

The neotypification and taxonomic status of *Amphiroa crassa* Lamouroux (Corallinales, Rhodophyta)

William WOELKERLING^{a*}, Adele HARVEY^a & Bruno de REVIERS^b

^a Department of Botany, La Trobe University, Bundoora, Victoria, Australia

^b Département Systématique et évolution, Muséum national d'histoire naturelle,
UMR 7138, CP 39, 57 rue Cuvier, 75231 Paris cedex 05, France

Abstract – A detailed account of the newly designated neotype specimen of *Amphiroa crassa* Lamouroux (Corallinales, Rhodophyta) is presented. Reasons necessitating its neotypification with a specimen remote from the reported type locality (Shark Bay, Western Australia) are outlined, and historical background information is provided. Brief comparisons with the recently typified type species of the genus, *A. tribulus*, and with four other Australian species (*A. anceps*, *A. beauvoisii*, *A. gracilis*, *A. klochkovana*) whose types have been studied in a modern context also are included. *A. crassa* differs from all of these species in that intergenicula produce a collar of untransformed, calcified peripheral region cells that surrounds and partly to largely encloses each geniculum.

Amphiroa / Lithophylloideae / Corallinaceae / Neotypification / Nomenclature

INTRODUCTION

Over 200 specific and infraspecific names have been ascribed to *Amphiroa* (Corallinales, Rhodophyta) since Lamouroux (1812: 186) established the genus. As noted by Harvey *et al.* (2009: 286-287), however, the number of biological species referable to *Amphiroa* as currently circumscribed (see Harvey *et al.*, 2009: 259-260, including Table 1) remains problematic, in part because the diagnostic value of many characters used to delimit and identify species needs critical reassessment, and in part because the type specimens of most species have not been studied in a modern context, thus rendering uncertain the correct application of names to specimens and the associated nomenclatural foundation essential for stability. Moreover, type specimens of a number of species of *Amphiroa* have yet to be formally identified and/or designated, and indeed, the formal typification of the type species of the genus [*Amphiroa tribulus* (Ellis et Solander) Lamouroux], and a detailed study of the type specimen, was only recently published (Woelkerling & Harvey, 2012).

Within the Corallinales (*sensu* Le Gall *et al.*, 2010: 305, Table 1), *Amphiroa* currently is referred to the Corallinaceae (*sensu* Harvey *et al.*, 2003: 993-994, Table 2); the genus includes those species of Corallinaceae possessing

* Corresponding author: W.Woelkerling@latrobe.edu.au

Table 1. Collection data on Australian specimens examined in conjunction with selection of a neotype for *Amphiroa crassa*. Herbarium abbreviations: **AD** = State Herbarium of South Australia, Adelaide, S. Australia; **BRI** = Queensland Herbarium, Brisbane, Qld., Australia; **PERTH** = Western Australian Herbarium, Perth, W. Australia

Queensland: Great Barrier Reef, Hicks Reef (*Dixon* 21.ii.2009, **AD**-A91159; **AD**-A91160; **AD**-A91161; **AD**-A91246 – Lizard Island Expedition). Great Barrier Reef, Yonge Reef (*Gurgel & Dixon* 11.ii.2009, **AD**-88757; **AD**-A88764; **AD**-A88765; **AD**-A88766; **AD**-A88767; **AD**-A88783 – Lizard Island Expedition). Great Barrier Reef, Yonge Reef (*Dixon* 12.ii.2009, **AD**-A90047; **AD**-A90048 – Lizard Island Expedition). Great Barrier Reef, Reef crest halfway between Bird Island and South Island (*Gurgel & Dixon* 8.ii.2009, **AD**-A88890 – Lizard Island Expedition). Great Barrier Reef, Waining Reef (*Gurgel & Dixon* 21.ii.2009, **AD**-A91352; **AD**-A91353; **AD**-A91100 – Lizard Island Expedition). Great Barrier Reef, Day Reef (*Gurgel & Dixon* 13.ii.2009, **AD**-A90084 – Lizard Island Expedition). Great Barrier Reef, Day Reef (*Huisman* 10.iv.2008, **AD**-A88065 – Lizard Island Expedition). Great Barrier Reef, Lizard Island (*Gurgel & Dixon* 23.ii.2009, **AD**-A91234; **AD**-A91235; **AD**-A91236 – Lizard Island Expedition). Great Barrier Reef, Lizard Island (*Huisman* 8.iv.2008, **AD**-A88016; **AD**-A88026 – Lizard Island Expedition). Great Barrier Reef, Lizard Island (*Gurgel & Perkins* 20.iv.2008, **AD**-A88191 – Lizard Island Expedition). Great Barrier Reef, Lizard Island, Day Reef (front north) (*Marklund* ??, **AD**-A89211A). Great Barrier Reef, Broomfield Reef (*Gurgel & Huisman* 15.xi.2009, **AD**-A90840 – Heron Island Expedition). Great Barrier Reef, North Sykes Reef (*Gurgel & Dixon* 11.ix.2008, **AD**-A88738 – Heron Island Expedition). Great Barrier Reef, Sykes Reef (*Gurgel & Huisman* 14.xi.2009, **AD**-A90559A; **AD**-A90559B; **AD**-A90618; **AD**-A90888 – Heron Island Expedition). Great Barrier Reef, North West Island (*Cribb* 18.viii.1968 **BRI**-AQ708173) (**neotype**). Great Barrier Reef, North West Island (*Dixon, Gurgel & Huisman* 31.viii.2008, **AD**-A88411 – Heron Island Expedition). Great Barrier Reef, North West Reef (*Gurgel & Huisman* 17.xi.2009, **AD**-A90666A; **AD**-A90666B; **AD**-A90666C; **AD**-A90743A; **AD**-A90743B; **AD**-A90743C – Heron Island Expedition). Great Barrier Reef, North Heron Reef, First Point (*Fusaro & Smoler* 12.xi.2009, **AD**-A90519 – Heron Island Expedition). Great Barrier Reef, North side of Heron Island, North Point (*Huisman & Dixon* 27.viii.2008, **AD**-A88386 – Heron Island Expedition). Great Barrier Reef, North Wistari Reef (*Gurgel & Huisman* 11.xi.2009, **AD**-A90994 – Heron Island Expedition). Great Barrier Reef, South West Wistari Reef (*Gurgel, Huisman & Dixon* 28.viii.2008, **AD**-A74946; **AD**-A74947 – Heron Island Expedition). Great Barrier Reef, Heron Island (*Cribb* 31.i.1963, **BRI**-AQ708168). Great Barrier Reef, Heron Island (*Cribb* 5.xi.1981, **BRI**-AQ708164). Great Barrier Reef, Heron Island (*Cribb* 4.xi.1975, **BRI**-AQ708166). Great Barrier Reef, Heron Island (*Cribb* 22.ix.1976, **BRI**-AQ708161). Great Barrier Reef, Masthead Island (*Cribb* 2.v.1968, **BRI**-AQ708171). Great Barrier Reef, Masthead Island (*Cribb* 23.v.1998, **BRI**-AQ615334). Great Barrier Reef, Masthead Island (*Cribb* 12.v.1968, **BRI**-AQ708171). Great Barrier Reef, Lady Musgrove Island (*Cribb* 22.vii.1968, **BRI**-AQ708172). Great Barrier Reef, Lady Musgrove Island (*Cribb* 22.vii.1968, **BRI**-AQ708172). Great Barrier Reef, ?? Island (*Cribb* 2.i.1972, **BRI**-AQ708165).

Western Australia: King and Conway Islands (15.87163° S 123.66347° E), north of Cape Leveque, Kimberley, region (*Huisman* 24.x.2011, **PERTH**, *Huisman* collection number 24.10.11.2.2).

secondary pit-connections between cells of adjacent filaments as well as genicula that do not produce dimerous, flange-like branches (see Woelkerling *et al.*, 2002: 370, Table 2 & 372, Table 3 and Harvey *et al.*, 2009: 259-260 for details).

Of the 19 validly and legitimately published names of taxa placed in *Amphiroa* by 1830 [see *Index Nominum Algarum* (<http://ucjeps.berkeley.edu/INA.html>) for continuously updated list], 16 were proposed by Lamarck or by Lamouroux and thus are (or have been) presumed to be based on material housed at **PC** (Muséum national d'Histoire Naturelle, Paris) or **CN** (Université de Caen, France). The present paper provides a detailed account of the newly designated neotype of *Amphiroa crassa* Lamouroux (in Lamouroux *et al.*, 1824: 52), a species originally based on material putatively collected from Shark Bay, Western Australia. Historical background information and comparisons with *A. tribulus* also are included.

Table 2. Characters separating the types of *Amphiroa crassa* and *A. tribulus*. Data sources: present paper (type of *A. crassa*); Woelkerling & Harvey 2012 (type of *A. tribulus*)

<i>Character</i>	<i>A. crassa</i>	<i>A. tribulus</i>
Branching of erect axes	Primarily dichotomous with rare trichotomies	Dichotomous to clustered with 2-6 branches arising from one point
Central midrib on flattened intergenicula	Not present	Present on some but not all intergenicula
Genicula at points of branching	Present at $\frac{1}{2}$ to $\frac{2}{3}$ of branch points but absent from $\frac{1}{3}$ to $\frac{1}{2}$ of branch points	Always present
Genicula formed up to 4 mm beyond a point of branching	yes	no
Mature genicula consisting of both transformed core-region cells and transformed peripheral-region cells	no	yes
Number of arching tiers of core cells per geniculum	Usually 14-16	5-8
Genicula partly to largely enclosed by a collar of untransformed peripheral region cells produced by the intergenicula	yes	no

MATERIALS, METHODS, TERMINOLOGY

Samples of neotype material for light microscopy were prepared by removing small pieces of fertile material and decalcifying in 0.6 M nitric acid. Material was rinsed in distilled water then stained in 5% aqueous potassium permanganate for 25-30 min. Material was again rinsed in distilled water and serially dehydrated in 30, 60, 90 and 100% ethanol for 30 min each. It was then left in medium grade 'L.R. White resin' (London Resin Co., Reading, Berkshire, England) for 12 h, and then embedded in L.R. White. Embedding entails placing the stained corallines in small depressions in plastic (PVC) trays filled with fresh resin, covering the depressions with plastic (melinex) coverslips to exclude oxygen and hardening in an oven set at 60-70°C for 4 h.

Material was then sectioned at 6-12 µm with a sledge microtome and sections permanently mounted on slides. Sections were first 'cleared' in 'Histo-Clear' (National Diagnostics, Atlanta, GA) then mounted in Ultramount No 4 with colourfast (Fronine Laboratory Supplies, Riverstone NSW, Australia). Slides were then placed on a hot plate and the mounting medium hardened overnight weighted down with brass blocks.

Herbarium abbreviations (listed here in bold caps) follow the *Index Herbariorum*, formerly in print (Holmgren *et al.*, 1990), now online electronically (Thiers, 2012 [continuously updated]). Morphological and anatomical terminology follows Harvey *et al.* (2009) and is ultimately based on Woelkerling (1988).

The International Code of Botanical Nomenclature (ICBN) cited is the Vienna edition (McNeill *et al.* 2006) because the amended *Code*, which was approved in August 2011 at the XVIII International Botanical Congress

(Melbourne) and is now in effect (McNeill *et al.* 2011: 1511), was not available online or in final printed form at the time the present paper was submitted. Based on data in McNeill & Turland (2011) and McNeill *et al.* (2011), however, the Articles of the amended *Code* explicitly cited in the present paper appear unchanged from the 2006 edition of the *Code*.

The amended *Code* is now known as *The International Code of Nomenclature for algae, fungi, and plants*, and in the amended *Code*, the general term *organisms* is used when referring to taxa traditionally treated as algae, fungi, and plants. In the context of nomenclature, therefore, algae and fungi are no longer termed plants; plants now encompass only bryophytes and vascular plants. In the present account, the terms ‘specimen’ (ICBN Art 8.2, 8.3) and ‘original material’ (ICBN Art 9, Note 2) are used in their nomenclatural sense, and the classical term *thallus* (pl. *thalli*) refers to the plant-like body of an alga.

RESULTS AND DISCUSSION

Historical background

Lamouroux (*in* Lamouroux *et al.*, 1824: 52) based *Amphiroa crassa* on material reported to come from ‘les côtes de la Nouvelle-Hollande, à la baie des Chiens-Marins’ (the coast of Australia in Shark Bay [Western Australia]) and received from Quoy & Gaimard, who were the naturalists on the 1817-1820 around the world expedition of the corvettes S.M. *Uranie* and *Physicienne* under the command of Louis de Freycinet (for further details, see Ducker, 1979). Lamouroux did not explicitly designate a type, indicate how many specimens he had, provide illustrations, cite other localities of occurrence, mention unpublished illustrations, or refer to specimens or illustrations published elsewhere. Subsequently, Lamouroux (1825-1826: 627) authored (posthumously) a very similar account in Quoy & Gaimard (1824-1826) based on the same material. The account in Quoy & Gaimard sometimes has been cited incorrectly as the protologue using an 1824 publication date, but available evidence (Sherborn & Woodward, 1901: 392; Woelkerling & Revers, 2008: 304) indicates that Lamouroux’s paper in Quoy & Gaimard was published in two instalments after his death (25-26.vii.1825): one (pp. 603-616) in livraison 14 (issued 17.xii.1825); and one (pp. 617-643), which includes the account of *Amphiroa crassa* (p. 627), in livraison 15 (issued 26.iv.1826).

In the protologue, Lamouroux (1824: 52) described his thalli as reddish-purple, 4-5 cm tall, rather regularly dichotomous with not very many intergenicula (*articulations*). Intergenicula were described as about 1 cm long and 1.25 mm broad in lower thallus portions but narrower towards the apices and terminating in 2-3 unequal short branchlets. The surfaces of the intergenicula were sometimes covered with a large number of small, round, scattered conceptacles (*tubercules*). Genucula (*disque corné*), which separate the intergenicula, were much smaller and very slender and sometimes covered by the chalky material of the intergenicula.

Since 1824, *A. crassa* apparently has always been retained in *Amphiroa* and apparently has not been treated as a synonym of another species. Weber-van Bosse (1904: 98, pl. 15, figs 1-7) provided the first illustrated account of *Amphiroa crassa* based on material from Indonesia collected during the Siboga Expedition, and she recognized two new infraspecific taxa. In conjunction with her account,

Weber-van Bosse (1904: 88) also studied specimens in the Lamouroux herbarium. Other older published records include those in compilations of Decaisne (1842: 124), Endlicher (1843: 49), Trevisan (1845: 33), Yendo (1905: 5) and De Toni (1924: 702). The species was overlooked in the compilations of Kützing (1849) and Areschoug (1852).

Lists of records or descriptions of material identified as *A. crassa* published since 1990 include those of Ramirez & Santelices (1991: 196; Chile), Silva *et al.* (1996: 221; Indian Ocean records), Millar (1999: 68; Queensland, Australia), N'Yeurt (2001: 761; Fiji), Littler & Littler (2003: 24; South Pacific), South & Skelton (2003: 723; Fiji records), and Skelton & South (2007: 38; Samoan Archipelago). All of these authors listed Shark Bay, Western Australia as the type locality, unaware that all original material is missing or lost.

Neotype selection and designation

No original specimens from Shark Bay, Western Australia labelled *Amphiroa crassa* by Lamouroux have been found after extensive searches (by Reviere & Woelkerling) in **CN**, which houses the main Lamouroux herbarium, or in **PC**, which contains a number of Lamouroux specimens or portions thereof. Although Weber-van Bosse (1904: 88) studied specimens (note the plural) of Lamouroux (without mention of locality data) and referred to these as types, she provided no illustrations of Lamouroux material and referred to the specimens as 'flat, broad and palmate' (words not used by Lamouroux in the protologue). No such Shark Bay specimens labelled *Amphiroa crassa* by Lamouroux or Weber-van Bosse were found in **CN** or **PC** during the present study, and it appears that all original material (ICBN, Art. 9, Note 2) is now missing or lost. In the absence of original material, ICBN Arts 9.6 & 9.11 specify that another specimen (*i.e.* a neotype) may be selected to serve as nomenclatural type for the application of a name, in this case *Amphiroa crassa*.

During the search for original material of *A. crassa*, we found a specimen (Fig. 1) in the Lamouroux herbarium (**CN**) affixed to an unlabelled herbarium sheet in a folder numbered "C. 8 f.27"; the folder also contained (Fig. 2) a loose strip of paper on which Lamouroux had written "*Amphiroa crassa*", "Freycinet", and "îles moluques" (= Moluccas Islands, now the Maluku Islands, Indonesia). Another loose annotation label written by E.B. Bornet, and a loose annotation label (not shown in Fig. 2) on which H.W. Johansen wrote "Type (?) *Amphiroa crassa*" also were present.

There is no firm evidence that this specimen constitutes original material as defined in ICBN Art. 9, Note 2. The small herbarium sheet (Fig. 1) to which the thallus is attached is unlabelled; and there are no annotations of Lamouroux or of Weber-van Bosse. The locality ('îles moluques') on the loose slip of paper (Fig. 2) found in the same herbarium folder is not mentioned in the protologue account of the species; the only locality cited is Shark Bay, Western Australia. The specimen itself is a fragment of a branch tip in which the intergenicula are 2-4 mm broad, wider than 1.25 mm broad as mentioned in the protologue, and the specimen is about 2.5 cm long and not 4-5 cm long as mentioned in the protologue. During the study of other corallines in the Lamouroux herbarium (Woelkerling & Reviere, unpublished data), several misplacements of loose labels/specimens were discovered, and such a possibility cannot be ruled out in the case of contents in folder "C. 8 f.27".



Figs 1-2. Specimen and labels in Lamouroux herbarium folder "C. 8 f.27" (CN). **1.** Specimen mounted on unlabelled herbarium paper in folder "C. 8 f.27". Scale rule in mm/cm. **2.** Two loose labels also present in folder "C. 8 f.27". Top label written by E.B. Bornet. Bottom label (presumably cut from original folder) written by J.V.F. Lamouroux. Scale rule in mm/cm.

Although it would be possible to choose the 'îles moluques' specimen as neotype, we have decided against this option, in part because the specimen is not from Australia, in part because some of the measurement data do not match those in the protologue, and in part because potentially diagnostic anatomical features associated with genicular structure and conceptacle anatomy could not be elucidated without destroying a significant part of the material.

Unfortunately, we know of no extant specimens of *A. crassa* gathered from Shark Bay, or of published records of Shark Bay material other than those linked to the original Lamouroux report (e.g. Decaisne, 1842: 124; Trevisan, 1845: 33; Weber-van Bosse, 1904: 98; Silva *et al.*, 1996: 221). Recent accounts of Shark Bay algae (Huisman *et al.*, 1990; Kendrick *et al.*, 1990) do not mention the species; searches of major Australian herbaria for Shark Bay specimens of *A. crassa* have not been fruitful; and John Huisman (personal communication), who has collected extensively along the coast of Western Australia, has not found the species any further west than the King & Conway Islands, north of Cape Leveque on the north coast of W.A., over 2000 km distant from Shark Bay. Thus it is not possible

to designate a neotype from Shark Bay or anywhere near to Shark Bay, and this leaves some doubt as to whether the Shark Bay locality reported by Lamouroux is correct. Indeed, the locality data may have been inadvertently misrecorded during the salvaging of collections after the wreck of the *Uranie* (Ducker, 1979: 29) at the Falkland Islands on 14 February 1820 on the homeward journey, long before Lamouroux ever received his material.

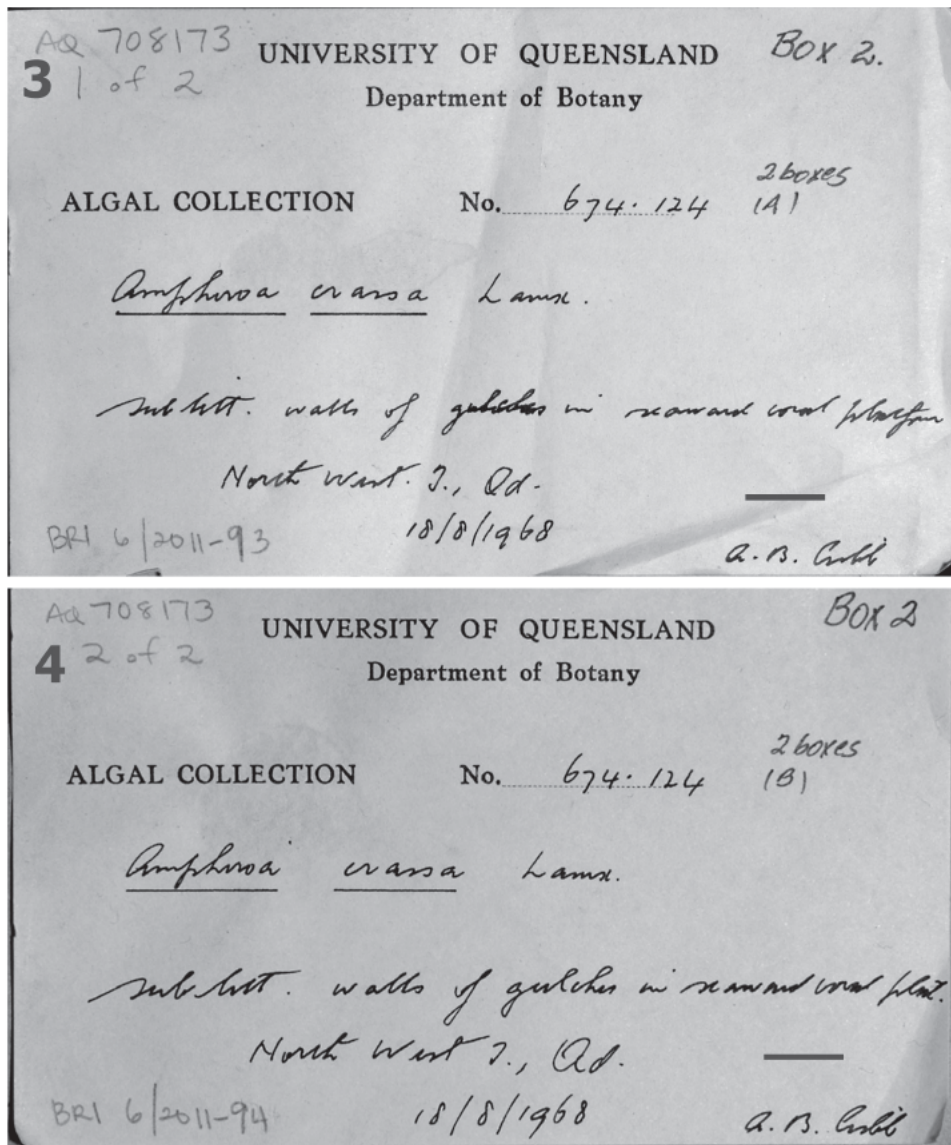
Nearly all of the 55 dried Australian collections (Table 1) identified as *A. crassa* during the present study were badly fragmented and thus comparatively unsuited for neotype selection. After fully considering the situation, the most intact collection that best shows the habit and features considered diagnostic of the species and is most in accord with the original description of Lamouroux was chosen as neotype. Thus **BRI** specimen AQ708173 (Figs 3-5), collected by A.B. Cribb from North West Island, Capricorn Group, Great Barrier Reef, Queensland, Australia on 18 August 1968 is designated here as the neotype specimen of *Amphiroa crassa*. **BRI** AQ708173 also bears the algal collection number 674.124, presumably assigned by A.B. Cribb when the collection was housed at the University of Queensland.

The neotype (Figs 3-28) includes material attached to eight pieces of paper (Fig. 5), all numbered 674.127, an additional numbered piece of paper devoid of attached material (not shown), and loose fragments composed of 1-several intergenicula (not shown). This material is housed in two small boxes that are clearly labelled (Figs 3-4) as being part of the same specimen. All requirements listed in ICBN Arts 8.2 & 8.3 for treating multiple individuals in more than one preparation (box) as parts of a single specimen have been met.

Account of neotype specimen

The designated neotype comprises (Figs 5-10) several individuals with more or less intact crustose basal portions (e.g. Fig. 5h, left-most individual, enlarged in Fig. 9), a number of branched axes or parts thereof lacking crustose basal portions, and some loose fragments (not shown). Individuals with crustose basal portions are 30-55 mm tall; branch axes without crustose basal portions are up to 100 mm long. Branching (Figs 5-8) is primarily dichotomous with rare trichotomies (Fig. 6, arrow 't'); lateral adventitious branches occur on some older intergenicula (Fig. 10, arrows). Intergenicula vary from compressed (Figs 6, 13) to more or less terete (Figs 7, 12) and are mostly (8) 10-17 (32) mm long and 0.7-2.2 mm in diameter. Branch tips also are compressed (Fig. 6) to or more or less terete (Fig. 7). Intergenicula with midribs were not observed. Most pieces bear conceptacles (Figs 8, 10, 11). Except for colour, which had faded in the designated neotype, the characters mentioned by Lamouroux (1824: 52) in the protologue fall within the range seen in neotype individuals. In addition, Weber-van Bosse (1904: 98) reported polychotomous branching in some of her specimens, but this was not found in the neotype and was not reported by Lamouroux (1824: 52).

Anatomically, branches are monomerous throughout, consisting of a single continuous system of branched, laterally coherent filaments. In median longitudinal section (Fig. 15), intergenicula consist of a broad central core (medullary) region in which filaments are oriented more or less parallel to the branch surface, passing into a peripheral (cortical) region where portions of core filaments or their derivatives bend outward to become more or less obliquely to perpendicularly oriented to the branch surface. Cells of adjacent core-region filaments are mostly 10-16 μm in diameter and aligned in 1-8 arching tiers of



Figs 3-4. Labels on the outside of the two boxes collectively housing the designated neotype of *Amphiroa crassa* (BRI AQ708713). Labels written by A.B. Cribb. Scale bars = 10.5 mm.

longer cells (mostly 65-90 μm long) followed by a single arching tier of shorter cells (mostly 13-48 μm long). Some tiers of shorter cells only span part of the core region (Fig. 15, arrowheads) Cells of adjacent peripheral-region filaments are not in arching tiers but can be laterally aligned; cells are mostly 8-10 μm in diameter and 8-18 μm long. Filaments (both in vegetative regions and in conceptacle roofs) terminate at the thallus surface in epithallial cells 7-9 μm in diameter and 2-5 μm long and with rounded or flattened outer walls (Fig. 14). Cells of adjacent

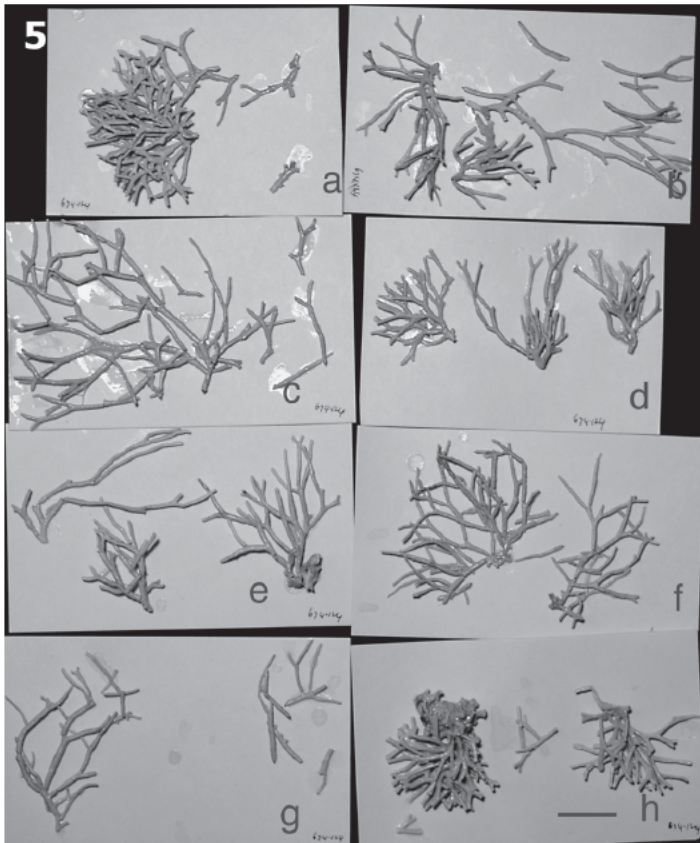
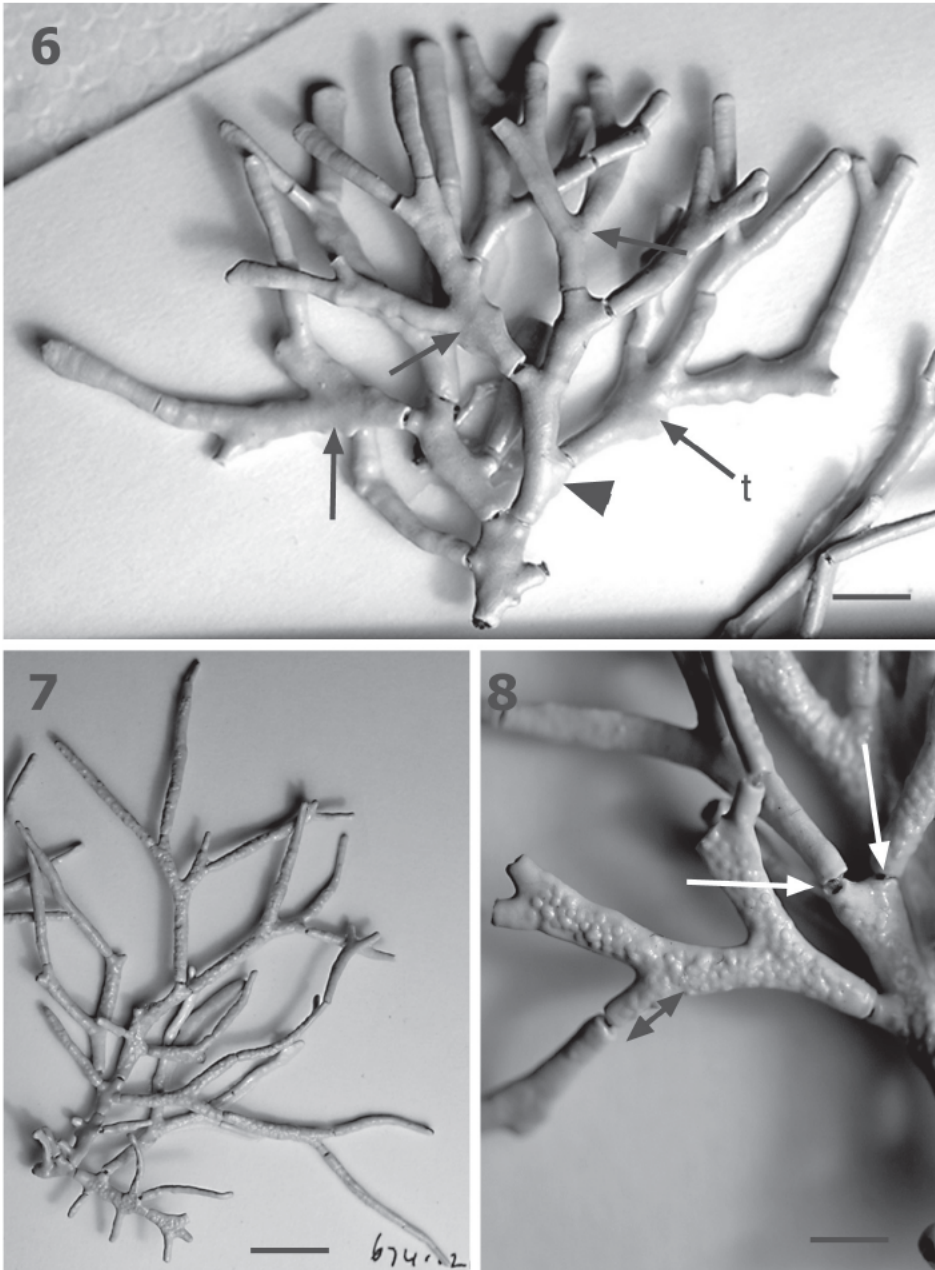


Fig. 5. Thalli and branch fragments of the neotype of *Amphiroa crassa* (BRI AQ708713). The number 674.127 on each herbarium sheet is a collection number added by A.B. Cribb. Loose fragments not shown. Scale bar = 22 mm.

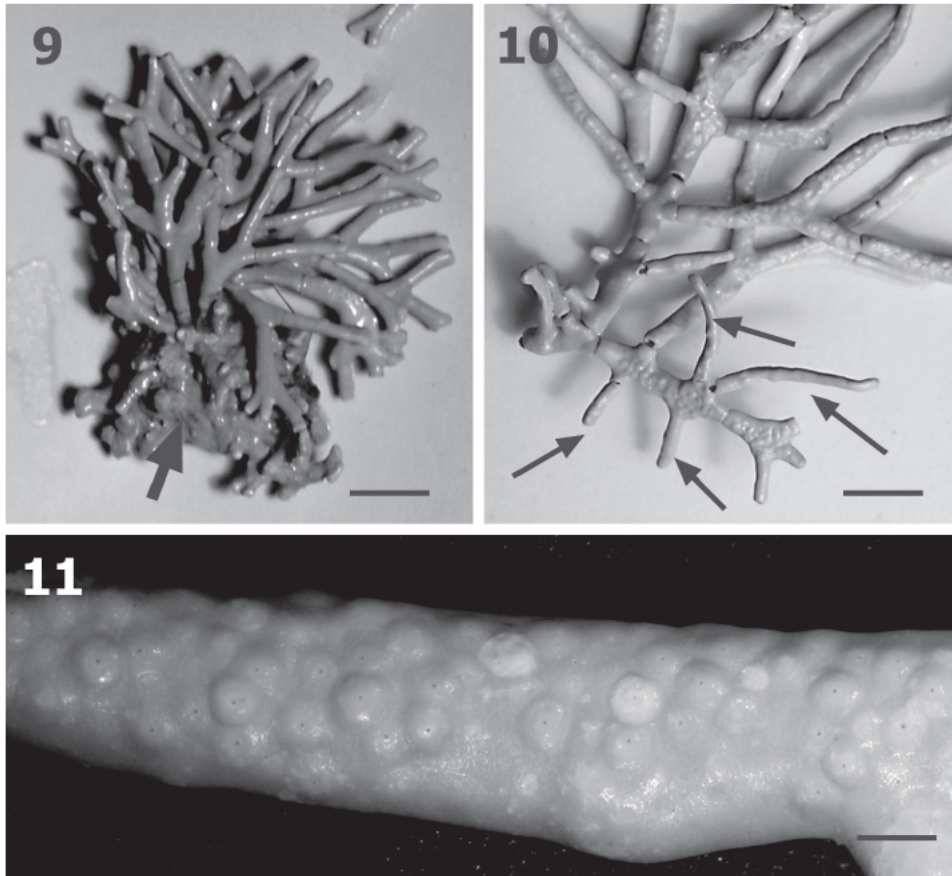
filaments are linked by secondary pit connections (Fig. 14); cell fusions do not occur. Lamouroux (1924: 52) did not deal with anatomical features, but data on those anatomical characters dealt with by Weber-van Bosse³ (1904: 98) are also evident in the neotype.

In surface view (Figs 6, 8, 16-17, 21, 22), genicula may be obvious, or they may be indistinct with constrictions in the thallus surface the only indications of their presence (Fig. 16 - a, b). Some genicula remain indistinct even at maturity, but more commonly, the calcified peripheral region surrounding the geniculum begins to split (Fig. 16 - c), and eventually forms a collar around the geniculum (Figs 17 - d, 22). When branches break, the collar commonly remains as a relict (Fig 17 - e, 23), and genicula, which are cartilaginous in texture, sometimes become partially or entirely dislodged from intergenicula (Fig. 21). Dislodged genicula almost always include calcified caps (Fig. 21) composed of bits of core filaments from intergenicula that have broken off (Figs 19, 21).

Genicula are entirely absent from $\frac{1}{3}$ to $\frac{1}{2}$ of the branching points (Figs 6, 8, 23). Genicula may be absent from both branches at a single branch junction (Fig. 6) or may be absent from only one branch at a single branch



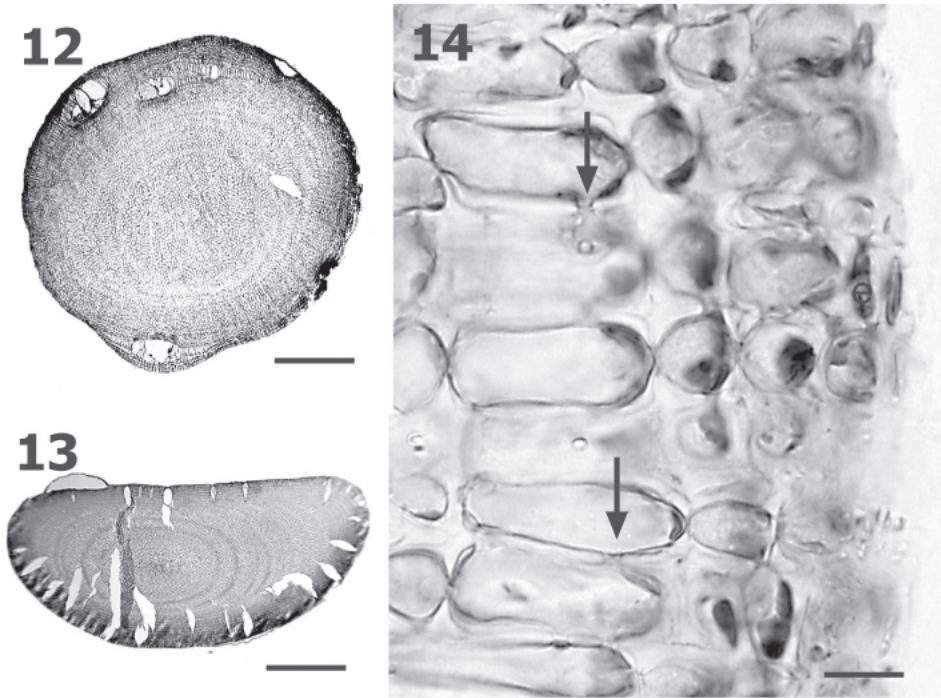
Figs 6-8. Neotype of *Amphiroa crassa* (BRI AQ708713). **6.** Thallus branch showing dichotomous branching and one trichotomy (arrow-t). Note lack of genicula at indicated branch junctions (arrows) and lack of one geniculum on one branch at indicated branch junction (arrowhead). Also note compressed intergenicula with compressed tips. Scale bar = 3.8 mm. **7.** Thallus branch showing more or less terete intergenicula with terete tips. Scale bar = 10 mm. **8.** Part of a branch showing two genicula at a branch junction (arrows) and one geniculum 2 mm past a branch junction (double-headed arrow). Scale bar = 1.9 mm.



Figs 9-11. Neotype of *Amphiroa crassa* (BRI AQ708713). **9.** Whole thallus with calcified non-geniculate base (arrow). Scale bar = 8 mm. **10.** Portion of a thallus with adventitious branches (arrows). Scale bar = 20 mm. **11.** Surface view of intergeniculum with numerous uniporate conceptacles. Scale bar = 500 μ m.

junction (Figs 6, 23). When present, genicula can develop at a branching point or up to 4 mm past the branching point (Figs 8, 17).

Formation of genicula (Figs 6-8, 16-23) occurs behind branch apices as a consequence of secondary decalcification and subsequent transformation of short segments of core region filaments but **not** of associated peripheral region portions of filaments, which remain calcified and unchanged in appearance. During development, core cells become decalcified, thick walled and darkly staining (Fig. 18). Eventually, portions of core region filaments that have been transformed into a geniculum become detached from the unchanged peripheral region, forming a gap (Figs 18-19). In Fig. 18, detachment has yet to be completed in the lower left part of the nearly mature geniculum. At first, the unchanged calcified peripheral region remains intact (Fig. 16 - a, b), but eventually, it commonly it forms a ring-like split (Figs 16 - c, 17 - d) which results in a collar of peripheral cells largely surrounding and enclosing the detached core. The calcified collar remains



Figs 12-14. Neotype of *Amphiroa crassa* (BRI AQ708713). **12.** Transverse section through a terete intergeniculum. Scale bar = 320 μm . **13.** Transverse section through a compressed intergeniculum. Scale bar = 560 μm . **14.** Section of peripheral region of intergeniculum showing rounded epithallial cells (right margin) and secondary pits (arrows). Scale bar = 6 μm .

attached to the adjacent intergeniculum (Fig. 16 - d, e; 19, 22, 23), and cells in collars do not decalcify, or become thick-walled, or stain darkly.

Anatomically, the mature geniculum is usually composed of 14-16 arching tiers of core cells with 1-8 arching tiers of longer core cells followed by a tier of shorter core cells (Fig. 20), as occurs in intergenicula. Transitions from calcified intergenicula to decalcified genicula occur between successive tiers of cells. Genicula from dried specimens often become very brittle during preparation (embedding, staining, sectioning) for light microscopic examination, and consequently often look more or less shattered or torn (Figs 18, 19, 23).

Of the characters mentioned in the protologue by Lamouroux (1824: 52), the most distinctive is that the genicula were slender and sometimes covered by the chalky material of the intergenicula (Figs 17, 22, 23). This feature, which refers to a collar of peripheral region cells that envelops the genicula, occurs in the designated neotype, as do other features mentioned in the protologue and mentioned in the account of Weber-van Bosse (1904: 98), who studied Lamouroux specimens.

The designated neotype of *Amphiroa crassa* includes both tetrasporangial and male individuals, but these cannot be differentiated from each other in surface view. Tetrasporangial conceptacles (Figs 24-26) protrude somewhat above the surrounding thallus surface, are uniporate, and are more or less densely scattered over the entire surface of intergenicula. Conceptacle roofs (Figs 24, 25)

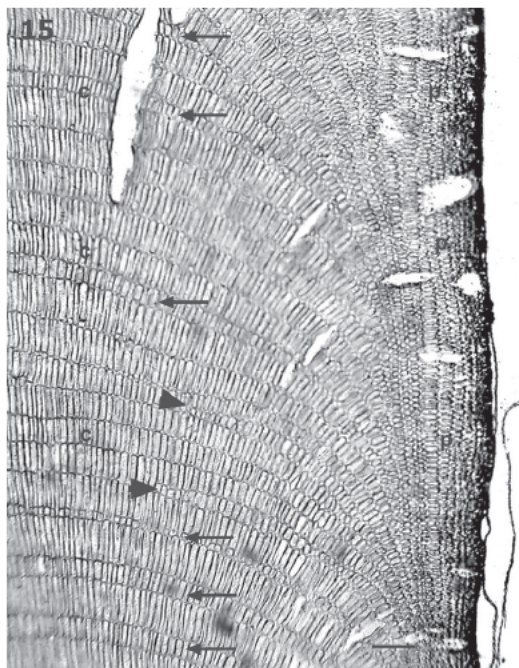
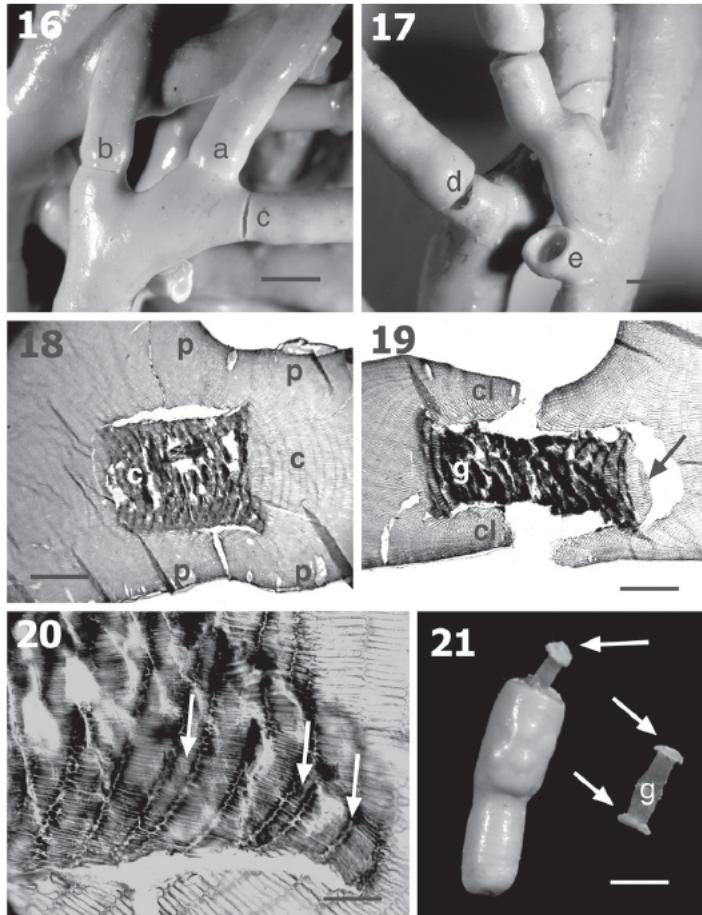


Fig. 15. Neotype of *Amphiroa crassa* (BRI AQ708713). Longitudinal section through the right side of part of an intergeniculum showing tiers of longer and shorter (arrows) cells. Note partial tiers of shorter cells (arrowheads). c = core region; p = peripheral region. Scale bar = 75 μ m.

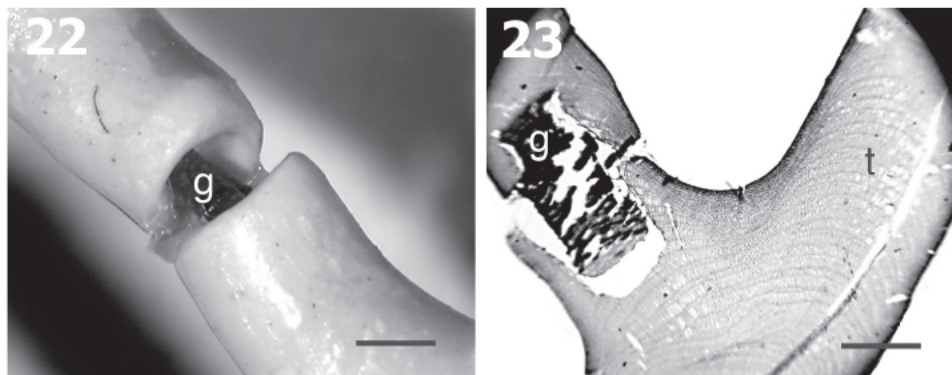
almost certainly are formed both from filaments interspersed with and peripheral to the developing tetrasporangia, and the chamber forms when portions of filaments degenerate. In some conceptacles (Fig. 24), filament degeneration remains incomplete. Conceptacle roofs are composed of the remaining terminal portions of those filaments and are mostly 5-6 cells long, and commonly include a layer of comparatively longer cells just above the chamber. The pore canal (Fig. 25) is flanked by cells that grow more or less parallel to the canal or slightly project laterally into the canal. Mature tetrasporangia are mostly 11-22 μ m in diameter and 27-45 μ m long and contain four zonately arranged tetraspores. Mature conceptacle chambers (including areas where filaments have not completely degenerated) are mostly 205-245 μ m in diameter and 55-90 μ m high. Older conceptacles sometimes become buried in the peripheral region of branches (Fig. 26); Weber-van Bosse (1904: 98) also reported buried conceptacles.

Spermatangial conceptacles (Figs 27-28) also protrude somewhat above the surrounding thallus surface and are scattered over the surfaces of intergenicula. Spermatangial filaments are confined to the conceptacle chamber floor and are unbranched. Mature conceptacle chambers are mostly 335-370 μ m in diameter and 55-90 μ m high. Female/carposporangial conceptacles were not detected in the neotype.

Both Lamouroux (1824: 52) and Weber-van Bosse (1904: 98) mentioned conceptacles, but neither provided information on contents. Weber-van Bosse (1904:98) mentioned that conceptacles were 320-340 μ m in diameter without specifying whether this was internal or external diameter, and she reported that conceptacles become buried in intergenicula, which also occurs in the neotype.



Figs 16-21. Neotype of *Amphiroa crassa* (BRI AQ708713). **16.** Surface view of developing genicula. Slight constrictions in thallus surface ('a', 'b') mark positions of two young genicula. Slightly older geniculum ('c') in which a horizontal split has appeared in thallus surface above underlying geniculum. Scale bar = 1.3 mm. **17.** Surface view of mature geniculum (d) connecting two intergenicula with surrounding calcified peripheral 'collars'. Also note a peripheral collar (e) remaining after part of a branch has broken away and geniculum has become dislodged. Scale bar = 1.3 mm. **18.** Longitudinal section through a maturing geniculum (dark staining region) and ends of flanking intergenicula (lighter areas). Note peripheral region cells still attached to immature geniculum in the lower left hand corner c = core region; p = peripheral region. Scale bar = 350 μ m. **19.** Longitudinal section through a mature geniculum (dark staining region) and flanking intergenicula (lighter areas). g = geniculum made up only of core region cells; cl = collar formed from peripheral region filaments originally connected to core region cells of geniculum. Note end of geniculum with attached intergenicular cells (arrow) broken away from main part of intergeniculum; compare with Fig. 21. Scale bar = 285 μ m. **20.** Enlarged longitudinal section through a geniculum showing alternating tiers of longer and shorter (arrows) cells. Note transition to intergenicula (on right) occurring between cells rows. Scale bar = 90 μ m. **21.** Surface view of genicula (g) with attached clumps of calcified intergenicula cells on the ends (arrows). Compare with Figure 19. Scale bar = 1.1 mm.



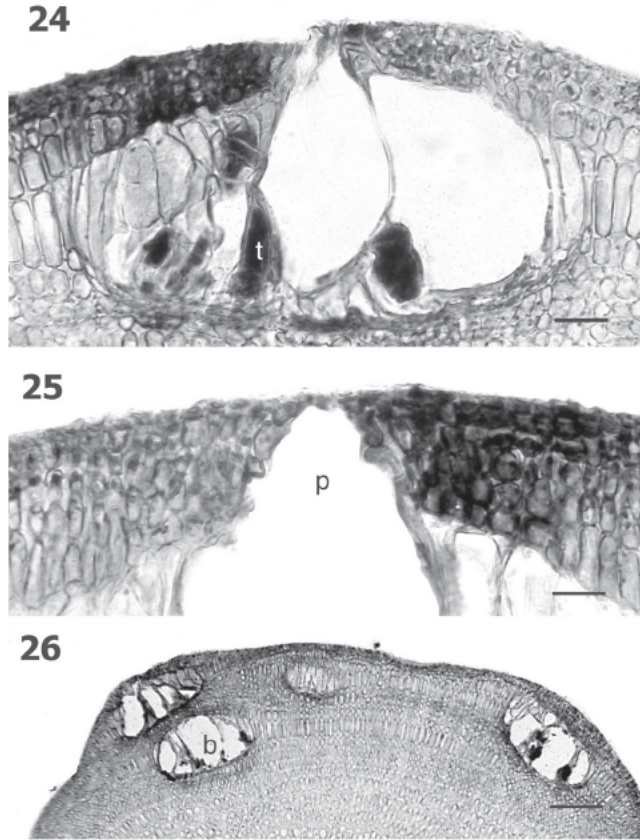
Figs 22-23. Neotype of *Amphiroa crassa* (BRI AQ708713). 22. Surface view showing collar of calcified peripheral cells around the geniculum (g). Compare with figure 23. Scale bar = 1 mm. 23. Longitudinal section through a branching point showing one branch with a mature geniculum (g) and one branch lacking a geniculum (t) Scale bar = 470 μ m.

Comparisons with *Amphiroa tribulus* and with temperate Australian species

In the first illustrated account of *Amphiroa crassa*, Weber-van Bosse (1904: 98, 99, plate 15, figs 1-7) felt the species was closely allied to *A. tribulus*, the type species of *Amphiroa*, but she was uncertain whether they were conspecific, in part because she had only scant material identified as *A. tribulus*. Subsequently, Setchell (1924: 153) commented without providing details that Pacific and Indian Ocean references under *A. tribulus* probably referred to *A. crassa*, and recently, Setchell's view was mentioned again by Skelton & South (2007: 40). Both species are recorded from the Indian Ocean (see records in Silva *et al.*, 1996: 221, 225) and from the South Pacific (Littler & Littler, 2003: 24, 26). In the tropical and subtropical western Atlantic, there are a number of records for *A. tribulus* [e.g. Taylor, 1960: 406, 407; Littler & Littler, 2000: 24; Dawes & Mathieson, 2008: 198; Wynne, 2011: 19]. There also are several records of *A. crassa* (Schramm & Mazé, 1865: 17; 1866: 40; Mazé & Schramm, 1878: 205; Murray, 1888: 338; 1889b: 21), considered uncertain by Taylor (1960: 407). Additional records for both species are available online from AlgaeBase (<http://www.algaebase.org>). However, except for Weber-van Bosse (1904: 88), who saw (but did not illustrate) Lamouroux specimens of *A. crassa*, none of these identifications/records is based knowledge of the types of either species. Indeed, *A. tribulus* was not formally typified until 2012 (Woelkerling & Harvey, 2012), and formal typification of *A. crassa* has first occurred in the present paper.

Now that both species have been formally typified, and data from the types are available, it is possible to undertake more informed comparisons. We have concluded from these comparisons (Table 2) that the two species are distinct morphologically-anatomically and that differences in seven vegetative characters are useful in distinguishing between them. Most concern differences in genicular anatomy. Characters relating to tetrasporangial conceptacle anatomy appear similar in the two types and thus are not diagnostically significant for separation of the two species; male conceptacles do not occur in the type of *A. tribulus*, so comparisons are not possible.

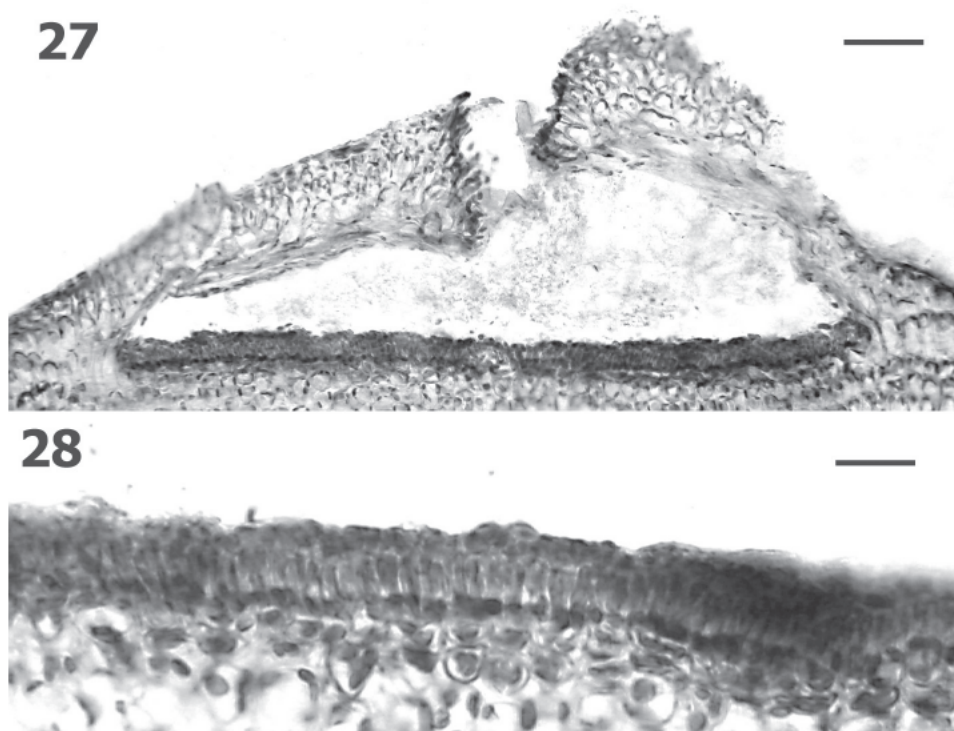
Amphiroa crassa is unknown in temperate Australian waters, but can readily be distinguished from the four species (Harvey *et al.*, 2009) that do occur



Figs 24-26. Neotype of *Amphiroa crassa* (BRI AQ708713). **24.** Section through a tetrasporangial conceptacle with tetrasporangia (t). Scale bar = 25 μm . **25.** Enlarged section through tetrasporangial conceptacle pore canal (p) region. Note that pore canal is flanked by cells that project laterally towards the canal. Scale bar = 20 μm . **26.** Transverse section through intergeniculum with a buried tetrasporangial conceptacle (b). Scale bar = 111 μm .

[*A. anceps* (Lamarck) Decaisne; *A. beauvoisii* Lamouroux; *A. gracilis* W.H. Harvey; *A. klochkovana* A. Harvey, Woelkerling & A. Millar] (see Harvey *et al.*, 2009: 261, table 2 for a comparison of the four). *A. crassa* differs from all four in that intergenicula produce a collar of untransformed, calcified peripheral region cells that surrounds and partly to largely encloses each geniculum (Figs 17-19, 22, 23). No such collars occur in the four species found in temperate Australia or in the type species of *Amphiroa*, *A. tribulus*.

A. gracilis and *A. klochkovana* also differ from *A. crassa* in that fascicled branching as well as some dichotomous branching occurs (Harvey *et al.*, 2009: 281, figs 45, 46, 49; 283, fig. 55); in *A. crassa*, by contrast, branching is primarily dichotomous with rare trichotomies (Figs 5-8). In *A. anceps*, genicula occur at all points of branching and all intergenicula are compressed to flattened (Harvey *et al.*, 2009: 264, figs 7, 8), whereas in *A. crassa*, genicula are absent from $\frac{1}{3}$ to $\frac{1}{2}$ of branch points, and intergenicula vary from terete to compressed (Figs 6, 7). In *A. beau-*



Figs 27-28. Neotype of *Amphiroa crassa* (BRI AQ708713). **27.** Section through a male conceptacle; note spermatangial branches confined to chamber floor. Scale bar = 40 μ m. **28.** Enlarged section through male conceptacle showing unbranched spermatangial filaments on the chamber floor. Scale bar = 13 μ m.

voisii, tetrasporangial conceptacle pore canals are flanked by ring of block-shaped cells (Harvey *et al.*, 2009: 276, fig. 37); such rings of block-shaped cells do not occur in *A. crassa* (Fig. 25).

CONCLUDING REMARKS

Further studies are needed to determine more fully what characters, both morphological-anatomical and molecular, distinguish *Amphiroa crassa* and *A. tribulus* from other species of *Amphiroa*, including those in temperate Australia. At present, no molecular comparisons of these species have been published and no DNA sequence data is currently available for the type specimens, but a number of morphological-anatomical features relating to genicula (Table 2) were found useful in the present study for separating the type of *A. crassa* from the type of *A. tribulus*. The full extent to which these features are stable within these two species, however, has yet to be determined.

As noted by Harvey *et al.* (2009: 286-287), the diagnostic value of many characters and character states currently used to separate species of *Amphiroa*

needs critical reassessment to determine variability within and across populations of individuals, a task beyond the scope of this study. The value of DNA sequence characters also requires assessment.

Similarly, further studies are needed to determine the status and disposition the two infraspecific taxa of *A. crassa* recognized by Weber-van Bosse: *A. crassa* f. *godeffroy* (Grunow) A. Weber-van Bosse, 1904: 98 (Basionym: *Amphiroa godeffroy* Grunow, 1874: 41) and *A. crassa* f. *minuta* Weber-van Bosse (1904: 98).

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