shorter cells (6–40 μm long). Cells of adjacent filaments in peripheral region not aligned in arching tiers, mostly 8–13 μm in diameter and 10–19 μm long; peripheral portions of filaments terminating at the thallus surface in epithallial cells 5–10 μm in diameter and 4–5 μm long and with rounded or flattened outer walls (Fig. 32). Peripheral-region and epithallial cells usually secondarily lost in genicula (Figs 21, 31). Cells of adjacent filaments linked by secondary pit connections (Fig. 33); cell fusions absent.

Genicula formed behind branch apices as a consequence of secondary decalcification of short segments of adjacent core-region filaments (Figs 28, 31); associated peripheral-region filaments remaining calcified; calcified portions subsequently cracking apart and usually sloughing off, sometimes leaving calcified spurlike extensions flanking the genicula (Figs 28, 29, 31). Mature genicula (as seen in median longitudinal section) composed of five or more successive arching tiers of transformed, thicker-walled (and more darkly staining) core-region cells (Fig. 31); transitions from calcified intergenicula to decalcified genicula occurring within single core-region cells or between successive cells of tiers; core cells in genicula similar in size to core cells in intergenicula, aligned in one to three arching tiers of longer cells followed by a single arching tier of shorter cells.

Tetrasporangial conceptacles uniporate, formed in peripheral regions of intergenicula; scattered over the surface of intergenicula (Fig. 29) and protruding above surrounding thallus surface (Fig. 29). Conceptacle pore canals flanked by filaments that grow parallel to the pore canal as well as basal filaments that project laterally toward the canal (Figs 35, 36); top of canal surrounded by a ring of large block-shaped cells (Figs 35–37) that may eventually degenerate to form a depression above the pore (Fig. 38). Mature roof filaments above chamber mostly three to five cells long (including epithallial cells).

Tetrasporangia formed peripheral to a central columella of sterile, elongate more or less degenerate cells (Figs 37, 38); conceptacle chamber floor more or less flat (Fig. 38) or sometimes with a central hump (Fig. 37). Each mature sporangium 25–55 μm in diameter and 70–85 μm long, containing four zonately arranged tetraspores. Bisporangia not seen. Mature conceptacle chambers 230–330 μm in diameter and 85–140 μm high.

Gametangial and carposporangial plants not recorded in Australian material.

PROTOLOGUE: Lamouroux 1816, p. 299.

ETYMOLOGY: The specific epithet honours the French entomologist and botanist A.M.F.J. Palisot de Beauvois (1752–1820), whose interests included invertebrate animals and cryptogamic plants. For further data on Palisot de Beauvois, see Lamy 1997.

SYNONYMS: No homotypic synonyms are known. Putative heterotypic synonyms, listed in Table 3, require reassessment. Further comments appear in the Discussion.

SUPERFLUOUS SUBSTITUTE NAME: *Amphiroa belvisii* J.V.F. Lamouroux in Lamouroux *et al.* (1824, p. 50) is an illegitimate superfluous substitute name (see ICBN Art. 52.1) for *A. beauvoisii*. Lamouroux *et al.* (1824, p. 50) cited the protologue of *A. beauvoisii* as a synonym in the original presentation of *A. belvisii*, thus rendering the latter illegitimate.

MISAPPLIED NAMES:

'Amphiroa anceps' auct. non (Lamarck) Decaisne

The Henderson specimen (MEL 664927) from Ballina, New South Wales (listed below) is the basis of the published records of Sonder (1871, p. 54, 1880, p. 20) and Millar (1990, p. 316) under the name *A. anceps*. These records are also included in Millar & Kraft (1993, p. 12). On the basis of conceptacle anatomy, MEL 664927 belongs to *A. beauvoisii*.

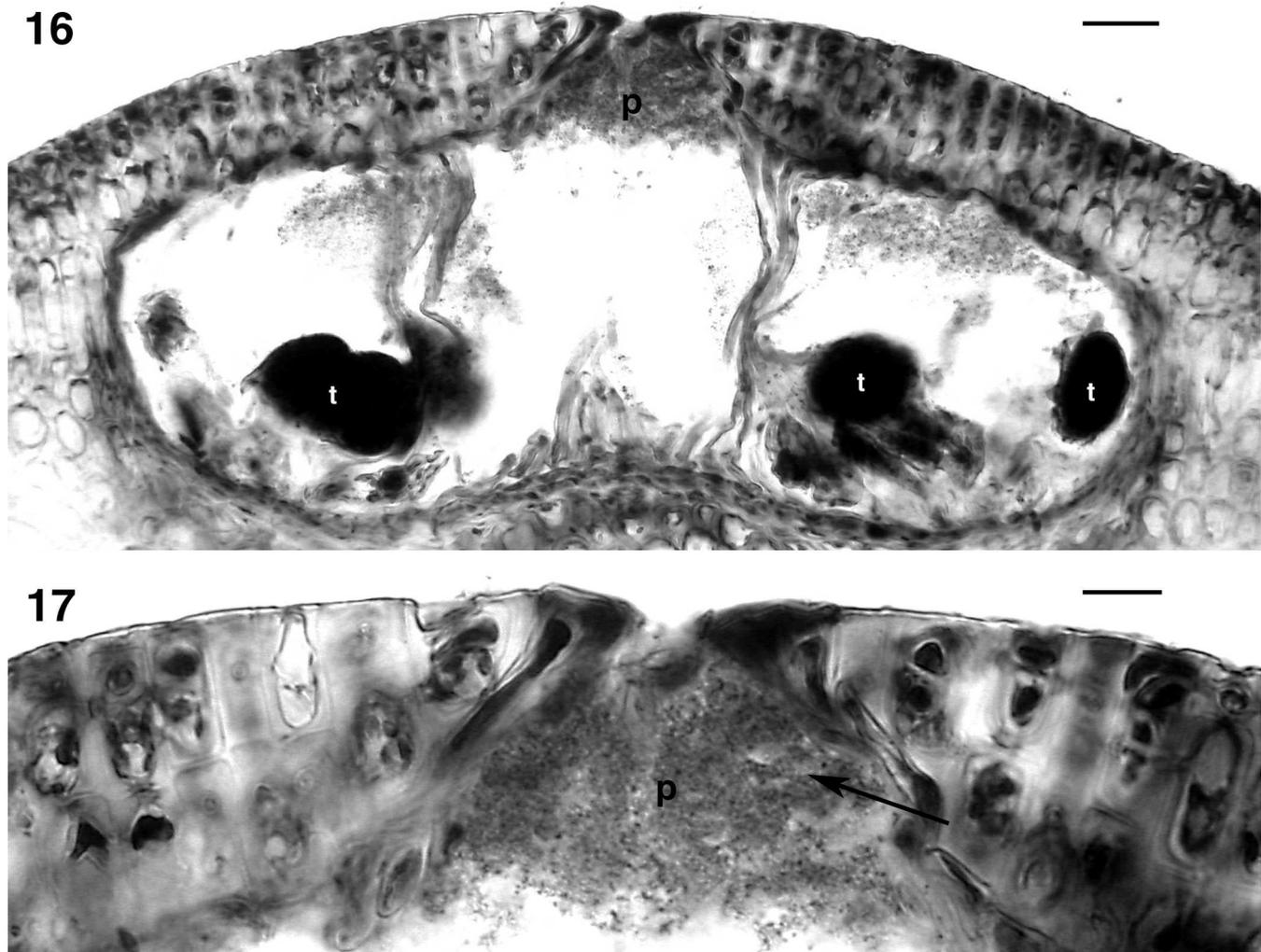
'Amphiroa ephedraea' auct. non (Lamarck) Decaisne

The W.H. Harvey specimen (NSW 713347) from Newcastle, New South Wales (listed below) was incorrectly identified by W.H. Harvey as *A. ephedraea* and distributed in 1857 as number 458M in set 57 of Harvey's exsiccata

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Fig. 14. Section through a mature tetrasporangial conceptacle showing remnants of tetrasporangia (t) and pore canal (p). (MEL 2063212). Scale bar = 45 μm .

Fig. 15. Enlarged section through tetrasporangial conceptacle pore canal (p) region. Note the absence of block-shaped cells like those found in *A. beauvoisii* (Fig. 36) (LTB 14054). Scale bar = 10 μm .



Figs 16–17. *Amphiroa anceps*.

Fig. 16. Section through a mature tetrasporangial conceptacle showing tetrasporangia (t) and pore canal (p) and conceptacle with a thinner roof compared with Fig. 14 (NSW 774014). Scale bar = 20 μ m.

Fig. 17. Enlarged section through tetrasporangial conceptacle pore canal (p) region showing a thinner roofed conceptacle – compare with Fig. 15. Note tetrasporangial conceptacle pore canals flanked only by filaments that project laterally toward the canal (arrow); rings of large block-shaped cells absent (LTB 14054). Scale bar = 8 μ m.

Duplicate Australian Algae. Further comments on this exsiccata occur in the account of *A. gracilis* below. On the basis of conceptacle anatomy, however, NSW 713347 belongs to *A. beauvoisii*.

W.H. Harvey (1863, p. xxix) subsequently incorrectly reported *A. ephedraea* from New South Wales, partly on the basis of his specimen 458M from Newcastle and partly on another specimen (458N) from Kiama, also labelled *A. ephedraea* by Harvey. The Kiama specimen, however, belongs to *A. anceps* (as noted in the account of that species).

Other published New South Wales records of *A. ephedraea* are summarized by Millar & Kraft (1993, p. 12) under their entry for *A. anceps*. We have been unable to determine with certainty, however, which of these *A. ephedraea* records might pertain to *A. beauvoisii* and which might pertain to *A. anceps* or some other species. This also is the case for southern and southwestern Australian records of *A. ephedraea* listed by Harvey (1863: xxix) and by Womersley & Johansen (1996, p. 285, in the synonymy of *A. anceps*).

Amphiroa ephedraea, studied in detail by Johansen (1968, 1969), has not been confirmed to occur in temperate Australia.

HOLOTYPE: CN, Lamouroux herbarium, unnumbered; gathered by an unknown collector from the coast of Portugal, donated by A.M.F.J. Palisot de Beauvois (Lamouroux 1816, p. 299).

The holotype is depicted here in Figs 18–23 and in Norris and Johansen (1981, fig. 7b). On a 1959 annotation label accompanying the holotype (Fig. 19), Roger Meslin mistakenly listed Palisot de Beauvois as the collector.

ADDITIONAL SPECIMENS EXAMINED: **New South Wales:** Tweed Heads – Cook Island (*Brand & Ringeltaube*, 23.x.1997, LTB 20958). Tweed Heads – west side of Cook Island (Coral Garden) (*Brand & Ringeltaube*, 25.x.1997, LTB 20980). Byron Bay – Boulders/seagrass foreshore at Lennox Head (*Woelkerling*, 30.iv.1997, LTB 20561). Byron

Table 3. Putative heterotypic synonyms of *Amphiroa anceps* and *A. beauvoisii* listed in the published literature. Taxa listed alphabetically by specific epithet. The tetrasporangial conceptacle pore canal anatomy of all taxa requires re-examination to determine whether it matches that of the species with which it has been synonymised.

A. Putative heterotypic synonyms of *Amphiroa anceps*

- Amphiroa bowerbankii* Harvey (1849, p. 97). Provisional synonymy proposed by Millar (1990, p. 317). Silva *et al.* (1996, p. 219, 221) and Desikachary *et al.* (1998, p. 61), however, continued to recognize *A. bowerbankii* as a distinct species.
- Amphiroa dilitata* J.V.F. Lamouroux (1816, p. 299). Synonymy proposed by Weber-van Bosse (1904, p. 93, 94); more recently considered a synonym by Womersley & Johansen (1996, p. 285).
- Amphiroa galaxauroides* O.G. Sonder (1848, p. 188). Synonymy proposed by Weber-van Bosse (1904, p. 93); more recently considered a synonym by Womersley & Johansen (1996, p. 285).
- Amphiroa nobilis* F.T. Kützing (1849, p. 703). Synonymy proposed by Weber-van Bosse (1904, p. 93); more recently considered a synonym by Womersley & Johansen (1996, p. 285).
- Galaxaura versicolor* O.G. Sonder (1845, p. 50). First proposed as a synonym of *Amphiroa galaxauroides* by Kützing (1849, p. 703). *Amphiroa galaxauroides* subsequently proposed as a synonym of *A. anceps* by Weber-van Bosse (1904, p. 93) but without mention of *G. versicolor*. More recently, both *A. galaxauroides* and *G. versicolor* treated as synonyms of *A. anceps* by Womersley & Johansen (1996, p. 285).

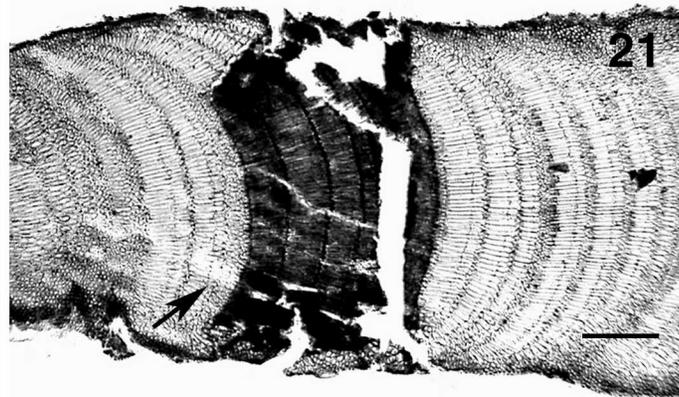
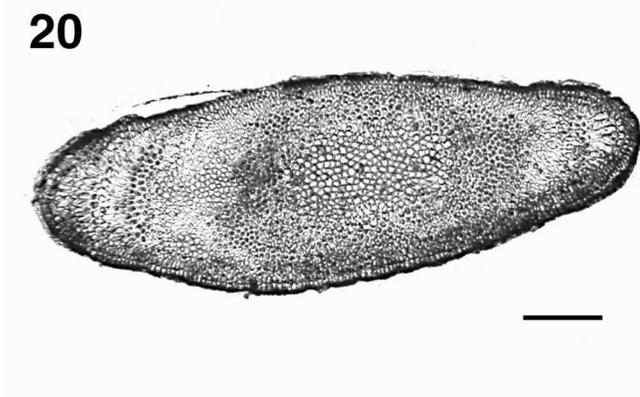
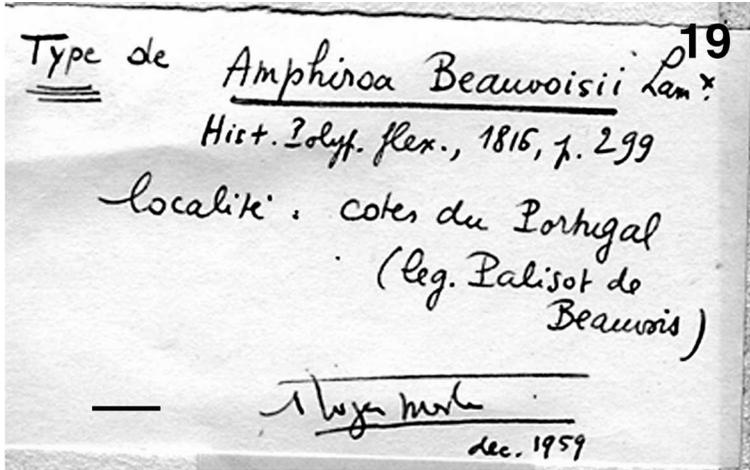
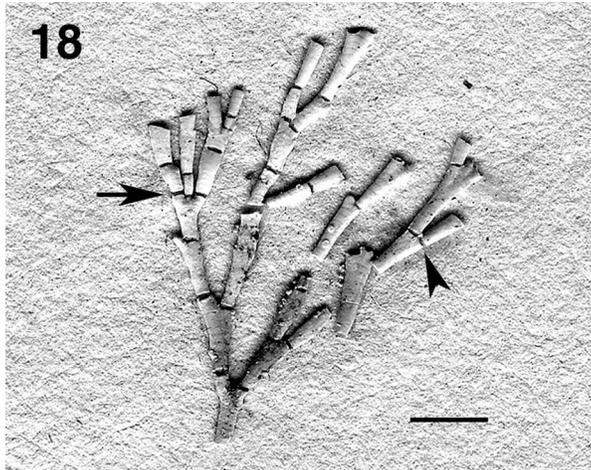
B. Putative heterotypic synonyms of *Amphiroa beauvoisii*

- Amphiroa algeriensis* F.T. Kützing (1858, p. 21). Synonymy proposed by Bornet (1892a, p. 349) [also see Ardissonne (1883, p. 455) under *Amphiroa exilis* W.H. Harvey]; more recently considered a synonym by Bressan & Babbini (2003, p. 120).
- Amphiroa annobonensis* R. Pilger (1919, p. 427). Synonymy proposed by Price *et al.* (1986, p. 10) on the basis of remarks by H.W. Johansen in Lawson & John (1982, p. 225).
- Amphiroa brasiliana* J. Decaisne (1842b, p. 125). Synonymy proposed by Moura & Guimarães (2005, p. 21, 25) (also see Weber-van Bosse 1904, p. 100).
- Amphiroa complanata* F.T. Kützing (1843, p. 388). Synonymy proposed by Bornet (1892a, p. 349) [also see Areschoug (1852, p. 535) and Ardissonne (1883, p. 455) under *A. exilis* W.H. Harvey]; more recently considered a synonym by Bressan & Babbini (2003, p. 120).
- Amphiroa drouetii* E.Y. Dawson (1953, p. 140). Synonymy proposed by Norris & Johansen (1981, p. 6, 12); more recently considered a synonym by Riosmena-Rodriguez & Siqueiros-Beltrones (1996, p. 137) and Moura & Guimarães (2005, p. 21).
- Amphiroa dubia* F.T. Kützing (1858, p. 24). Synonymy proposed by Seagrief (1984, p. 4) on the basis of a personal communication from H.W. Johansen.
- Amphiroa exilis* W.H. Harvey (1849, p. 95). Synonymy proposed by Bornet (1892a, p. 349); more recently considered a synonym by Bressan & Babbini (2003, p. 120) and Moura & Guimarães (2005, p. 21).
- Amphiroa exilis* var. *crassiuscula* W.H. Harvey (1849, p. 95, as β *crassiuscula*). Synonymy proposed in Seagrief (1984, p. 4) on the basis of a personal communication from H.W. Johansen; more recently considered a synonym by Moura & Guimarães (2005, p. 21). Yendo (1905, p. 4) previously had proposed the new combination *A. beauvoisii* β *crassiuscula* (W.H. Harvey) Yendo on the basis of Harvey's taxon *A. exilis* β *crassiuscula*.
- Amphiroa franciscana* var. *robusta* E.Y. Dawson (1953, p. 150). Synonymy proposed by Norris & Johansen (1981, p. 6, 12); more recently considered a synonym by Moura & Guimarães (2005, p. 21).
- Amphiroa linearis* F.T. Kützing (1858, p. 22). Synonymy proposed by Norris & Johansen (1981, p. 6, 12); more recently considered a synonym by Moura & Guimarães (2005, p. 21).
- Amphiroa mexicana* W.R. Taylor (1945, p. 189). Synonymy proposed by Mateo-Cid *et al.* (2008, p. 9, 17).
- Amphiroa parthenopia* G. Zanardini (1874, p. 268). Synonymy proposed by De Toni (1905, p. 1813) [also see Ardissonne (1883, p. 455) under *A. exilis* W.H. Harvey]; more recently considered a synonym by Bressan & Babbini (2003, p. 120).
- Amphiroa peninsularis* W.R. Taylor (1945, p. 188). Synonymy proposed by Norris & Johansen (1981, p. 6); more recently considered a synonym by Riosmena-Rodriguez & Siqueiros-Beltrones (1996, p. 137) and Moura & Guimarães (2005, p. 21). Dawson (1953, p. 146) previously had treated *A. peninsularis* as a synonym of *A. zonata* K. Yendo, which Norris & Johansen listed as another synonym of *A. beauvoisii*.
- Amphiroa polyzona* C. Montagne (1846, p. 136). Synonymy proposed by Bornet (1892a, p. 349); more recently considered a synonym by Bressan & Babbini (2003, p. 120).
- Amphiroa pustulata* G. Martens (1836, p. 489). Synonymy proposed by Bornet (1892a, p. 349) [also see Areschoug (1852, p. 535) under *A. exilis* W.H. Harvey]; more recently considered a synonym by De Toni (1905, p. 1813).
- Amphiroa zonata* K. Yendo (1902, p. 10). Synonymy proposed by Norris & Johansen (1981, p. 6, 12) (also see Weber-van Bosse 1904, p. 99); more recently considered a synonym by Riosmena-Rodriguez & Siqueiros-Beltrones (1996, p. 137) and Moura & Guimarães (2005, p. 21). Yoshida & Baba (1998, p. 538), however, treat *A. zonata* as a distinct species.

Note: Norris & Johansen (1981, p. 12) also suggested that *Amphiroa echigoensis* K. Yendo (1902, p. 16) (also see Weber-van Bosse 1904, p. 99) and *Amphiroa galapagnensis* W.R. Taylor (1945, p. 189) may be synonymous with *A. beauvoisii*. Yoshida & Baba (1998, p. 532), however, treat *A. echigoensis* as a distinct species.

Bay – ‘Boulders Beach’, Lennox Head (*Woelkerling, Millar & Hardin*, 3.v.1997, LTB 20547). Byron Bay – NW side Julian Rocks (*Millar & Hardin*, 30.iv.1997, LTB 20522). Broken Head, 7 km south of Byron Bay (*Wills*, 08.i.2001, NSW 456227). Ballina (*Henderson*, no date, MEL 664927, Herbarium of O.W. Sonder). Coffs Harbour – Korffs Islet (*Millar & Hardin*, 13.viii.1996, LTB 20624). Coffs Harbour – Muttonbird Island (*Wills*, 11.i.2001, NSW 456226). Newcastle (*W.H. Harvey*, May–June 1855, NSW 713347/ Harvey 458M) (This specimen is from W.H. Harvey's *Duplicate Australian Algae*, set no. 57 sold to Rev. J.H.

Pollexfen). Jarvis Bay – Green Patch reef (*Woelkerling*, 25.iii.1996, LTB 20085). Jarvis Bay – Plantation Point (*Woelkerling*, 24.iii.1996, LTB 20111). Jarvis Bay – ‘The Rockfall’ 0.5 km north of Perpendicular Point (*Millar & Hardin*, 25.iii.1996, LTB 20078). Disaster Bay – Saltwater Creek, Ben Boyd National Park (*Leach*, 10.xii.1976, LTB 11280/MEL 2066863). **Victoria:** Rye Ocean Beach (*Woelkerling*, 14.ii.1977, LTB 11277/MEL 2063218). Port Fairy (*Woelkerling*, 4.i.1979, LTB 11707/MEL 2066862) (this specimen depicted in *Woelkerling* 1988, p. 60, fig 43 as *A. beauvoisii*).



Figs 18–21. *Amphiroa beauvoisii*. Holotype specimen (CN).

Fig. 18. Habit of holotype showing mostly dichotomous (arrowhead) complanate branching. Note one trichotomy (arrow) and compressed intergenicula. Scale bar = 410 mm.

Fig. 19. Label accompanying the holotype written by Roger Meslin. Another label (not shown) with the superfluous name *Amphiroa belvisii* also accompanies the holotype. Scale bar = 10 mm.

Fig. 20. Transverse section through a compressed intergeniculum showing core-region filaments in cross-sectional view. Arching tiers of cells not observable in this view. Scale bar = 125 μm.

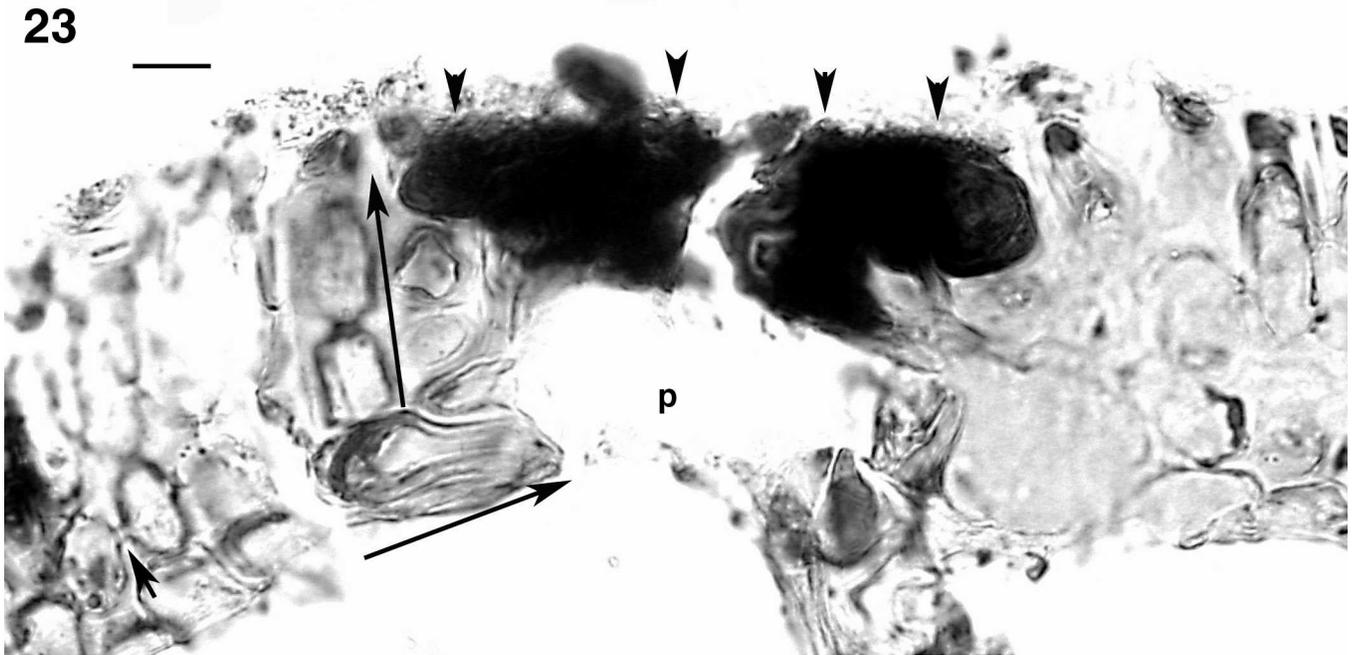
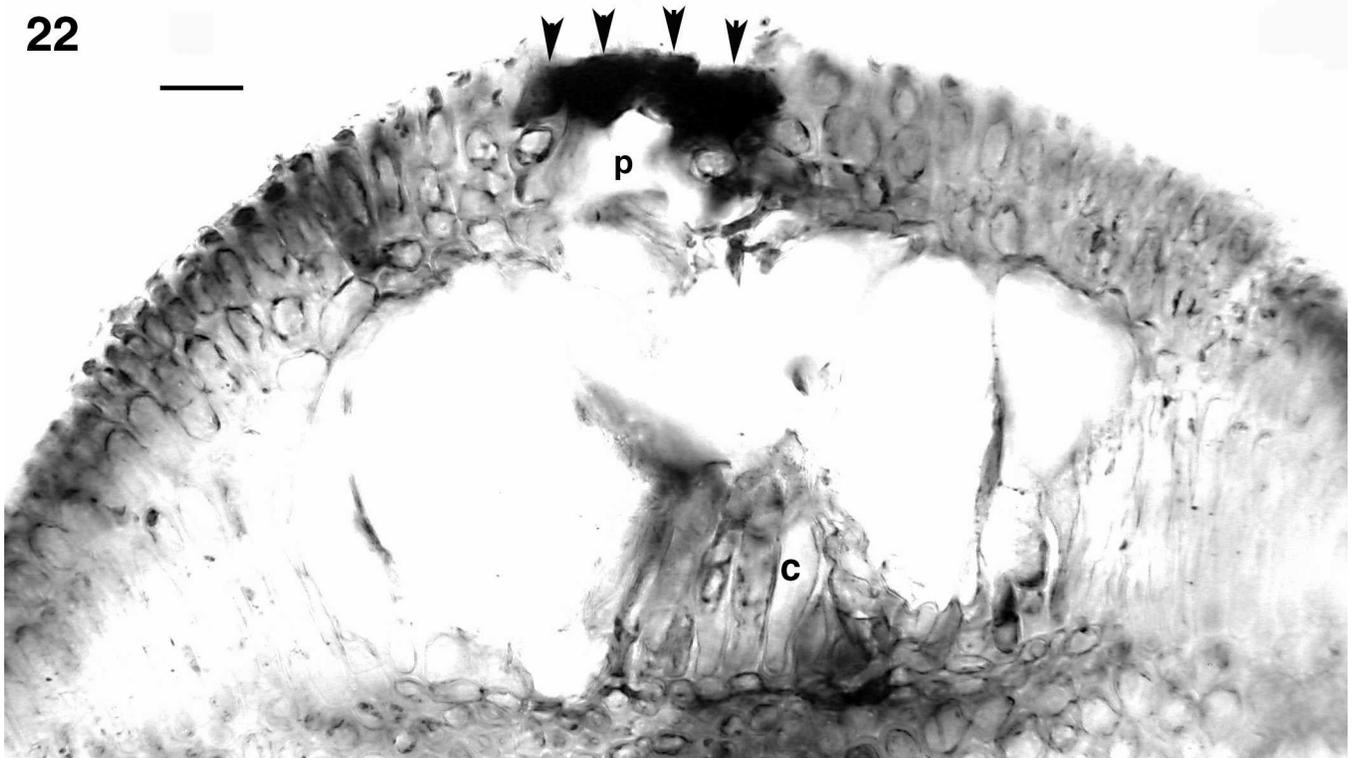
Fig. 21. Longitudinal section through a geniculum (dark staining area) and intergeniculum (lighter area). Note single tier of shorter cells (arrow) separated by tiers of longer cells and remnants of calcified, ruptured peripheral-region filaments flanking the central part of the geniculum. Scale bar = 155 μm.

HOLOTYPE MORPHOLOGY AND ANATOMY: All features evident in the holotype of *A. beauvoisii* (Figs 18–23) are concordant with those in temperate Australian specimens (Figs 24–38). The holotype (Figs 18–19) consists of part of a single branched erect axis 22 mm long (Fig. 18) composed of alternating calcified intergenicula and uncalcified genicula, and eight small fragments (not shown), several with genicula. Branching is complanate (in one plane) (Fig. 18) and essentially dichotomous with one trichotomy (Fig. 18); intergenicula are compressed to flat (Fig. 20).

Anatomical data were obtained from one of the eight fragments; it had both an intact geniculum and an intact conceptacle. Cells of adjacent filaments in the core region were aligned in three to four arching tiers of longer cells followed by a single arching tier of shorter cells; this pattern occurs both in intergenicula and more darkly staining genicula (Fig. 21). The single geniculum sectioned consisted of five tiers of cells of core region filaments (Fig. 21). Cells of adjacent filaments in the peripheral region of inter-

genicula are not aligned in arching tiers, and peripheral portions of filaments terminate at the thallus surface in epithallial cells with rounded or flattened outer walls. Cells of adjacent filaments are linked by secondary pit connections; cell fusions are absent.

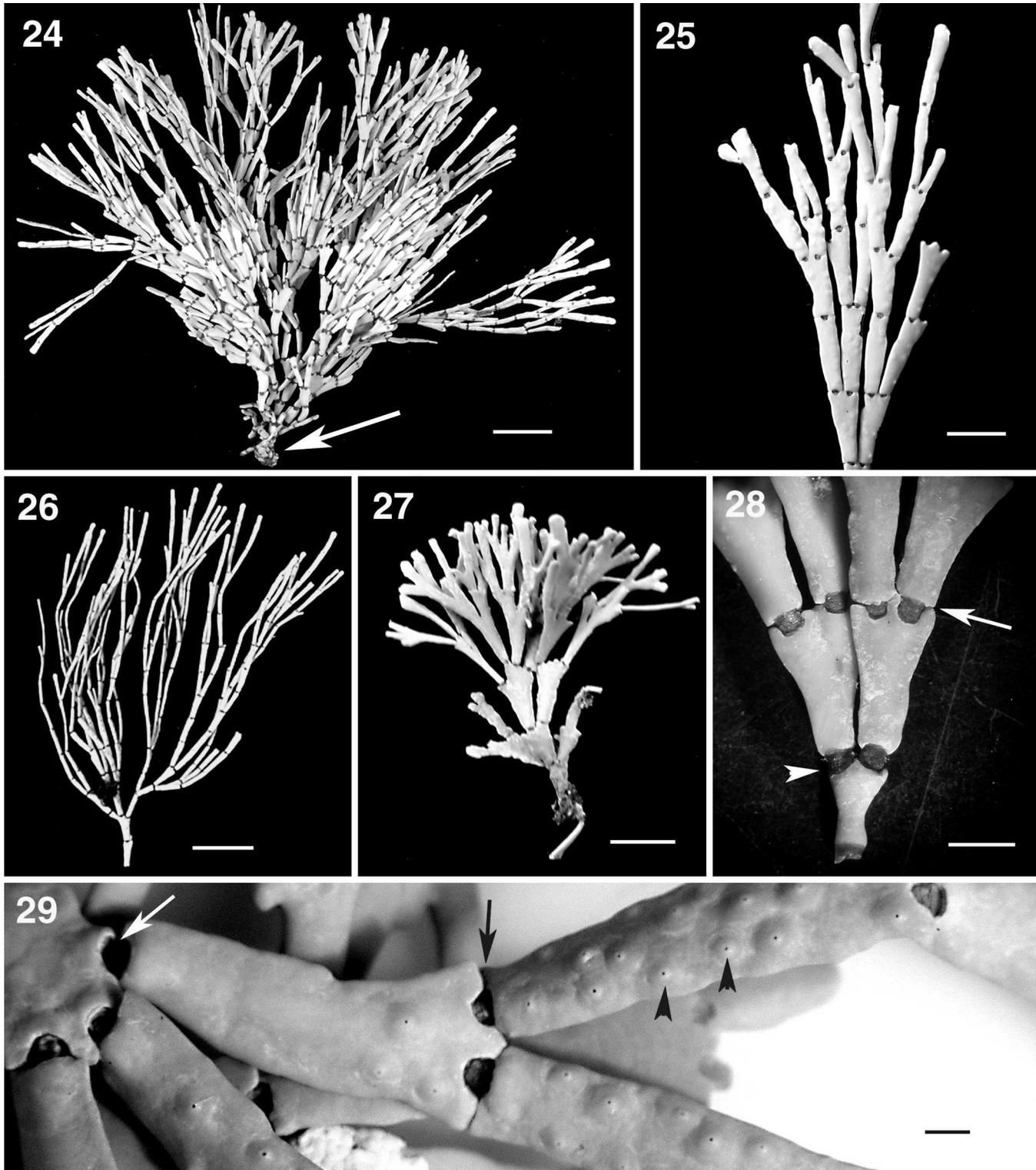
At least one intact conceptacle and several conceptacles with broken roofs occur on the main part of the holotype. Conceptacle roofs protrude slightly above the surrounding thallus surface. In median vertical section, the pore canal of the conceptacle from the holotype fragment (Figs 22, 23) is bordered by filaments that grow parallel to the pore canal as well as basal filaments that project laterally toward the canal (Fig. 23). Although mucilaginous material was also present in the pore canal, the top of the canal was surrounded by a degenerating ring of large block-shaped cells (Figs 22, 23) (compare Figs 35 and 36). Mature roof filaments above the chamber are mostly three cells long (including epithallial cells). A central columella composed of sterile, elongate more or less degenerate cells occurs (Fig. 22), and the conceptacle chamber is 190 μm in diameter and 95 μm high. The



Figs 22–23. *Amphiroa beauvoisii*. Holotype conceptacle (CN).

Fig. 22. Section through a tetrasporangial conceptacle showing pore canal (p), mostly obscured, large block-shaped cells (arrowheads) lining the top of pore canal and remnants of a central columella (c). The block-shaped cells are mostly obscured by dark-staining mucilaginous material (compare with Figs 37, 38). Scale bar = 20 μ m.

Fig. 23. Pore canal region in the section adjacent to that shown in Fig. 22. Note pore canal (p), mostly obscured large block-shaped cells (arrowheads) (compare with Figs 37, 38) lining the upper back of the pore canal and the two directions of filament growth (long arrows) flanking the pore canal. Secondary pit connection between cells of adjacent roof filaments (short arrow) is evident near left margin. Scale bar = 2 μ m.



Figs 24–29. *Amphiroa beauvoisii*. Morphological variation in temperate Australian plants.

Fig. 24. Entire plant with basal holdfast (arrow) and branches of flattened intergenicula that are more or less of equal width throughout plant (LTB 20547). Scale bar = 10 mm.

Fig. 25. Branch tip showing young, flattened intergenicula and young genicula in which surrounding calcified peripheral regions are still largely intact. (LTB 20561). Compare with Fig. 28 showing a mature geniculum in surface view and Fig. 31 showing a longitudinal section through a young geniculum. Scale bar = 4 mm.

Fig. 26. Portion of a plant with slender (less than 1 mm wide) compressed intergenicula and relatively few points of branching. (MEL 2063218). Scale bar = 11 mm.

Fig. 27. Portion of a plant in which most intergenicula bear two to three (four) branches, resulting in a dense, bushy appearance. Note how some intergenicula are wider distally than proximally (LTB 20980). Scale bar = 5 mm.

diameter is slightly less than found in Australian specimens, but this does not appear to be taxonomically significant.

The presence of a columella provides strong circumstantial evidence that the type specimen is tetrasporangial. In all species where gametangial conceptacles are known, no columella occurs; the entire floor of gametangial conceptacles is occupied either by spermatangial or by carpogonial branches.

INTERGENICULA AND GENICULA: In the type (Fig. 21) and some temperate Australian specimens (Fig. 31), the peripheral region of intergenicula tends to be narrow compared with the broader core region, but in other specimens (e.g. LTB 11707 – see Woelkerling 1988, p. 60, fig. 43), the peripheral region can occupy up to half the diameter of the intergeniculum.

During genicular formation, short segments of core-region filaments involving five or more successive tiers of cells undergo secondary decalcification, but associated peripheral-region portions of the filaments remain calcified. The calcified portions eventually crack apart; occasionally (e.g. Fig. 21; Woelkerling 1988, p. 60, fig. 43), cracked fragments are relatively persistent; whereas, more commonly (e.g. Fig. 31), they slough off, sometimes leaving calcified spurlike extensions flanking the geniculum (Figs 28, 29). Successive genicula in a branch may or may not have such spurlike extensions (Fig. 28).

TETRASPORANGIAL CONCEPTACLE DEVELOPMENT: Conceptacle primordia in temperate Australian specimens of *A. beauvoisii* arise from groups of subepithallial initials. In the youngest stage seen (Fig. 34) the overlying epithallial cells have become uplifted, forming a protective dome above the developing primordia. In the next stage seen (Fig. 35), uplifted epithallial cells are still evident, but these presumably degenerate as the conceptacle matures (Figs 37, 38).

Conceptacle primordia are formed just beneath epithallial cells and apparently continue to divide to form three distinct groups of cells/filaments: (1) central sterile columella-forming filaments; (2) interspersed sterile roof-forming filaments; and (3) sporangial initials (Fig. 35). Central sterile filaments become darkly stained and apparently stop growing at two to three cells long, thereby leaving a gap in the developing roof that ultimately forms the pore canal. As the conceptacle matures these cells elongate to form a central columella. A columella was evident in most mature conceptacles to varying degrees (Figs 37, 38).

At this early stage of development (Fig. 35), roof-forming filaments are up to five cells long with elongate lowermost cells. Uppermost portions of roof filaments remain intact to form the mature conceptacle roof and pore canal. The lowermost cells continue to elongate and largely degenerate to form the conceptacle chamber; some lowermost, however, persist in the mature conceptacle, occurring

as elongate filaments still attached to the conceptacle roof (Figs 37, 38).

Early in tetrasporangial conceptacle development (Fig. 35) the conceptacle pore canals are bordered by filaments that grow parallel to the pore canal as well as basal filaments that project laterally toward the canal; large block-shaped cells are also evident terminating roof filaments surrounding the pore canal. Large block-shaped cells are evident in the mature pore (Fig. 36) and are sometimes more easily observed in sections on the periphery of the pore canal. Large block-shaped cells may persist in the mature conceptacle (Fig. 37) or degenerate to form a depression above the pore (Fig. 38). To our knowledge, pore canals are never completely occluded by large block-shaped cells (Fig. 36).

Sporangial initials occur at the periphery of the developing conceptacle and, at this early stage (Fig. 35), are subtended by small stalk cells. Sporangial initials subsequently mature and divide to form tetrasporangia with four zonately arranged tetraspores in the mature conceptacle (Figs 37, 38).

HABITAT AND DISTRIBUTION: During the current study, *A. beauvoisii* was confirmed to occur in southeastern and southern Australia, intertidally in rock pools and to depths of 15 m. Plants have been collected from the NSW/Queensland border (Tweed Heads) southward and westward to Port Fairy, Victoria (on the southern coast). All plants were epilithic, and only tetrasporangial plants were found. Figs 24–27 illustrate the range in growth form for the species, ranging from thin intergenicula (Fig. 26) through to wide intergenicula (Fig. 27). Intermediates between these two extremes were also found (Figs 24, 25). The full geographic range along the temperate Australian coast, however, has not been determined.

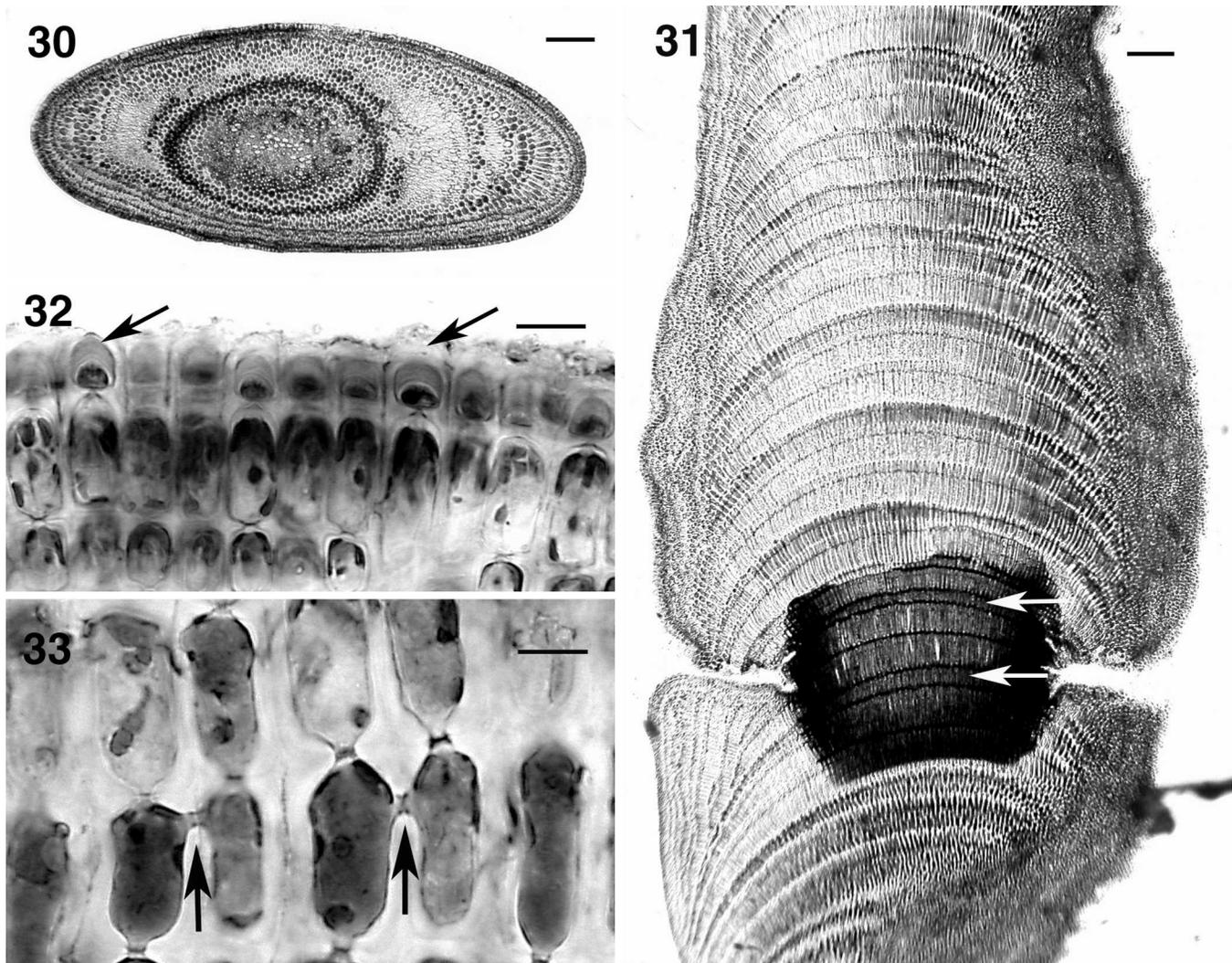
According to Norris & Johansen (1981, p. 12), *A. beauvoisii* is likely the most widespread species of the genus, and reportedly occurs in most tropical and subtropical regions, as well as in the Mediterranean Sea, the southwestern Indian Ocean, South Africa and now southeastern and southern Australia. This reported distribution, however, requires re-evaluation to confirm that the records are based on specimens that have the same tetrasporangial pore canal anatomy as occurs in the type and in southeastern and southern Australian specimens. Further comments occur below in the Discussion.

RELATIONSHIPS TO OTHER SPECIES: The relationships of *A. beauvoisii* to other species found in temperate Australia are considered in the Discussion. Comparisons of *A. beauvoisii* with other species (including the putative heterotypic synonyms listed in Table 3) are difficult to make at present because of the lack of modern data on type specimens (particularly on conceptacle anatomy) and the consequent

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Fig. 28. Portion of a branch with mature intergenicula, where surrounding calcified peripheral-region filaments have either partly disappeared after rupturing, leaving small spurlike extensions (arrow), or have disappeared entirely (arrowhead). (MEL 2066863) Scale bar = 2 mm

Fig. 29. Surface view of intergenicula with numerous, scattered, uniporate conceptacles (arrowheads). Conceptacles occur on both faces of intergenicula. Note both trichotomous (white arrow) and dichotomous (black arrow) branching. (LTB 20078). Scale bar = 500 μm .



Figs 30–33. *Amphiroa beauvoisii*. Vegetative anatomy.

Fig. 30. Transverse section through a compressed intergeniculum showing core-region filaments in cross-sectional view. Arching tiers of cells not observable in this view. Dark-staining ring in core region unexplained. (LTB 20561). Scale bar = 100 μ m.

Fig. 31. Longitudinal section through a young geniculum (dark-staining area) and intergeniculum (lighter area) (compare with surface view in Fig. 28). Note tiers of shorter cells (arrows) separated by tiers of longer cells both in geniculum and flanking intergenicula. Also note that margins of geniculum do not necessarily correspond to ends of cell tiers, and note that calcified peripheral region surrounding geniculum is still largely intact but has begun to crack apart. (LTB 20980). Scale bar = 100 μ m.

Fig. 32. Transverse section through intergeniculum showing rounded epithelial cells (arrows) terminating filaments at thallus surface (MEL 2066863). Scale bar = 10 μ m.

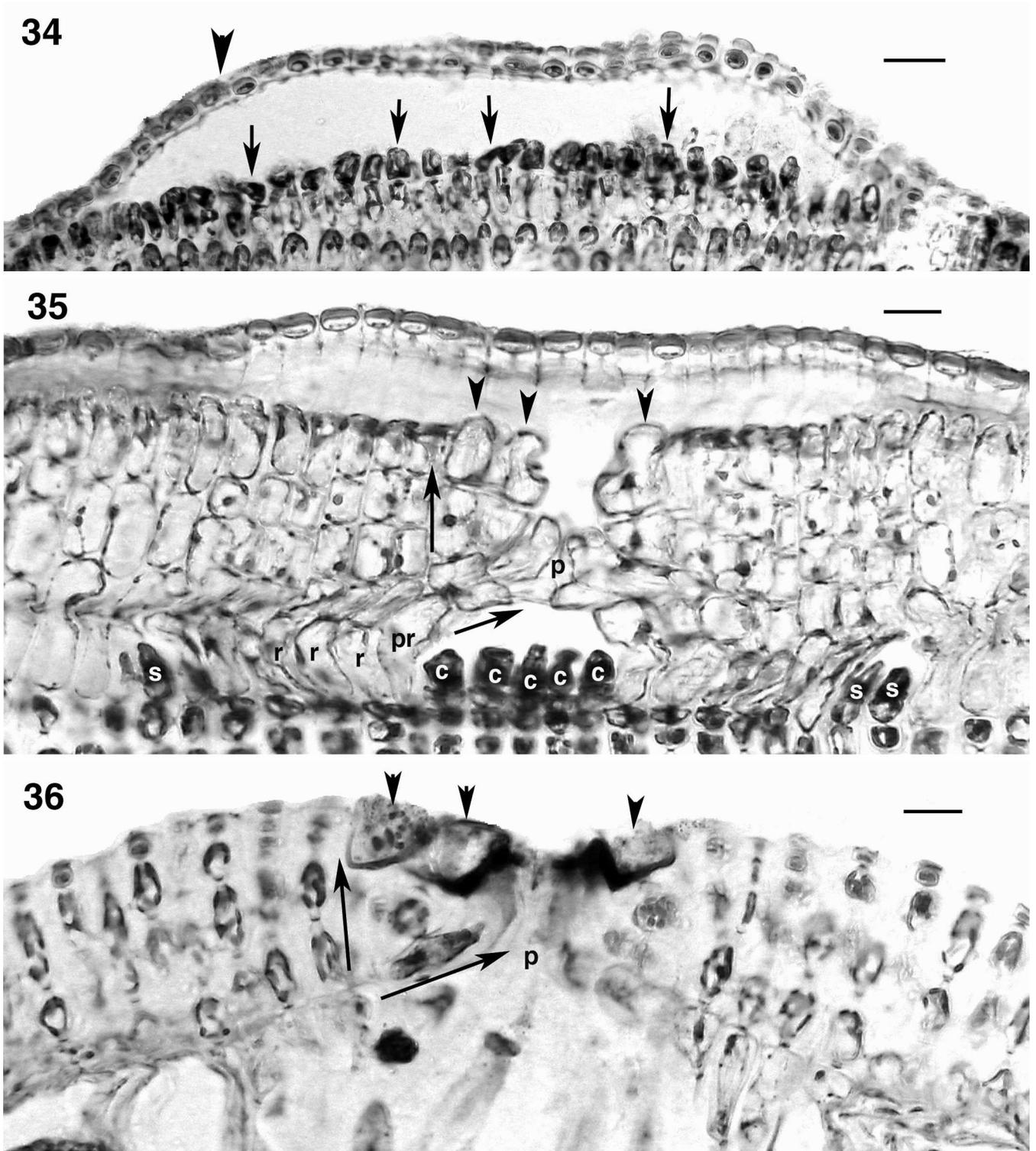
Fig. 33. Transverse section through intergeniculum showing secondary pit-connections (arrows) between cells of adjacent peripheral-region filaments (LTB 20561). Scale bar = 7 μ m.

uncertainty that published identifications of specimens are correct.

Murata and Masaki (1978, p. 406, fig. 7), for example, illustrate large block-shaped cells in the tetrasporangial conceptacle of a specimen identified as *Amphiroa zonata* Yendo. *Amphiroa zonata* has a flattened thallus similar to *A. beauvoisii* (Yoshida & Baba 1998, p. 536, pl. 3–14, figs C, D). Whether these species are concordant, however, requires further investigation including detailed data on type material. If the two are concordant, *A. beauvoisii* is the older name and has nomenclatural priority. Moura & Guimarães (2005, figs 59, 88) also show sections of tetrasporangial conceptacles with large block-shaped cells in specimens identified as *Amphiroa fragilissima* (Linnaeus)

Lamouroux and *Amphiroa van-bosseae* Lemoine respectively. The thallus of both these specimens, however, are terete (Moura & Guimarães 2005, figs 53, 73) and therefore not concordant with the type of *A. beauvoisii*.

Temperate Australian specimens of *A. beauvoisii* are concordant with the type, as demonstrated above. Whether specimens identified as *A. beauvoisii* in some other studies are concordant with the type is uncertain, however, as no definitive data on tetrasporangial conceptacle pore canal anatomy are included. Norris & Johansen (1981, pp. 6–12), for example, provide no data on tetrasporangial conceptacle pore canal anatomy, and thus it is not possible to verify from their paper that all of their material is conspecific with the type and with Australian specimens of *A. beauvoisii*.



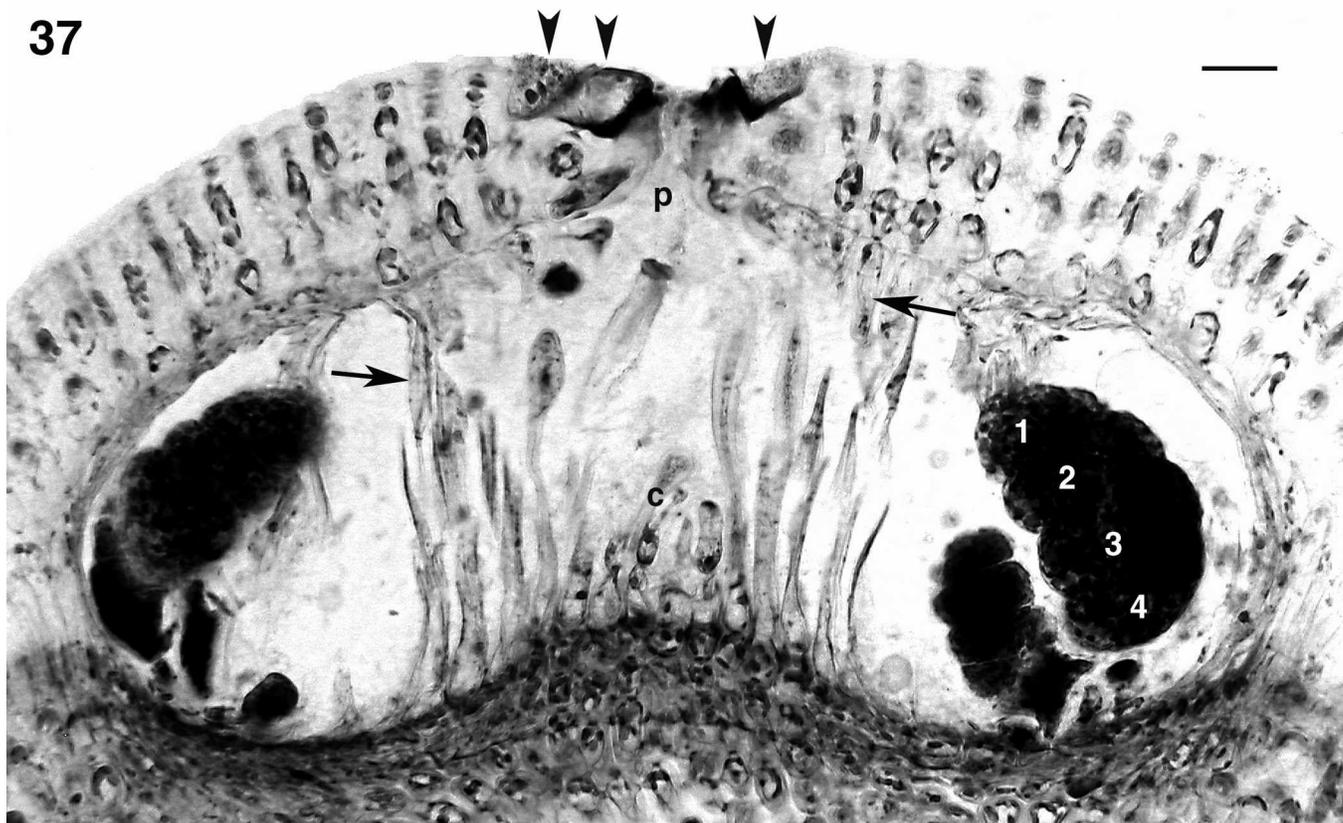
Figs 34–36. *Amphiroa beauvoisii*. Tetrasporangial conceptacle development.

Fig. 34. Section showing very early stage of tetrasporangial conceptacle development. Note conceptacle primordia (arrows) below uplifted epithallial cells (arrowhead) (LTB 20085). Scale bar = 20 μ m.

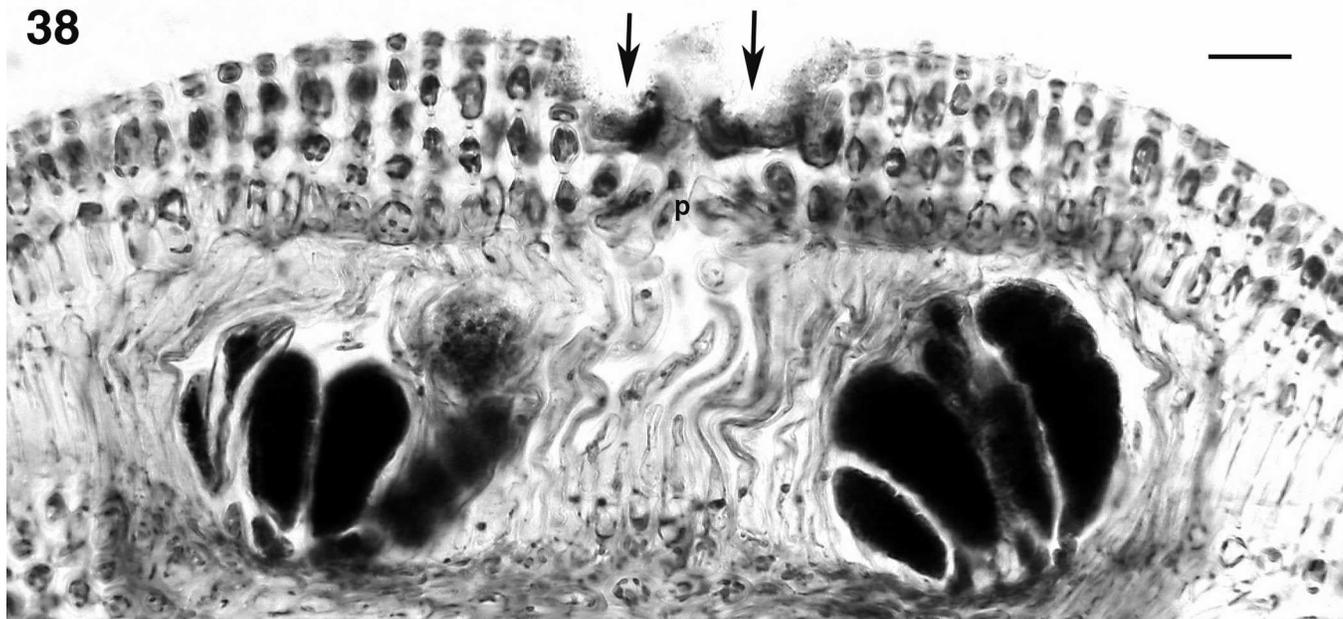
Fig. 35. Later stage showing developing pore canal (p), large block-shaped cells (arrowheads) terminating filaments lining the top of the pore canal and the two directions of growth (arrows) of filaments flanking the pore canal. Also note sporangial initials (s), filaments forming the developing conceptacle roof (r), filaments flanking the developing pore canal (pr) and the developing columella (c) (LTB 20958). Scale bar = 12 μ m.

Fig. 36. Section through a mature pore (p) showing large block-shaped cells (arrowheads) terminating filaments at the top of the pore canal and the two directions of growth (arrows) of filaments flanking the pore canal (p) (LTB 20561). Scale bar = 10 μ m.

37



38



Figs 37–38. *Amphiroa beauvoisii*. Tetrasporangial conceptacle anatomy.

Fig. 37. Section through a mature tetrasporangial conceptacle showing sporangia with four zonately arranged spores (numbered), the pore canal (p), large block-shaped cells (arrowheads), remaining elongate cells of filaments that helped form the conceptacle roof (arrows) and the now degenerating central columella (c). Also note the distinct central hump on the conceptacle chamber floor. (LTB 20561). Scale bar = 20 μ m.

Fig. 38. Section through a mature tetrasporangial conceptacle showing depression (arrows) at the top of the pore canal (p) formed as a result of partial disintegration of large block-shaped cells. Also note the virtual absence of a central hump on the conceptacle chamber floor. (LTB 20522). Scale bar = 20 μ m.

Riosmena-Rodriguez & Siqueiros-Beltrones (1996, p. 141, fig. 11) and Moura & Guimarães (2005, p. 30, fig. 41) show sections of tetrasporangial conceptacles, but these do not include the pore canal region, and no comments on pore canal anatomy are included in the text. The section of Rosas-Alquicira *et al.* (2008, p. 137, fig. 3A) appears to include a pore canal, but its anatomy cannot be properly interpreted. In the absence of clear data on tetrasporangial pore canal anatomy, uncertainty surrounds the accuracy of the species identifications in these studies and precludes meaningful comparisons with Australian specimens and the type.

Mateo-Cid *et al.* [2008, p. 10, fig. 11; p. 15, fig. 21 (as *Amphiroa mexicana* W.R. Taylor); p. 18, fig. 25], on the other hand, included several illustrations of tetrasporangial conceptacle pore canals in Mexican specimens they identified as *A. beauvoisii*. Unfortunately, however, these specimens are incorrectly identified because the tetrasporangial pore canal anatomy differs from that in the type of *A. beauvoisii*. Further comments on the above are included in the Discussion.

Amphiroa gracilis W.H. Harvey (1855, p. 547)

Figs 39–53

SYNOPTIC DESCRIPTION: Temperate Australian plants epilithic; attached ventrally to substrate by a calcified, crustose, nongeniculate base and producing branched erect axes up to 100 mm long that consist of alternating calcified segments (intergenicula) and secondarily decalcified segments (genicula). Branching dichotomous to clustered, with 2–8 (–15) branches arising from most intergenicula (Figs 41, 45, 46); all intergenicula terete, up to 6 mm long and mostly 300–500 µm in diameter.

Erect axes monomerous, consisting throughout of a single continuous system of branched, laterally coherent filaments; in median longitudinal section (Figs 42, 48); axes of intergenicula and genicula with a broad uninterrupted central core (medullary) region in which filaments are oriented more or less parallel to the branch surface, passing in both intergenicula and genicula into a narrower peripheral (cortical) region in which portions of core filaments or their derivatives bend outward to become more or less diagonally or perpendicularly oriented to the branch surface. Cells of adjacent filaments in core region mostly 9–16 µm in diameter, aligned in two to eight arching tiers of longer cells (35–90 µm long) followed by a single arching tier of shorter cells (10–45 µm long). Cells of adjacent filaments in peripheral region not aligned in arching tiers, mostly 6–11 µm in diameter and 8–16 µm long; peripheral portions of filaments terminating at the thallus surface in epithallial cells 6–11 µm in diameter and 3.0–4.5 µm long and with rounded or flattened outer walls (Fig. 53). Cells of adjacent filaments linked by secondary pit connections (Fig. 50); cell fusions absent.

Genicula formed behind branch apices as a consequence of secondary decalcification of short segments of axes, including both core- and peripheral-region filaments. Mature genicula (as seen in median longitudinal section) composed of 10 or more successive arching tiers of transformed, thicker-walled (and more darkly staining) core-region cells (Figs 42, 48) with two to four (to seven)

tiers of longer cells followed by a single tier of shorter cells, and of associated peripheral-region filaments; transitions from calcified intergenicula to decalcified genicula occurring within single tiers of cells or between successive cells of tiers. Core-region cells and peripheral-region cells in genicula similar in size to those in intergenicula; peripheral-region surface commonly with small cracks or chinks (Figs 42, 48).

Tetrasporangial conceptacles uniporate, formed in peripheral regions of intergenicula, scattered over the surface of intergenicula (Fig. 51) and protruding above surrounding thallus surface. Conceptacle pore canals flanked by filaments that project laterally toward the canal (Figs 44, 53); rings of large block-shaped cells absent. Mature roof filaments above chamber mostly four to six cells long (including epithallial cells).

Tetrasporangia formed peripheral to a central region with sterile, elongate, more or less degenerate cells including a columella (Figs 43, 52); conceptacle chamber floor more or less flat. Each mature sporangium 35–55 µm in diameter and 70–110 µm long, containing four zonately arranged tetraspores. Bisporangia not seen. Mature conceptacle chambers 345–355 µm in diameter and 70–100 µm high.

Gametangial and carposporangial plants unknown.

PROTOLOGUE: W.H. Harvey (1855, p. 547).

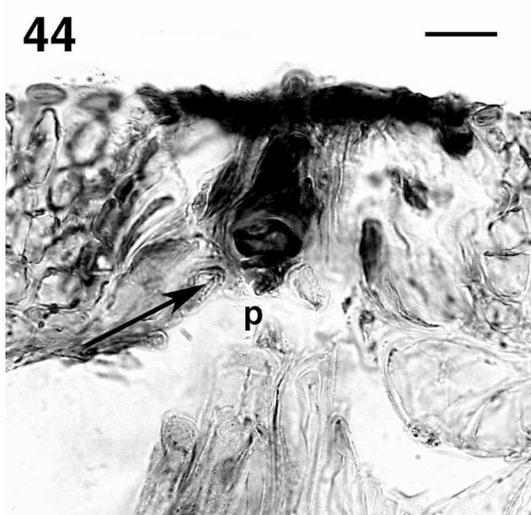
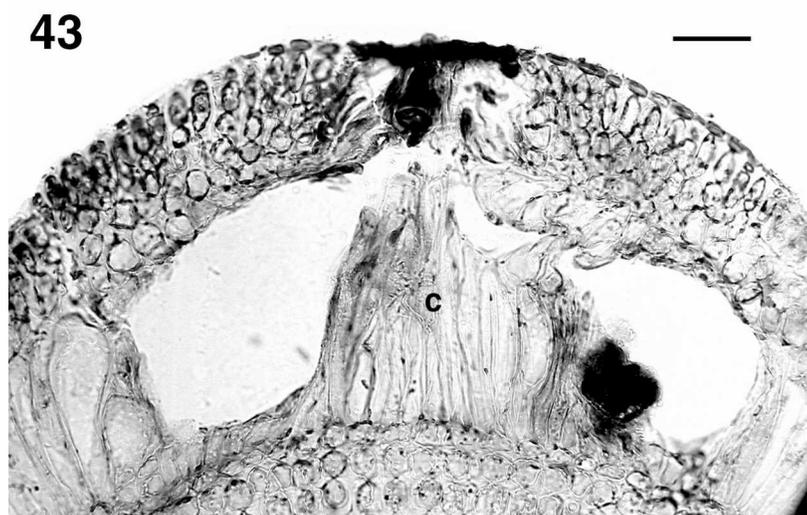
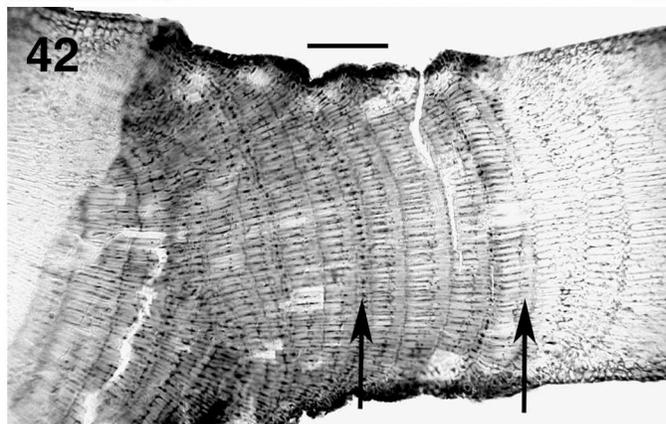
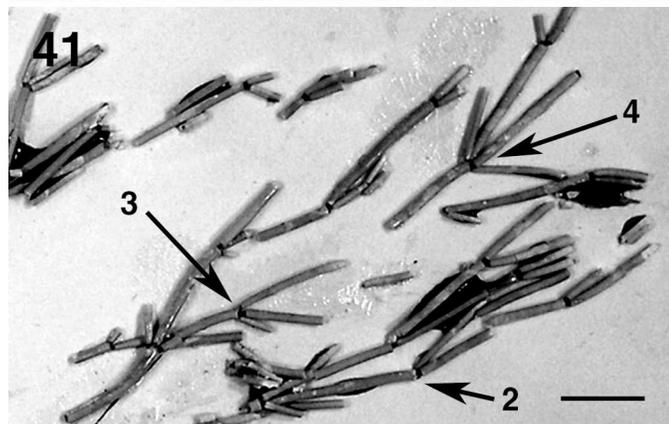
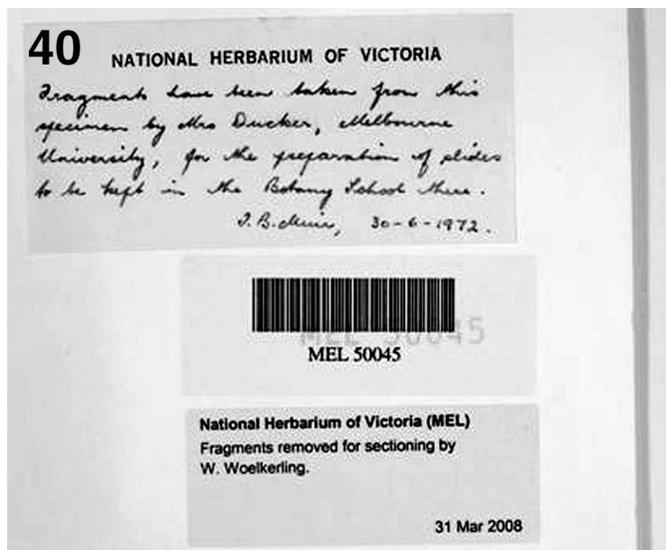
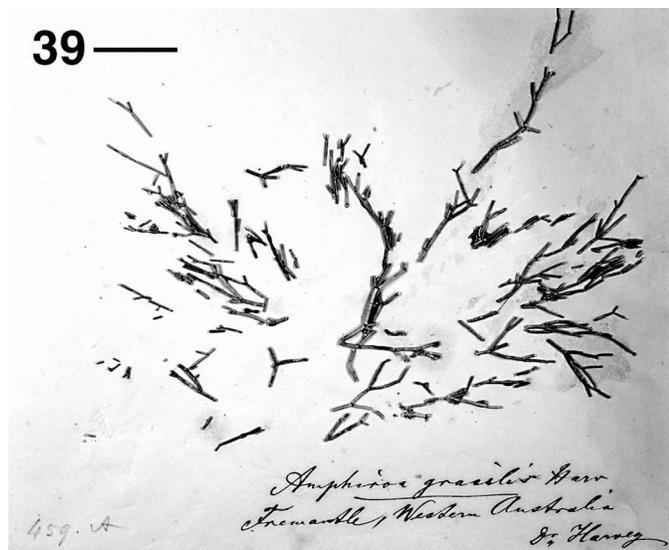
ETYMOLOGY: *gracilis*, from the Latin, meaning thin or slender; probably referring to the slender nature of the intergenicula. Harvey (1855) did not explain the etymology.

SYNONYMS: *Metagoniolithon gracile* (W.H. Harvey) Yendo (1905, p. 12) is the only known homotypic synonym. No heterotypic synonyms have been identified.

LECTOTYPE: TCD, Harvey ‘Trav. Set. 218’; designated by Womersley & Johansen (1996, p. 288). Type locality: Rottneest Island, Western Australia. Lectotype not seen during present study but said by Womersley & Johansen (1996, p. 288) to be in fragments.

SPECIMENS EXAMINED: **Western Australia:** Freemantle (*W.H. Harvey*, no date, MEL 50045 = specimen 459A of the exsiccata *Australian Algae* distributed by Harvey in 1857). Freemantle (*W.H. Harvey*, no date, NSW 711489 = specimen 459A of the exsiccata *Duplicate Australian Algae* distributed by Harvey in 1857). Freemantle (*W.H. Harvey*, no date, NSW 712049 = specimen 459A of the exsiccata *Duplicate Australian Algae* distributed by Harvey in 1857). Rottneest Island, Radar reef (*Woelkerling*, 9.ii.1978, LTB 10910).

Harvey’s sets of *Duplicate Australian Algae* were accompanied by a printed list entitled LIST OF DR. HARVEY’S DUPLICATE AUSTRALIAN ALGAE that included 601 numbered specimens. Many of these specimens, and the full list of species, can be viewed at www.aussiealgae.org. Each actual specimen sheet bears a number followed by a letter denoting a locality. Harvey’s key to the localities is reproduced in Ducker (1988, p. 364). Ducker (1988) also contains Harvey’s extensive correspondence concerning the trip on which he collected the specimens and a reproduced copy (Ducker 1988, pp 362, 363) of the “Subscription Prospectus of Specimens of Australian Algae” sent out by Harvey before his trip.



Figs 39–44. *Amphiroa gracilis*. Specimen identified by W.H. Harvey (MEL 50045-Harvey 459A).

Fig. 39. Fragmented specimen identified by W.H. Harvey in MEL. Note Harvey’s annotation 459A (lower left in pencil) signifying specimen number and collection locality for his sets of *Duplicate Australian Algae*. Information at lower right also written by W.H. Harvey. Scale bar = 20 mm.

Fig. 40. Labels accompanying Harvey’s specimen in MEL. Upper label written by Doris Sinkora, who curated the algae at MEL from the early 1970s until her retirement in 1988.

Fig. 41. Fragments of W.H. Harvey’s specimen showing dichotomous (arrow 2), trichotomous (arrow 3) and quadrachotomous (arrow 4) branching. All intergenicula are cylindrical. Scale bar = 5 mm.

Fig. 42. Longitudinal section through a geniculum that consists both of decalcified core-region filaments and decalcified peripheral-region filaments. Note single tier of shorter cells (arrows) separated by tiers of longer cells. Scale bar = 100 µm.

The Harvey specimens of *A. gracilis* cited above are all labelled with the locality name Freemantle and have the locality letter "A" written after the number 459. In Harvey's printed locality list, however, locality "A" is listed as 'the neighbourhood of Freemantle, Western Australia', which almost certainly also encompasses specimens collected on Harvey's visits to Garden Island and Rottneest Island (see Harvey 1855 for details) and specimens from Swan River (see Womersley & Johansen 1996, p. 288). No dates occur on the specimens, and it is entirely possible that various specimens numbered 459 were collected on different dates from different localities in the general neighbourhood of Freemantle. None of the specimens cited above can be considered isotypes (as suggested by Ducker 1979a, p. 96) because there is no evidence that they are true duplicates (see ICBN Art. 8.3, footnote) of the lectotype designated by Womersley & Johansen (1996, p. 288), which is numbered 218 (see Harvey 1855, p. 534, 547) and is labelled 'Rottneest Island'.

Further information on Harvey's sets of *Duplicate Australian Algae* appears in Anonymous (1857), Sayre (1969, p. 77), Ross (1976), Blackler (1977), Ducker (1977, 1988), and May (1977) and at www.aussiealgae.org.

SPECIMEN IDENTIFIED BY HARVEY: All features evident in Harvey's material of *A. gracilis* (Figs 39–44) are concordant with those in recently collected material from Rottneest Island, Western Australia (Figs 45–53).

The Harvey specimen in MEL (Figs 39, 40) is fragmented, consisting of several broken and incomplete segments, some with two to four branches arising from a single geniculum (Fig. 41). The lectotype (not seen) is similarly in fragments (Womersley & Johansen 1996, p. 288). All intergenicula in Harvey's specimen in MEL are terete.

The single geniculum sectioned (Fig. 42) included intact core-region and peripheral-region filaments. Cells or adjacent core-region filaments are arranged in arching tiers with two to four longer tiers of cells followed by one shorter tier. The arching tiers occupy most of the diameter of the geniculum; the peripheral region consists only of the two to four outward-curving terminal cells of filaments.

Several conceptacles protruding slightly above the surrounding intergenicular surface remain on the Harvey specimen in MEL. The single conceptacle examined (Figs 43, 44) contained the remains of a central columella and the remnants of what is presumed to be a tetrasporangium. The conceptacle roof consists mostly of four to five layers of cells (Fig. 43). The pore canal (Fig. 44) is bordered by cells that project laterally toward the canal; rings of large block-shaped cells are not present. The pore canal appears occluded by what are probably remnants of a tetrasporangium. The conceptacle chamber measured 355 µm in diameter and 100 µm high.

RECENTLY COLLECTED MATERIAL: Data on the more recently collected specimen illustrated in Figs 45–53 are incorporated into the species description. Branching (Figs 45, 46, 49) occurs mostly in clusters, commonly with six or more branches arising from a single intergeniculum. Some branches remain short, consisting of only one intergeniculum; whereas, others produce more intergenicula and further branches. All intergenicula are terete in transverse section (Fig. 47). Gencula (Fig. 48) consist of secondarily decalcified segments of axes and include both core-region filaments and peripheral-region filaments. Cells of adjacent filaments are linked by secondary pit connections (Fig. 50).

Tetrasporangial conceptacles (Figs 51–53) are scattered over the intergenicula and protrude slightly above the surrounding thallus surface (Fig. 51). Within conceptacle chambers (Fig. 52), tetrasporangia occur peripheral to a columella; sometimes remains of filaments that contributed to roof formation also persist. No distinct central hump was observed on the chamber floor.

Tetrasporangial conceptacle roofs (Fig. 52) are mostly four- to six-cells thick above the chamber, and the pore canals are flanked only by filaments that project laterally toward the canal (Fig. 53); rings of large block-shaped cells do not occur.

HABITAT AND DISTRIBUTION: During the current study, *A. gracilis* was confirmed to occur around Freemantle and at Rottneest Island, Western Australia on rock at depths of 1–3 m. According to Womersley & Johansen (1996, p. 288), *A. gracilis* grows in outer reef pools and to depths of at least 5 m, and it is known from Kalbarri, Western Australia to Troubridge Hill, South Australia. We are unaware of any published records outside this region.

RELATIONSHIPS TO OTHER SPECIES: The relationships of *A. gracilis* to other species found in temperate Australia are outlined in the Discussion.

Only limited comparisons of *A. gracilis* with other species are possible at present because of the lack of modern data on type specimens (particularly on conceptacle anatomy) and the consequent uncertainty that published identifications of specimens are correct. According to Johansen (1968, 1969), *A. ephedraea* also consists of terete intergenicula and has gencula composed both of core- and peripheral-region filaments, and according to Moura & Guimarães (2005), *A. vanbosseae* also possesses these characters. The types of both species, however, need to be studied in a modern context to confirm that they also possess these features. Clustered branching of the sort reported here for *A. gracilis* is not reported for *A. ephedraea* or *A. vanbosseae*; in the protologue of *A. ephedraea*, Lamarck (1815, p. 238, as *Corallina*) describes the branching as dichotomous, whereas in the protologue of

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Fig. 43. Section through a tetrasporangial conceptacle with remains of a columella (c) and remains of a sporangium on the right. Scale bar = 35 µm.

Fig. 44. Enlarged section through tetrasporangial conceptacle pore canal (p) region showing single direction of filament growth (arrow) flanking the pore canal and the absence of large block-shaped cells like those (Figs 37, 38) found in *A. beauvoisii*. Pore canal is occluded by probable remains of a sporangium. Scale bar = 15 µm.

A. vanbosseae, Lemoine (1930, p. 73) describes the branching as very irregular. Thus the present limited evidence suggests that the three taxa seem specifically distinct from one another on the basis of differences in branching.

Because branches in *A. gracilis* commonly occur in clusters of three or more, Yendo (1905, p. 12) referred the species to *Metagoniolithon*. In *A. gracilis* and all other species of *Amphiroa*, however, cells of adjacent filaments are linked by secondary pit connections and genicula include one or more tiers of arching cells. By contrast, in all species of *Metagoniolithon*, cells of adjacent filaments are linked by cell fusions and genicula are composed entirely of untiered filaments. As noted by Harvey *et al.* (2003, p. 992, fig. 2; p. 994, table 3), these morphological differences taken together with available molecular evidence support placement of the two genera in different subfamilies of the Corallinaceae: *Amphiroa* in the Lithophylloideae and *Metagoniolithon* in the Metagoniolithonoideae.

***Amphiroa klochkovana* sp. nov.**

Figs 54–63

Amphiroa klochkovana, characteribus *Amphiroae* sed e speciebus alteris combinatione characterum sequentium differt: genicula e filamentis areae centralis atque filamentis areae peripheralis constata, parietibus cellularum non calcificatis; ramificatio dichotoma vel fasciculata, ramis usque ad 6 ex eodem geniculo orientibus; intergenicula infera plerumque complanata sed intergenicula supera pro parte maxima teretia; poricanales conceptaculi tetrasporangialis per filamenta, quae ad canalem lateraliter projecta, omnino limitati, filamentis cellulas magnas cuboidales carentibus.

Amphiroa klochkovana, with the characteristics of *Amphiroa*; differing from other species in having the following combination of features: genicula composed both of decalcified core-region filaments and decalcified peripheral-region filaments; branching dichotomous to clustered with up to six branches arising from the same geniculum; most lower intergenicula flattened but most upper intergenicula terete; and tetrasporangial conceptacle pore canals bordered entirely by filaments that project laterally toward the canal and that lack large block-shaped cells.

The diagnostic characteristics of *Amphiroa* and of the higher taxa to which it belongs are given in Table 1.

SYNOPTIC DESCRIPTION: Temperate Australian plants epilithic; attached ventrally to substrate by a calcified, crustose, nongeniculate base and producing branched erect axes up to 145 mm long that consist of alternating calcified segments (intergenicula) and secondarily decalcified segments (genicula). Branching dichotomous to clustered, with two to four (to six) branches arising from most intergenicula (Figs 54, 55); most lower intergenicula compressed to flattened (Figs 54, 56) but most upper intergenicula more or less terete (cylindrical) (Figs 54, 57); changes from compressed or flattened intergenicula to terete intergenicula usually abrupt. Compressed to flattened intergenicula mostly 7–15 mm long, mostly 0.8–4.0 mm wide, and 600–1300 μm thick; terete intergenicula mostly 5.5–10 mm long and 500–900 μm in diameter.

Erect axes monomerous, consisting throughout of a single continuous system of branched, laterally coherent filaments; in median longitudinal section (Figs 58, 59); axes of intergenicula and genicula with a broad uninterrupted central core (medullary) region in which filaments are oriented more or less parallel to the branch surface, passing in both intergenicula and genicula into a narrower peripheral (cortical) region in which portions of core filaments or their derivatives bend outward to become more or less diagonally or perpendicularly oriented to the branch surface. Cells of adjacent filaments in core region mostly 8–14 μm in diameter, aligned in two to eight arching tiers of longer cells (35–90 μm long) followed by a single arching tier of shorter cells (10–30 μm long). Cells of adjacent filaments in peripheral region not generally aligned in arching tiers, mostly 8–14 μm in diameter and 10–16 μm long; peripheral portions of filaments terminating at the thallus surface in epithallial cells 6–10 μm in diameter and 5–7 μm long and with rounded or flattened outer walls (Fig. 60). Cells of adjacent filaments linked by secondary pit connections (Fig. 60); cell fusions absent.

Genicula formed behind branch apices as a consequence of secondary decalcification of short segments of axes, including both core- and peripheral-region filaments. Mature genicula (as seen in median longitudinal section) usually composed of 10 or more successive arching tiers of transformed, thicker-walled (and more darkly staining) core-region cells (Figs 58, 59) with two to eight tiers of longer cells followed by a single tier of shorter cells, and of associated peripheral-region filaments; transitions from calcified intergenicula to decalcified genicula occurring within single tiers of cells or between successive cells of tiers. Core-region cells and peripheral-region cells in genicula similar in size to those in intergenicula; peripheral-region surface commonly with small cracks or chinks (Fig. 58).

Tetrasporangial conceptacles uniporate, formed in peripheral regions of intergenicula; scattered over the surface of both compressed to flattened and terete intergenicula (Fig. 61) and protruding above surrounding thallus surface (Fig. 61). Conceptacle pore canals flanked by filaments that project laterally toward the canal (Fig. 63); rings of large block-shaped cells absent. Mature roof filaments above chamber mostly four to five cells long (including epithallial cells).

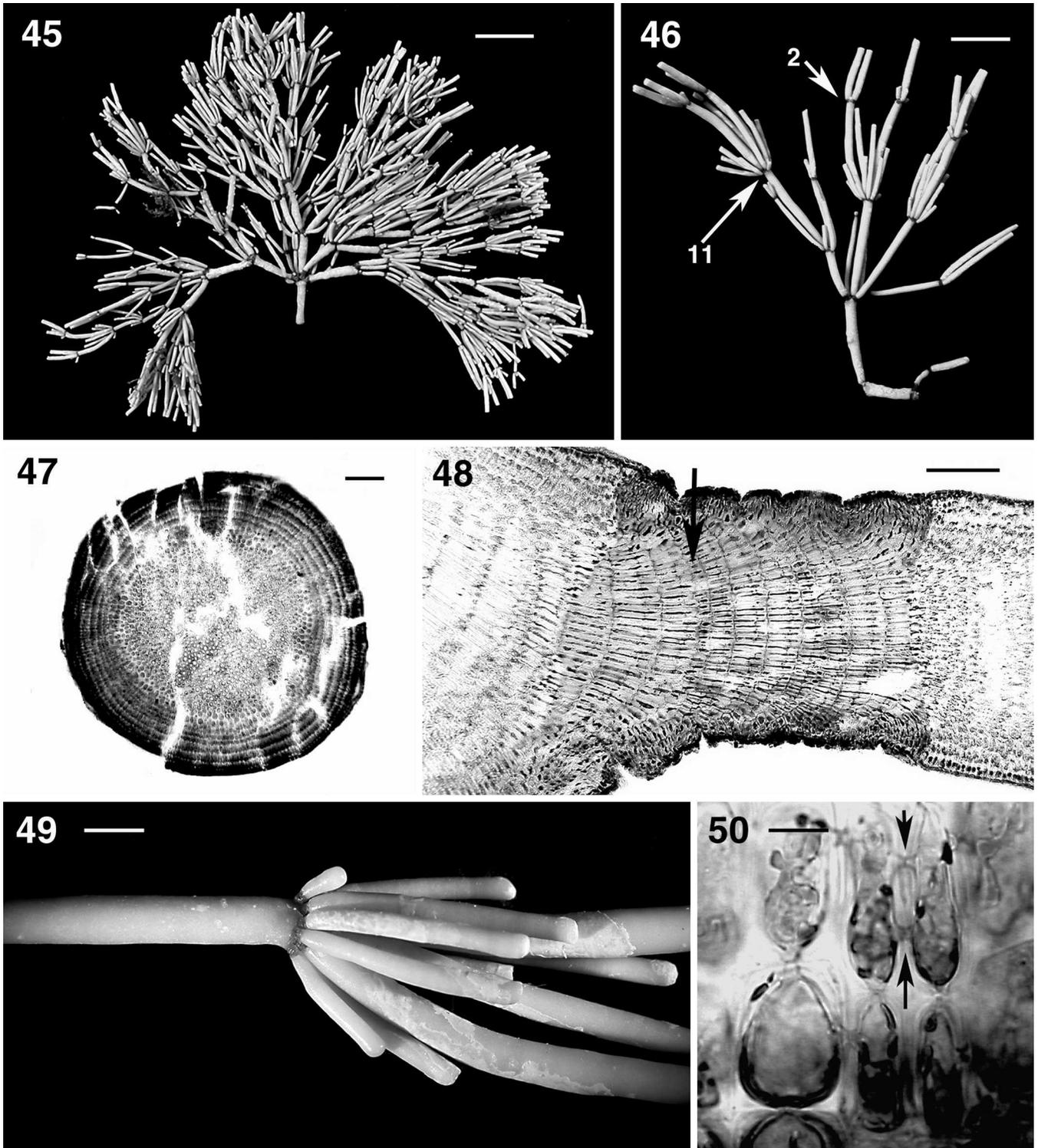
Tetrasporangia formed peripheral to a central region with sterile, elongate, more or less degenerate cells including a columella (Fig. 62); conceptacle chamber floor more or less flat (Fig. 62). Each mature sporangium 55–80 μm in diameter and 90–140 μm long, containing four zonately arranged tetraspores. Bisporangia not seen. Mature conceptacle chambers 370–520 μm in diameter and 110–120 μm high.

Gametangial and carposporangial plants unknown.

ETYMOLOGY: The specific epithet honours the Russian phycologist Nina Klochkova for her substantial interest in and contributions to our understanding of coralline red algae occurring in Russian waters. In translation, N.G. Klochkova (Н.Г. КЛОЧКОВА) also is known as N.G. Kloczcova.

HOLOTYPE: LTB 20485 (Figs 54–63).

TYPE LOCALITY: S.W. Split Solitary Island, Coffs Harbour, New South Wales, Australia (*A. Millar & Hardin*,



Figs 45–50. *Amphiroa gracilis*. Specimen from Rottnest Island, W. Australia (LTB 10910).

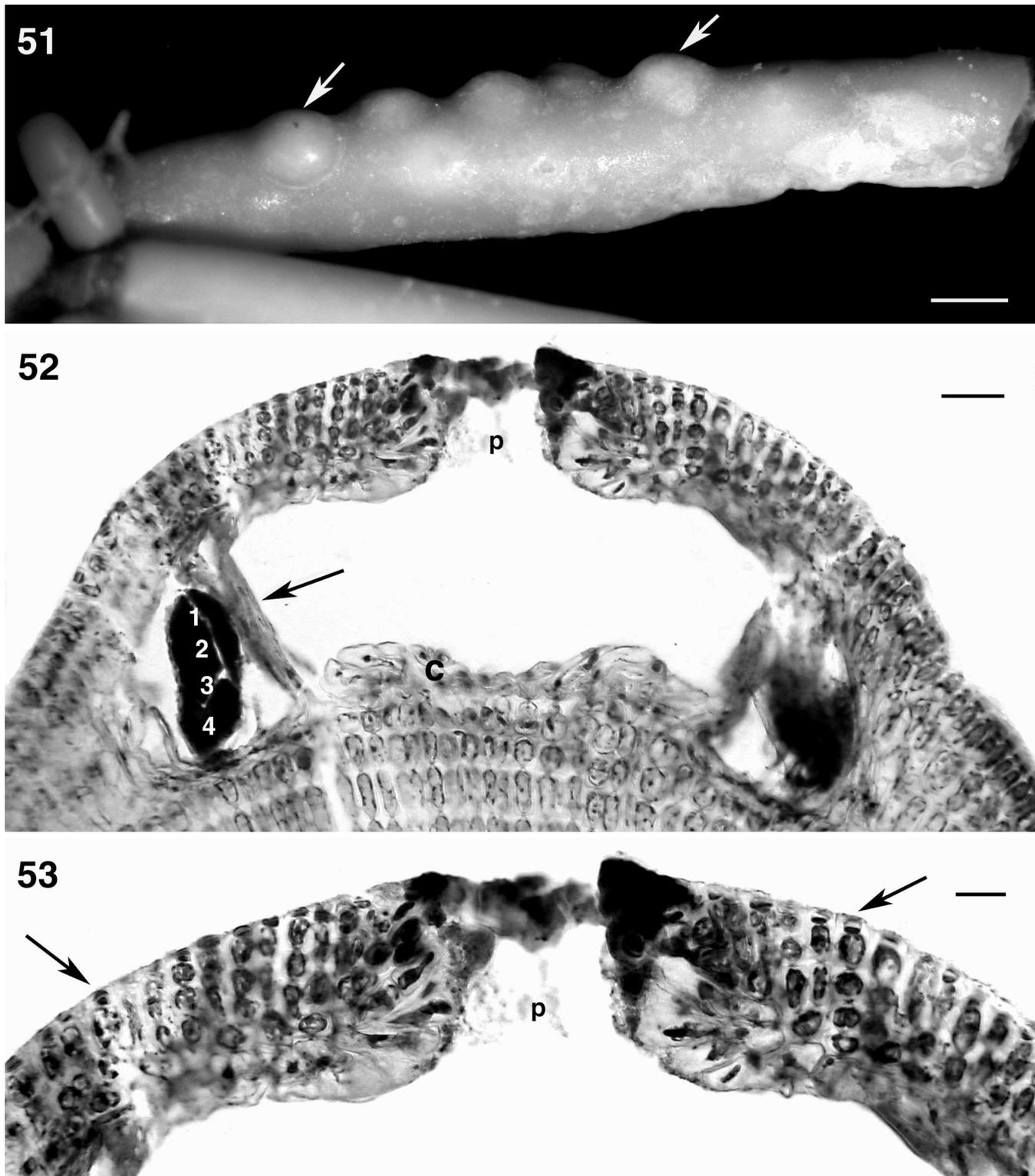
Figs 45, 46. Portions of plants showing cylindrical intergenicula and dichotomous (Fig. 46, arrow 2) to fastigate (Fig. 46, arrow 11) branching. Scale bars: Fig. 45 = 10 mm; Fig. 46 = 5 mm.

Fig. 47. Transverse section through a cylindrical intergeniculum showing core-region filaments in cross-sectional view. Arching tiers of core filament cells not observable in this view, but cells near surface are seen in surface view as a result of filaments curving toward the thallus surface. Scale bar = 100 μ m.

Fig. 48. Longitudinal section through a geniculum that consists both of decalcified core-region filaments and peripheral-region filaments. Note single tier of shorter cells (arrow) separated by tiers of longer cells. Scale bar = 100 μ m.

Fig. 49. Surface view of geniculum from which 12 branches originate. Scale bar = 1 mm.

Fig. 50. Transverse section through intergeniculum showing secondary pit connections (arrows) between cells of adjacent peripheral-region filaments. Scale bar = 8 μ m.

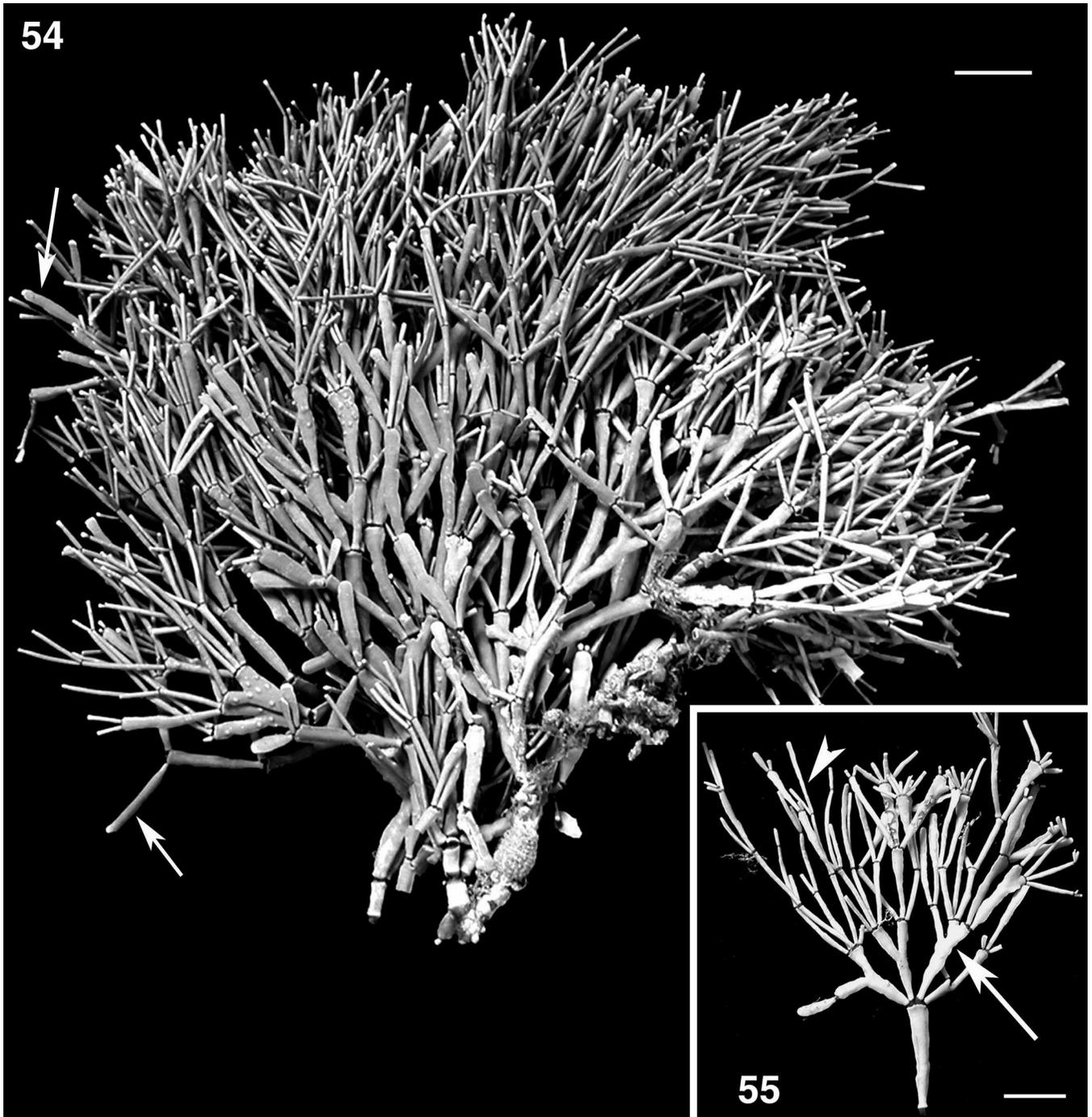


Figs 51–53. *Amphiroa gracilis*. Specimen from Rottneest Island, W. Australia (LTB 10910).

Fig. 51. Surface view of intergenicula with scattered, uniporate conceptacles (arrows). Scale bar = 500 μ m.

Fig. 52. Section through a tetrasporangial conceptacle showing sporangia with four zonately arranged spores (numbered), remnant elongate cells of filaments (arrow) that helped form the conceptacle roof, the pore canal (p) and remnants of a central columella (c). Scale bar = 30 μ m.

Fig. 53. Enlarged section through tetrasporangial conceptacle pore canal (p) region. Note that all flanking filaments are projecting laterally toward the canal. Also note the absence of large block-shaped cells like those (Fig. 36) found in *A. beauvoisii*. Mucilage is visible at top of pore canal. Also note epithelial cells (arrows) with rounded or flattened outer walls. Scale bar = 10 μ m.



Figs 54–55. *Amphiroa klochkovana*. Holotype morphology. (LTB 20485).

Fig. 54. Habit photo of plant in holotype collection. Note occasional compressed intergenicula (arrows) toward the tips of the branches. Scale bar = 10 mm.

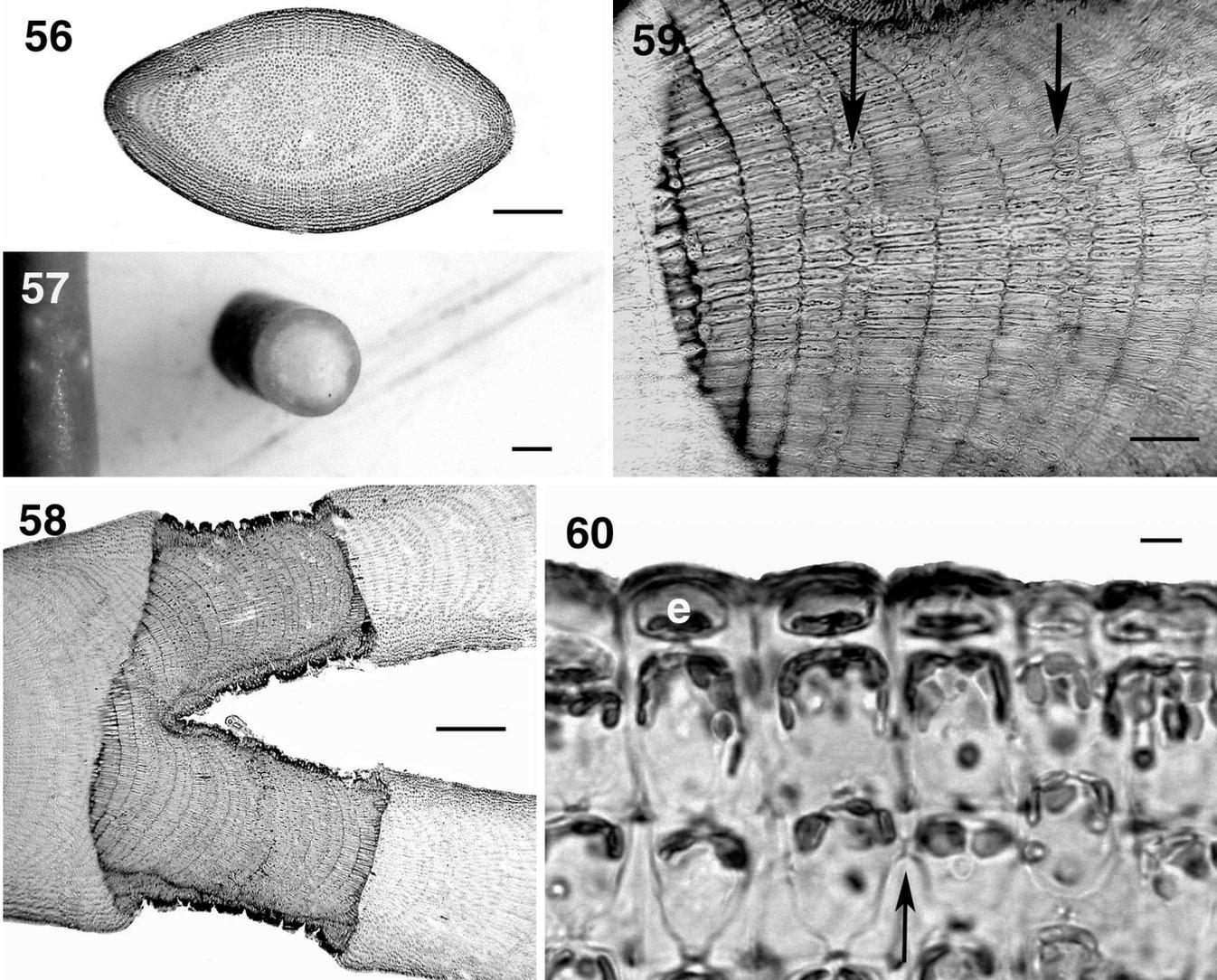
Fig. 55. Portion of a branch axis showing fascicles of branches arising from single intergenicula. Note both compressed (arrow) and terete (arrowhead) intergenicula. Scale bar = 10 mm.

20.vi.1996). Holotype designated here. The holotype specimen includes several individuals in addition to those depicted in Figs 54 and 55; this is in accord with ICBN Art. 8.1 & 8.2.

ADDITIONAL SPECIMENS EXAMINED: **New South Wales:** Coffs Harbour – Split Solitary Island (*A. Millar & R. Millar*, 23.ii.1989, NSW 289249). Coffs Harbour – Split

Solitary Island (*A. Millar & Hardin*, 14.viii.1996, LTB 20637). Sydney – Collaroy (*Lucas*, May 1922, NSW 766737). Sydney – near Narrabeen (*Lucas*, May 1909, NSW 766735)

MORPHOLOGY AND ANATOMY: Features of the holotype are depicted in Figs 54–63. Changes from compressed or flattened intergenicula to terete intergenicula in *A. kloch-*



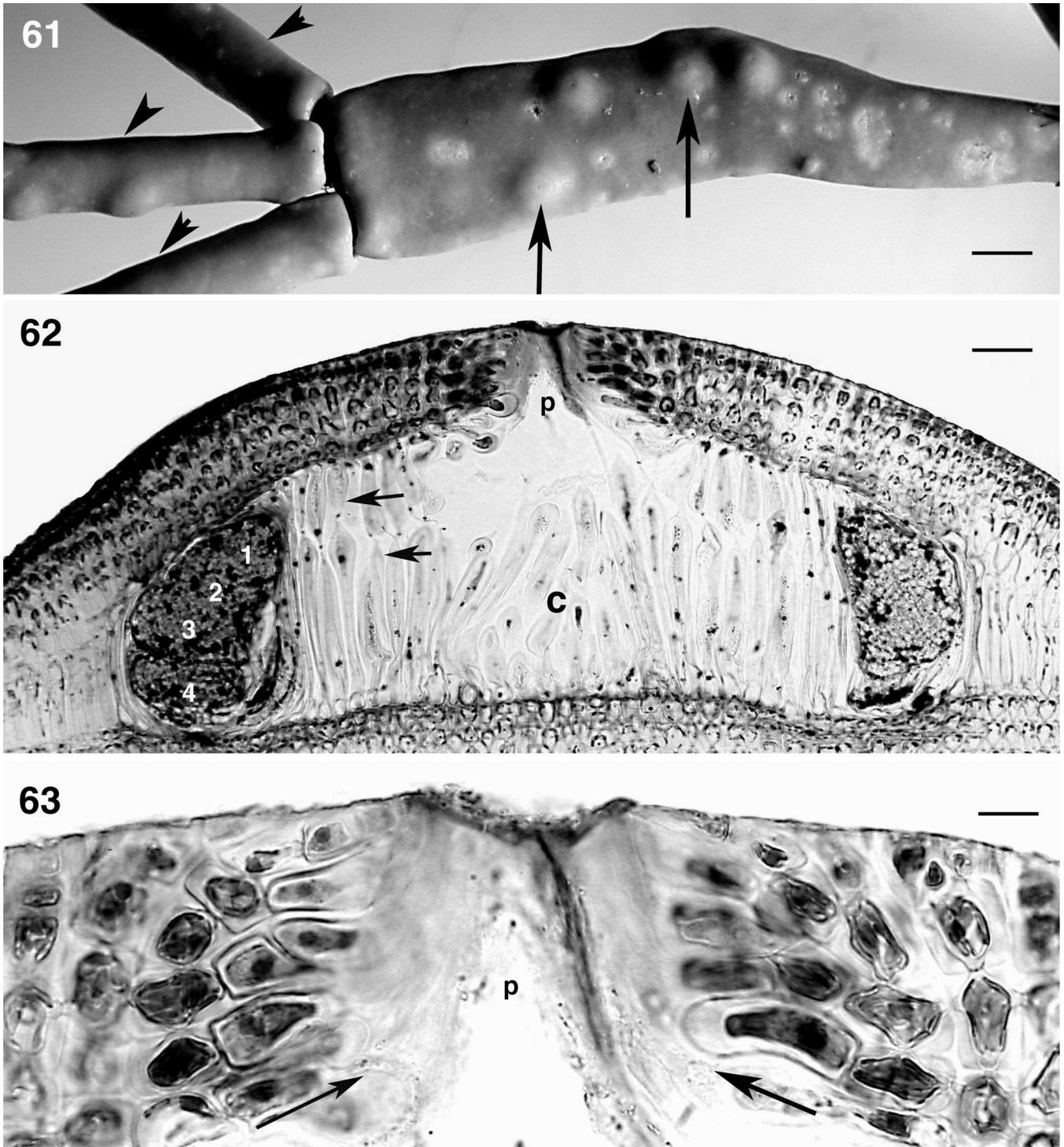
Figs 56–60. *Amphiroa klochkovana*. Vegetative anatomy of holotype. (LTB 20485).
Fig. 56. Transverse section through a compressed intergeniculum showing core-region filaments in cross-sectional view. Arching tiers of cells not observable in this view. Scale bar = 210 μ m.
Fig. 57. Transverse view of a cylindrical intergeniculum. Scale bar = 200 μ m.
Fig. 58. Longitudinal section through a geniculum (dark staining area) and intergeniculum (lighter area). Note that calcified peripheral region surrounding geniculum is still largely intact but has begun to crack apart. Scale bar = 45 μ m.
Fig. 59. Closer view of a geniculum showing a single tier of shorter cells (arrows) separated by tiers of longer cells. Note that ends of geniculum do not necessarily correspond to ends of cell tiers. Scale bar = 200 μ m.
Fig. 60. Transverse section through intergeniculum showing rounded epithallial cells (e) terminating filaments at thallus surface and secondary pit connection (arrow) between cells of adjacent peripheral-region filaments. Scale bar = 5 μ m.

kovana are abrupt, usually occurring at points of branching. At transition points, terete intergenicula usually arise from flattened intergenicula; the reverse pattern is uncommon. Occasionally, however, an intergeniculum is more or less terete at the lower end and flattened at the upper end (Fig. 54). The predominant form of intergenicula in very young plants is unknown; no such plants were seen.

HABITAT AND DISTRIBUTION: *Amphiroa klochkovana* presently is known only from four localities: two in the Split Solitary Islands off Coffs Harbour and two in the Sydney region. The Split Solitary Islands material was collected at depths of 15–20 m; whereas, the Sydney specimens lack depth information.

RELATIONSHIPS TO OTHER SPECIES: *Amphiroa klochkovana* appears to be unique amongst known species of *Amphiroa* in producing erect branches up to 145 mm long in which (1) most lower intergenicula are compressed to flattened; (2) most upper intergenicula are essentially terete; (3) genicula are composed of both decalcified core-region and decalcified peripheral-region filaments; and (4) up to six branches originate from a single intergeniculum. An extensive search of the literature has failed to find another species with the above combination of characters.

On the basis of anatomical data from modern detailed studies of species of *Amphiroa*, we are aware of four other species in which genicula are composed of both decalcified core-region filaments and decalcified peripheral-region



Figs 61–63. *Amphiroa klochkovana*. Conceptacles in holotype. (LTB 20485).

Fig. 61. Surface view of intergenicula with scattered, uniporate conceptacles. Conceptacles (arrows) occur on both faces of compressed intergenicula as well as on cylindrical (terete) intergenicula. Note single compressed intergeniculum bearing three more or less cylindrical intergenicula (arrowheads). Scale bar = 650 μm .

Fig. 62. Section through a tetrasporangial conceptacle showing sporangia with four zonately arranged spores (numbered), remaining elongate cells of filaments (arrows) that helped form the conceptacle roof, the pore canal (p) and a central columella (c) (LTB 20485). Scale bar = 30 μm .

Fig. 63. Enlarged section through a tetrasporangial pore canal (p) region showing single direction of growth (arrows) of filaments flanking the pore canal, and the absence of block-shaped cells like those (Fig. 36) found in *A. beauvoisii* (LTB 20485). Scale bar = 6 μm .

filaments: *A. ephedraea* (Lamarck) Decaisne (according to Johansen 1968, 1969); *A. foliacea* Lamouroux (according to Lee 2008); *A. gracilis* W.H. Harvey (see Womersley & Johansen 1996 and this study); and *A. vanbosseae* Lemoine (according to Moura & Guimarães 2005). *Amphiroa ephedraea*, *A. gracilis*, and *A. vanbosseae*, however, produce only terete intergenicula; whereas, *A. foliacea* produces only flattened intergenicula. None of these species is reported to contain the mixture of terete and flattened intergenicula found in *A. klochkovana*.

Further comparisons with the temperate Australian species *A. gracilis* Harvey, which also produces multiple branches from a single intergeniculum, appear in the Discussion.

DISCUSSION

Comparisons of species

Of the four known temperate Australian species of *Amphiroa*, *A. beauvoisii* and *A. anceps* both have intergenicula that overwhelmingly are compressed to flattened throughout the plant, and both have genicula composed only of secondarily decalcified segments of core-region filaments. By contrast, intergenicula are entirely terete in plants of *A. gracilis* and both terete and compressed in *A. klochkovana*. Genicula of both species are composed both of secondarily decalcified core-region filaments and secondarily decalcified peripheral-region filaments.

Our comparisons of temperate Australian and type specimens of *A. beauvoisii* and *A. anceps* have shown that they cannot be separated at species level by thallus morphology and that there are no taxonomically significant differences in internal vegetative anatomy either. Erect axes of our specimens of both species are composed of compressed intergenicula and are complanately branched in a dichotomous manner with occasional trichotomies. Tetrasporangial conceptacles of both species are scattered over intergenicula and protrude somewhat above the surrounding intergenicular surface.

The two species clearly differ, however, in tetrasporangial conceptacle pore canal anatomy, and these differences are evident in both type material and modern Australian specimens. In *A. beauvoisii* (Figs 22, 23, 35–37), pore canals are bordered by filaments that grow parallel to the pore canal as well as basal filaments that project laterally toward the canal, and the top of the pore canal is bordered by a ring of large block-shaped cells. In *A. anceps* (Figs 6, 14–17), by contrast, all filaments bordering the pore canal project laterally toward the canal, and the top of the pore canal is not bordered by a ring of large block-shaped cells.

Comparisons of gametangial and carposporangial plants of *A. beauvoisii* and *A. anceps* could not be undertaken because such plants are unknown in Australia.

Our studies of *A. klochkovana* and *A. gracilis* have shown that they cannot be separated at species level using characters associated with tetrasporangial conceptacle anatomy. In both species, the conceptacle pore canal is flanked by filaments that project laterally toward the canal, and rings of large block-shaped cells do not occur. Conceptacle roofs are otherwise similar in both species, a

columella (whose presence or absence may not be taxonomically significant) occurs in both species, and all measured characters have overlapping range values.

Although *A. klochkovana* and *A. gracilis* also have the same genicular anatomy, they clearly differ in intergenicular morphology. In *A. klochkovana*, both terete and compressed to flattened intergenicula consistently occur. In upper portions of plants, most intergenicula are terete with only very occasional flattened or compressed intergenicula present. In lower portions of plants, most intergenicula are compressed to flattened and relatively few are terete. In *A. gracilis*, by contrast, all intergenicula are terete. We have not found specimens that could be considered intermediate between the two species. In addition, the two species are widely separated geographically: *A. klochkovana* is not known south of Sydney on the east coast of Australia; whereas, *A. gracilis* is not known east of Troubridge Hill, Yorke Peninsula, South Australia on the south coast of Australia.

Gametangial and carposporangial plants of both *A. klochkovana* and *A. gracilis* are unknown.

Species delimitation in *Amphiroa*: tetrasporangial conceptacle anatomy

The discovery that *A. beauvoisii* and *A. anceps* differ in reproductive anatomy but not necessarily in vegetative morphology or anatomy has flow-on implications concerning specimen identification, reported geogeographic distribution, putative heterotypic synonymy and the diagnostic value of conceptacle anatomy at species level.

First, past identifications of specimens as *A. beauvoisii* or as *A. anceps* need to be reassessed in relation to tetrasporangial conceptacle pore canal anatomy. Because conceptacle anatomy has not been taken into account previously, there are likely to be numerous misidentifications in the literature, not only between *A. beauvoisii* and *A. anceps*, but also between these two and other species.

Norris & Johansen (1981, p. 12) described *A. beauvoisii* as a highly variable species morphologically; whereas, Riosmena-Rodriguez & Siqueiros-Beltrones (1996, p. 140) concluded that external and internal characters vary within a narrow range and the external morphology does not vary between specimens as in other taxa. The overall morphological and anatomical variability of *A. beauvoisii* as a species cannot be determined fully until past identifications of specimens are reassessed. Most published descriptions of *A. beauvoisii* also require reassessment to ensure that the specimens upon which the descriptions are based are correctly identified.

Second, both *A. beauvoisii* (Norris & Johansen 1981, p. 12) and *A. anceps* (Womersley & Bailey 1970, p. 313; Huisman & Walker 1990, p. 411) have been described as widespread in tropical and subtropical (and warm temperate) seas, but because of uncertainties of specimen identification, these biogeographic statements also require reassessment. Nearly all current literature records require verification, including those listed under the species names in the continuously updated electronic resource AlgaeBase (<http://www.algaebase.org>). It is not possible at present, therefore, to provide a reliable statement on the biogeographic distribution of *A. beauvoisii* and *A. anceps*.

Third, the types of all taxa previously treated as heterotypic synonyms of either *A. beauvoisii* or of *A. anceps* require reassessment to determine if tetrasporangial conceptacle pore canal anatomy matches that in *A. beauvoisii* or that in *A. anceps* or whether it differs from both. At least 16 putative heterotypic synonyms of *A. beauvoisii* and five of *A. anceps* are recorded in the literature (Table 3).

Finally, it now seems likely that differences in conceptacle anatomy will become evident for other species within *Amphiroa*, and these differences are likely to have diagnostic value in differentiating other species within the genus. The studies of Woelkerling & Campbell (1992), Keats (1997), and Harvey *et al.* (2005), for example, have shown that differences in tetrasporangial conceptacle pore canal anatomy and conceptacle roof anatomy are diagnostically reliable in differentiating species within *Lithophyllum*, the most biodiverse nongeniculate genus of Lithophylloideae. Results from the present study provide firm evidence that such differences also can be diagnostically reliable in differentiating species within *Amphiroa*, the most biodiverse geniculate genus of Lithophylloideae.

Species delimitation in *Amphiroa*: other characters

Our results suggest that in addition to conceptacle anatomy, differences in genicular anatomy and differences in intergenicular morphology are diagnostically valuable in separating species occurring in temperate Australia. Norris & Johansen (1981), Riosmena-Rodriguez & Siqueros-Beltrones (1996), Dolan (2001) and Moura & Guimarães (2005) also have used differences in genicular anatomy and intergenicular morphology to separate species. Rodriguez & Siqueros-Beltrones (1996, pp. 144–145) and Moura & Guimarães (2005, pp. 51–56) also discuss other characters they found useful for separating species occurring in the Gulf of California and along the coast of Brazil. Their conclusions now need to be tested on other species in other regions, a task beyond the scope of the present project.

Similarly, the diagnostic value of many characters used in species identification keys [e.g. see Taylor (1945, pp. 185–186), Dawson (1953, pp. 134–135), Taylor (1960, p. 403), Womersley and Johansen (1996, p. 285), Stegenga *et al.* (1997, p. 576), Yoshida and Baba (1998, p. 531), Desikachary *et al.* (1998, pp. 58–59), Johansen (in Abbott 1999, p. 177), Littler and Littler (2000, p. 20), John *et al.* (2003, p. 71), Oliviera *et al.* (2005, p. 74)] needs critical reassessment: In most cases, the variability of these characters within and across populations of individuals remains uncertain.

Type specimens and species names

The application of species names to specimens of *Amphiroa* is based much more on tradition than on a detailed knowledge of type specimens. This certainly has been the case for *A. beauvoisii* and *A. anceps*, whose types had not previously been studied in detail in a modern context. The end result of a lack of adequate data on types is a substantial body of published species lists, catalogues, floras, and other studies using names whose correct application remains shrouded in uncertainty. This problem has been recognized as particularly acute for the nongeniculate corallines (see

Woelkerling 1984, pp. 5–18, Woelkerling 1988, p. 1), and it also is a major problem for many geniculate genera, including *Amphiroa*. Until there is a much greater body of knowledge of the morphology and anatomy of type specimens, the application of names to specimens as noted by Woelkerling (1988, p. 3) will continue to lack the nomenclatural foundation essential for stability.

Molecular data

To our knowledge, species delimitation within *Amphiroa* has never been assessed using molecular as well as morphological data, and indeed, extant gene sequence data is not suited for such studies. Molecular data in Genbank (<http://www.ncbi.nlm.nih.gov>) (searched 25.viii.2008) occur for specimens identified as *A. dilatata* Decaisne (AF097876), *A. fragilissima* (Linnaeus) Lamouroux (EF033529, EF033599, U04039 and U60744), *Amphiroa hancockii* W.R. Taylor (AY234233) and *Amphiroa tribulus* (Ellis & Solander) Lamouroux (AY234234). The data for *A. dilatata*, *A. hancockii*, *A. tribulus* and for two collections of *A. fragilissima* (U04039, U60744), however, are unaccompanied by voucher specimens and thus are of no taxonomic value because the identifications cannot be verified. (Voucher specimens associated with published DNA sequences should always be deposited in registered public herbaria to allow further study or verification of published data.) Similarly, the vouchers for the two collections of *A. fragilissima* (U04039, U60744) need to be compared with the type of *A. fragilissima* to confirm correct identification, and as far as we know, the type has not been studied in a modern context.

There is clearly a need for further research to be undertaken where specimens (from type localities and matching the type specimens in all morphological and reproductive details) are analysed for the molecular sequences to help guide the true taxonomic and phylogenetic affinities of *Amphiroa* species.

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