

The utility of morphological characters in gastropod phylogenetics: an example from the Calyptraeidae

RACHEL COLLIN*

Committee on Evolutionary Biology, University of Chicago, Culver Hall, Rm. 402,
1025 E. 57th St., Chicago, IL 60637, USA; and
Department of Zoology, The Field Museum of Natural History, 1400 S. Lake Shore Drive,
Chicago, IL 60605, USA; and
*Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002, USA

Received 22 February 2002; accepted for publication 31 October 2002

Organismal taxonomy is often based on a single or a small number of morphological characters. When they are morphologically simple or known to be plastic, we may not have great confidence in the taxonomic conclusions of analyses based on these characters. For example, calyptraeid gastropod shells are well known for their simplicity and plasticity, and appear to be subject to frequent evolutionary convergences, but are nevertheless the basis for calyptraeid taxonomy. In a case like this, knowing how the pattern of relationships inferred from morphological features used in traditional taxonomy compares to the patterns of relationships inferred from other morphological characters or DNA sequence data would be useful. In this paper, I examine the relative utility of traditional taxonomic characters (shell characters), anatomical characters and molecular characters for reconstructing the phylogeny of calyptraeid gastropods. The results of an ILD test and comparisons of the recovered tree topologies suggest that there is conflict between the DNA sequence data and the morphological data. Very few of the nodes recovered by the morphological data were recovered by any other dataset. Despite this conflict, the inclusion of morphological data increased the resolution and support of nodes in the topology recovered from a combined dataset. The RIs and CIs of the morphological data on the best estimate topology were not any worse than these indices for the other datasets. This analysis demonstrates that although analyses can be misled by these convergences if morphological characters are used alone, these characters contribute significantly to the combined dataset. © 2003 The Linnean Society of London. *Biological Journal of the Linnean Society*, 2003, 78, 541–593.

ADDITIONAL KEYWORDS: *Calyptraea* – *Cheilea* – *Crepidula* – *Crucibulum* – gastropod taxonomy.

'In the cabinets of the Naturalist, the shells of the *Crepidulae* and *Calyptraeae* attract by the singularity rather than the beauty of their forms'. Richard Owen (1834)

INTRODUCTION

Natural variability and morphological plasticity are common characteristics of organisms. When such variation occurs in combination with simple morphology, taxonomic and systematic analyses are extraordinarily difficult. A combination of variability and relatively

simple morphologies is particularly common in colonial marine invertebrates such as sponges and corals, lichens, algae and unicellular organisms. This situation often results in difficulty in species identification, lack of confidence in systematic conclusions, generally poorly resolved phylogenetic hypotheses and unstable taxonomies.

These problems are also common in groups with complex morphologies when only one or a few character complexes have traditionally been used for systematics. In these cases, it is useful to know how the traditional systematic characters compare to the other available characters in their ability to resolve different levels of phylogenetic relationships. The use of a

*Correspondence. E-mail: collinr@naos.si.edu

single morphological feature is particularly common in the study of marine molluscs where species and genera are often described on the basis of shell morphologies, and the complex soft anatomy has historically not been used (see Schander & Sundberg, 2001). This preference for hard-parts in molluscan taxonomy and systematics has two causes: (1) material from which anatomical observations can be made is or has not been available to molluscan workers; or (2) detailed examination of molluscan anatomy has not led to the discovery of characters that are useful in taxonomic or phylogenetic analyses. This second point receives some support from phylogenetic analyses of muricid gastropods by Kool (1993) and Vermeij & Carlson (2000), who find that anatomical characters can resolve nodes deep in rapanine phylogeny but that they cannot be used to resolve the relationships of closely related species. In contrast shell characters can confidently be used to identify muricid species and can be useful in resolving the tips of trees. Unfortunately not all molluscan groups have shells with numerous, clearly identifiable morphological characters. For example oysters (ostreaeids), true limpets (patellogastropods), hoof shells (hipponicids) and slipper limpets (calyptraeids) have simple shell morphologies that are plastic, often making it difficult to identify different species. In this paper, I compare the utility of character complexes traditionally used in gastropod systematics to produce resolved calyptraeid phylogenies with data from other morphological systems and to DNA sequence data.

CALYPTRAEID BIOLOGY

Calyptraeids (Figs 1,2) are sedentary filter-feeding caenogastropods that are often abundant in the intertidal and shallow subtidal. This group has a worldwide temperate and tropical distribution, and unlike many other gastropods their highest diversity is in the Americas while the lowest diversity is in the Indo-Pacific. They are absent from the Arctic and Antarctic. The genus *Crepidula* is probably the best studied group of calyptraeids. A variety of species are commonly used in developmental (e.g. Conklin, 1897; Moritz, 1938; Pechenik, 1980; Lima & Pechenik, 1985; Pechenik *et al.*, 1996; Dickinson *et al.*, 1999), ecological (e.g. Hoagland, 1977, 1978; Matusiak & Fell, 1982; Loomis & VanNieuwenhuyze, 1985; Shenk & Karlson, 1986; Shenk & Karlson, 1986; McGee & Targett, 1989) and behavioural (Hoagland, 1978; Vermeij *et al.*, 1987; Collin, 1995) research. They have been the major focus of research on protandrous sex-change in marine invertebrates (Coe, 1942a,b; Hoagland, 1978; Collin, 1995) and *Crepidula fornicata* and *C. onyx* are well studied examples of invasive, exotic species in marine habitats (Carlton, 1979; Deslous-Paoli, 1985; Woodruff

et al., 1986; Sauriau *et al.*, 1998). Despite the wide range of studies on the biology of these gastropods, the systematics and taxonomy of calyptraeids have received little attention during this century (see Hoagland, 1977 for the most recent taxonomic revision).

CALYPTRAEID TAXONOMY

The taxonomy of calyptraeids, as with most gastropods, has traditionally been based on shell morphology (Table 1). Generally, the family has been defined by a limpet-shaped shell with a shelly septum extending into the body cavity of the shell (Figs 1 and 2). The family usually includes slipper shells (*Crepidula* Lamarck 1799), cup and saucer limpets (*Crucibulum* Schumacher, 1817) and hat shells (*Calyptraea* Lamarck, 1799). Early taxonomists used 'Calyptraea' as a far more inclusive family including many limpet-shaped taxa. For example Lamarck included *Parmophorus*, *Emarginula*, *Siphonaria*, *Fissurella*, *Pileopsis*, *Calyptraea*, *Crepidula* and *Ancylus* in his Calyptraea, de Blainville (1818) included *Crepidula*, *Calyptraea*, *Capulus*, *Hipponix* and *Notrema* and Sowerby (1852) included *Calyptraea*, *Crucibulum*, *Crepidula*, *Capulus*, *Emarginula*, *Cemoria*, *Fissurella*, *Rimula* and *Ancylus*. Subsequently the concept of the family was narrowed to include only *Crepidula*, *Crucibulum* and *Calyptraea*. This scheme has been the foundation of most subsequent studies. *Cheilea* Modeer 1793 was often included in the Calyptraeidae (e.g. Broderip, 1834; Sowerby, 1852; Abbott, 1974; Hoagland, 1977) on the basis of shell morphology but workers who have examined their soft morphology and anatomy place them in the Hipponicidae (e.g. Fischer, 1880; Thiele, 1929; Wenz, 1940; Simone, 2002).

The generic level assignments of species within the Calyptraeidae are also contentious or uncertain and vary widely among authors. Most recent authors divide the family into three groups: *Crepidula*, with flat septum and posterior shell apex, *Crucibulum* with a cone-shaped shell and cup-shaped septum, and *Calyptraea* with a cone-shaped shell and spiral septum. However, Broderip (1834) placed all *Crepidula* and *Crucibulum* species in the genus *Calyptraea* because all these animals are anatomically similar (Owen, 1834). Other workers, more inclined to split taxa, have introduced up to 14 subgenera (that are often raised to genus level) in *Crepidula* alone (Hoagland, 1977), and numerous divisions of the other genera have also been proposed. In the most recent revision, Hoagland (1977) concluded that such division of this genus is not warranted. Such unstable supraspecific taxonomy suggests that traditional characters do not robustly support any single taxonomic scheme.

Table 1. Shell characters of nominal genera and subgenera discussed in this paper*

Genus and subgenus	Original author	Type species	Shell shape	Apex	Shelf shape	Muscle scars	Other characters	Distribution
<i>Crepidula</i> <i>s.l.</i>	Lamarck (1799)	<i>C. fornicata</i>	Oval	Posterior	Flat, attached on both sides	0, 1, 2		World-wide temperate and tropical
<i>Bostrycapulus</i>	Olsson & Harbison (1953)	<i>C. aculeata</i>	Oval	Posterior-lateral	Flat, attached on both sides	1	Spines, medial ridge on shelf	World-wide temperate
<i>Crepidatella</i>	Lesson (1830)	<i>C. dilatata</i>	Rounded	Posterior-lateral	Slightly cupped, free on right side	1		Eastern Pacific, South Atlantic
<i>Maoricrypta</i>	Finlay 1927	<i>C. costata</i>	Oval	Posterior	Flat, attached on both sides	2		New Zealand
<i>Zeacrypta</i>	Finlay 1927	<i>C. monoxyla</i>	Oval	Posterior	Flat, attached on both sides	2		New Zealand
<i>Janacus</i>	Mörch 1852	<i>C. unguiformis</i>	Flat, oval	Posterior	Flat, attached on both sides	0	White	World-wide temperate and tropical
<i>Crucibulum</i> <i>s.s.</i>	Schumacher (1817)	<i>C. rugosa-costatum</i>	Conical	central	Cup-shaped	0		World-wide temperate and tropical
<i>Calyptraea</i> <i>s.s.</i>	Lamarck (1799)	<i>C. chinensis</i>	Conical	Central	Spiral ramp	1		World-wide temperate and tropical
<i>Trochita</i>	Schumacher (1817)	<i>T. trochiformis</i>	Conical	Central	Spiral ramp	1	Thick, ribbed	World-wide
<i>Sigapatella</i>	Lesson (1830)	<i>S. novozelandiae</i>	Conical	Central	Spiral ramp	1		New Zealand
<i>Zegalarus</i>	Finlay 1926		Conical	Central	Spiral ramp	1		New Zealand
<i>Bicatillus</i> <i>s.s.</i>	Swainson 1840	<i>B. extinctorum</i>	Conical	Central	Tiny, flattened cup-shaped	1		Asia
<i>Siphopatella</i> <i>s.s.</i>	Lesson (1830)	<i>S. washi</i>	Flat	Lateral	Flat, folded	1		Old world

*Definitive characters, if any, are highlighted in bold text.

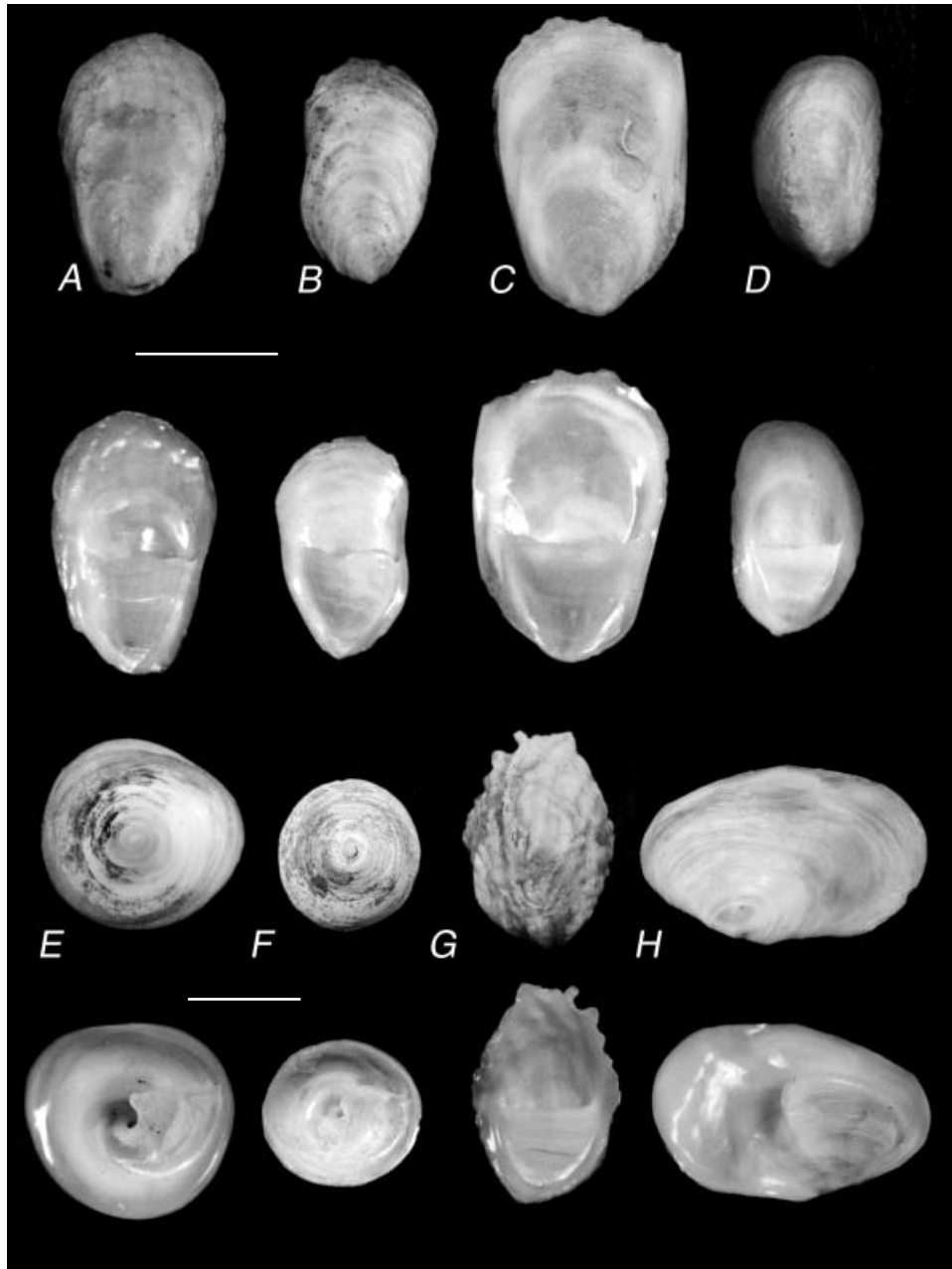


Figure 1. Representative calyptraeid shells I. (A) *Crepidula williamsi*, Santa Barbara, California FMNH 299415. (B) *Crepidula depressa*, Florida FMNH 299412. (C) *Maoricrypta monoxyla*, Leigh, New Zealand, from hermit crabs FMNH 299413. (D) *Maoricrypta monoxyla*, Leigh, New Zealand, FMNH 299413 from *Turbo smaragdus* Gmelin (1791). (E) *Calyptraea mamillaris*, Panama FMNH 299416. (F) *Calyptraea fastigata*, Washington FMNH 299422. (G) *Maoricrypta costata* Leigh, New Zealand FMNH 299414. (H) *Siphopatella walshi*, Oman. Scale bar = 1 cm.

MATERIAL AND METHODS

MATERIAL EXAMINED

I have examined live, formalin and/or ethanol preserved material of 67 species listed in Table 2 ($\approx 30\%$ of the species in the family). I examined the external

appearance and dissected all animals under a Wild M4 dissecting microscope (Figs 1–9). In some cases, only one or two individuals were available for study. Therefore, not all the characters were coded in these cases, as this would require destruction of the specimen, and both males and females are needed to complete the

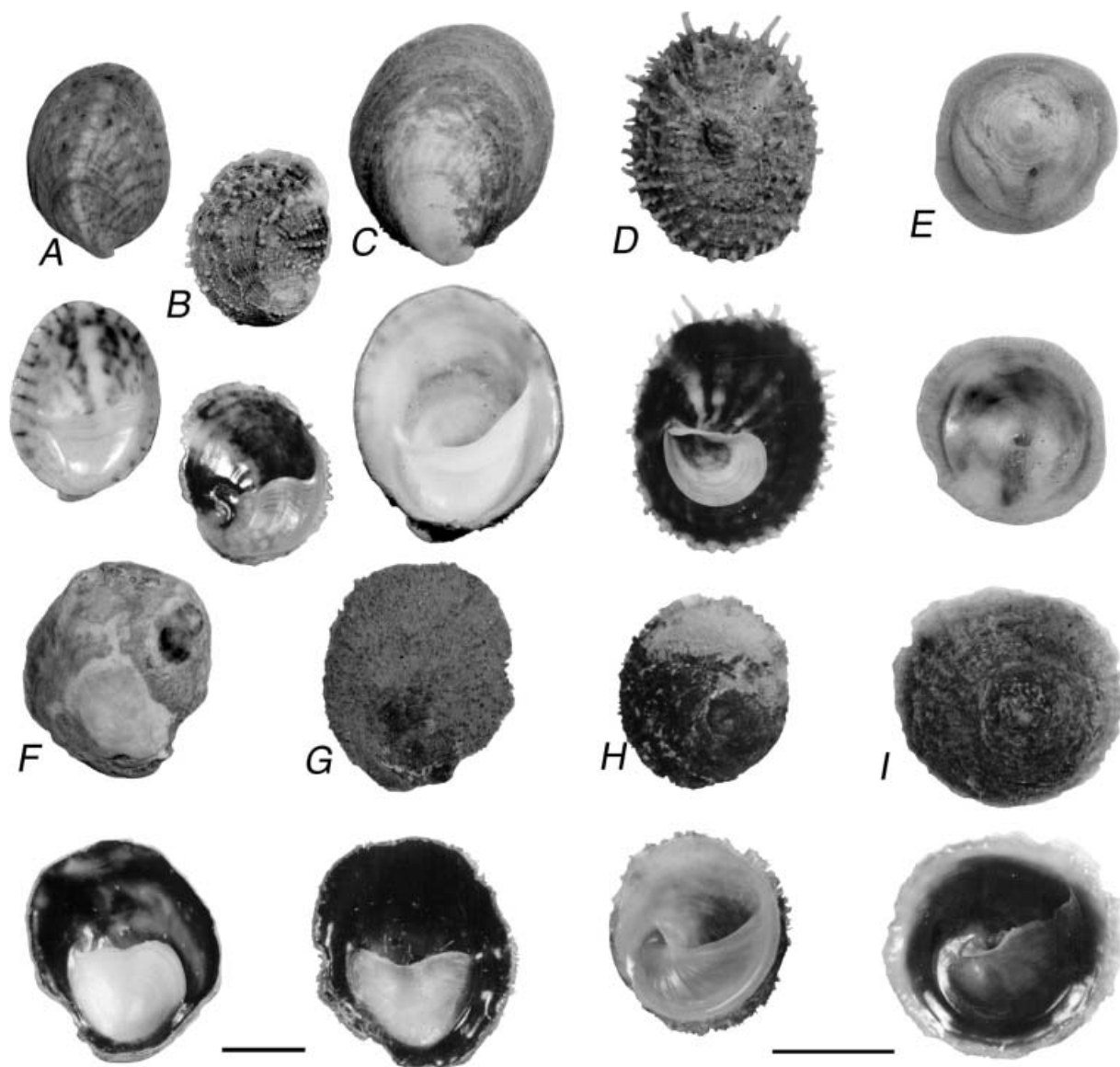


Figure 2. Representative calyptraeid shells II. (A) *Crepidula maculosa*, Florida FMNH 299419. (B) *Crepidula* (*Bostrycapulus*) *aculeata*, Panama. (C) *Crepidula grandis*, Japan FMNH 299421. (D) *Crucibulum spinosum* Panama FMNH 299418. (E) *Bicatillus extintorum*, Singapore FMNH 299402. (F) *Crepidatella* n.sp., Totorelillo, Chile FMNH 299417. (G) *Crepidula* cf. *onyx*, Panama FMNH 299420. (H) *Sigapatella novaezelandiae*, Portabello, New Zealand FMNH 299423. (I) *Trochita calyptraeformis*, Peru FMNH 29924. Scale bar = 1 cm.

dataset. Almost all morphological features that were identified as variable during a preliminary examination of a subset of taxa were coded, regardless of expected phylogenetic utility. This allows a fair comparison between the utility of morphological and DNA characters (where quickly and slowly evolving characters and invariable characters occur in the same sequence). Anatomical details and character codings are discussed in Appendix 1.

Outgroups were selected on the basis of traditional beliefs about caenogastropod relationships. Because hipponicids, trichotropids and capulids have all been considered close relatives of the calyptraeids (Broderip, 1834; Reeve, 1859; Hoagland, 1986; Bandel & Riedel, 1994), they were included as outgroups. A variety of outgroups were used because it is not clear which are the closest relatives of the calyptraeids. Outgroup polarization of characters using living taxa

Table 2. Summary of taxa and vouchers number for material used in this study

Species	Author	Locality	Voucher numbers*	Collector(s)
CALYPTRAEIDAE				
<i>Crepidula (Bostrycapulus) Olsson & Harbison (1953)</i>				
<i>Crepidula aculeata</i> Florida	Gmelin (1791)	Mote Marine Laboratory, Lido Key, Florida, USA 27°20' N, 82°42' W	ANSP A19745 FMNH 282365 BM20010455	R. Collin and J. Wise
<i>Crepidula cf. aculeata</i> Panama		Venado, Pacific Coast, Panama 8°55' N, 79°38' W	FMNH 282273 ANSP A19740 BM 20010452	R. Collin
<i>Crepidula cf. aculeata</i> Australia		Edwards Reef, Sydney, Australia 33°51' S, 151°13' E	FMNH 282302 ANM C400000	R. Collin, W. Ponder and P. Selvarakumaraswamy
<i>Crepidula cf. aculeata</i> Argentina		Playa Orenge, San Antonio Oeste, Argentina 40°53' S, 64°29' W	FMNH 282297 ANSP A 19744 BM20010456	R. Collin
<i>Crepidula cf. aculeata</i> Brazil		Gois Beach, Santos Bay, São Paulo, Brazil 24°00' S, 46°21' W	FMNH 282350	L. Simone
<i>Crepidula cf. aculeata</i> Mexico		Bahía de La Paz, Mexico 24°07' N, 110°24' W	FMNH 282193 FMNH 282194	R. Collin
<i>Crepidula cf. aculeata</i> South Africa		Wooleys Pool, Muizenberg, South Africa 34°4' S, 18°20' E	FMNH 282277 BM20010453	R. Collin, T. Ridgeway and K. Ruck
<i>Crepidula gravispinosa</i>	Kuroda & Habe (1950)	Chijiwa, Nagasaki, Japan	FMNH 282336	M. Katoh
<i>Crepidula (Crepidatella) Lesson (1830)</i>				
<i>Crepidatella capensis</i>	Quoy & Gaimard (1832–1833)	Muizenberg, Cape Province, South Africa 34°4' S, 18°20' E	FMNH 282278	R. Collin, T. Ridgeway and K. Ruck
<i>Crepidatella dilatata</i>	Lamarck (1822)	Corral Bay, San Carlos, Chile 39°51' S, 73°27' W	BM 20010461	R. Collin and A. Reidemann
<i>Crepidatella fecunda</i>	Gallardo (1979)	Bahía de Coquimbo, IV Region, Chile 29°59' S, 71°19' W	FMNH 299425	R. Collin and D. Véliz
<i>Crepidatella lingulata</i>	Gould (1846)	Shady Cove, Friday Harbor, Washington, USA. 48°20' N, 123 01' W	FMNH 282293 FMNH 285019	R. Collin and B. Pernet

<i>Crepidula (Maoricrypta Zeacrypta) Finlay (1927)</i> <i>Crepidula immersa</i>	Angas (1847)	Edithburg, York Penninsula, South Australia 35°03' S, 137°26' E	FMNH 282298	R. Collin
<i>Crepidula monoxyla</i>	Lesson (1830)	Leigh, North Island, New Zealand 36°10' S, 174°30' E	FMNH 282305 ANSP A19732 BM20010467	R. Collin
<i>Crepidula (Janacus) Mörch (1852)</i> <i>Crepidula argentinata</i>	Simone <i>et al.</i> (2000)	Mar del Plata, Argentina 30°00' S, 57°21' W	ANSP A19738 FMNH 282346 BM20010457	M. Clédon
<i>Crepidula atrasolea</i>	Collin (2000)	Harbor Branch Oceanographic Institution, Florida, USA 28°30' N, 81°20' W	FMNH 282209 FMNH 282213	R. Collin
<i>Crepidula coquimbensis</i>	Brown & Olivares (1996)	Bahía de Herradura, Coquimbo, IV Region, Chile 29°58' S, 71°21' W	FMNH 282311	R. Collin
<i>Crepidula depressa</i>	Say (1822)	Sanibel Marina, Florida, USA 26°27' N, 82°02' W	FMNH 282201 ANSP 19187 FMNH 282211	R. Collin
<i>Crepidula fimbriata</i>	Reeve (1859)	Friday Harbor, Washington, USA 48°20' N, 123 01' W	FMNH 299426	R. Collin and B. Pernet
<i>Crepidula lessoni</i> Panama	Broderip (1834)	Chumical, Pacific Coast, Panama 8°30' N, 79°40' W	FMNH 282271 BM20010465	R. Collin
<i>Crepidula nummaria</i>	Gould (1846)	Santa Cruz, California, USA 36°40' N, 122°02' W	FMNH 282245	J. Pearse
<i>Crepidula cf. perforans</i>	Gallardo (1977)	Santa Barbara, California, USA 34°20' N, 120°01' W	FMNH 282243	S. Anderson and R. Collin
<i>Crepidula philippiana</i>	Say (1822)	Los Molinos, Chile. 39°51' S, 73°27' W	FMNH 282349	A. Reidermann
<i>Crepidula plana</i>	d'Orbigny (1841)	Woods Hole, Massachusetts, USA 41°30' N, 70°40' W	FMNH 282207, 282210, 282214, 282215	MBL Biological Supply Co.
<i>Crepidula protea</i>	Menke (1851)	Santos Bay, São Paulo, Brazil 23°20' S, 46°25' W	MZSP 32264	L. Simone
<i>Crepidula striolata</i>		Rio Mar, Pacific Coast, Panama 08°18' N, 79°50' W	FMNH282331	R. Collin

Table 2. Continued

Species	Author	Locality	Voucher numbers*	Collector(s)
<i>Crepidula williamsi</i>	Coe (1947)	Santa Barbara, California, USA 34°20' N, 120°01' W	FMNH 282177–282178	R. Collin and D. Zachrl
<i>Crepidula</i> aff. <i>williamsi</i> Alaska		Kodiak Island, Alaska, USA 57° 12' N, 153° 24' W	FMNH 287485	J. Voight
<i>Crepidula</i> aff. <i>williamsi</i> Washington		Friday Harbor, Washington, USA 48°20' N, 123 01' W	FMNH 299429	R. Collin and B. Pernet
<i>Crepidula</i> s.l. Lamarck (1822) (in addition to Janacus)				
<i>Crepidula adunca</i>	Sowerby (1825)	Friday Harbor, Washington, USA 48°20' N, 123 01' W	FMNH 282185	R. Collin
<i>Crepidula</i> cf. <i>aplysoides</i>	Reeve (1859)	Isla Margarita, Venezuela 11°01' N, 64°03' W	FMNH 293348	P. Miloslavich
<i>Crepidula arenata</i>	Broderip (1834)	La Paz, BCS, Mexico 24°17' N, 110°17' W	FMNH 282364	R. Collin
<i>Crepidula cerithicola</i>	Adams (1852)	Punta Charmé, Pacific Coast, Panama 08°30' N, 79°40' W	FMNH 282332	R. Collin
<i>Crepidula complenata</i>	Krauss (1848)	Langebaan Lagoon, Cape Province, South Africa 33°04' S, 18°02' E	FMNH 282295 ANSPA19748 BM20010462	R. Collin and G. Branch
<i>Crepidula convexa</i>	Say (1822)	Wildwood Crest, Cape May, New Jersey, USA 38°50' N, 74°59' W	FMNH 282261, 282262, 282299 BM20010463	R. Collin and S. Padowitz
<i>Crepidula excavata</i> Mexico	Broderip (1834)	Magdalena Bay, BCS, Mexico	FMNH 282344	R. Collin
<i>Crepidula fornicata</i>	Linnaeus (1758)	Woods Hole, Massachusetts, USA 41°30' N, 70°40' W	FMNH 282306	MBL Biological Supply Co.
<i>Crepidula grandis</i>	Middendorff (1849)	Japan	FMNH 299421	P. Callomon
<i>Crepidula incurva</i> Mexico	Broderip (1834)	La Paz, Baja, Mexico. 24°17' N, 110°17' W	FMNH 282179–282181	R. Collin
<i>Crepidula incurva</i> Panama	Broderip (1834)	Chumical, Pacific coast, Panama 8°30' N, 79°40' W	FMNH 282333	R. Collin

<i>Crepidula incurva</i> Peru	Broderip (1834)	Zorritos, Peru 3°45' S, 80°40' W	FMNH 299431	R. Collin and A. Indacochea
<i>Crepidula maculosa</i>	Conrad (1846)	Panacea, Florida, USA 30°00' N, 84°30' W	FMNH 299368	Gulf Specimen Co.
<i>Crepidula marginalis</i>	Broderip (1834)	Venado, Pacific Coast, Panama 8°55' N, 79°38' W	FMNH282272	R. Collin
<i>Crepidula naticarum</i>	Williamson (1905)	Santa Barbara, California, USA 34°20' N, 120°01' W	FMNH 282176 ANSP A19731 BM20010468	S. Anderson
<i>Crepidula navicula</i>	Mörch (1877)	Morrocoy, Venezuela	FMNH 293349	P. Miloslavich
<i>Crepidula</i> cf. <i>convexa</i> Bocas		Bocas del Toro, Panama 9°20' N, 82°15' W	FMNH 282355	R. Collin
<i>Crepidula onyx</i> California	Sowerby (1824)	Santa Barbara, California, USA 34°20' N, 120°01' W	ANSP A19741 BM20010469	S. Anderson and R. Collin
<i>Crepidula</i> aff. <i>onyx</i> Panama		Venado, Pacific Coast, Panama 8°55' N, 79°38' W	FMNH 299420	R. Collin
<i>Crepidula</i> cf. <i>onyx</i> Argentina		Playa Orego, San Antonio Oeste, Argentina 40°53' S, 64°29' W	FMNH 282287 ANSP A19739 BM20010471-72	R. Collin and T. Borchado
<i>Crepidula porcellana</i>	Lamarck (1822)	Calheta Funda, Sal Island, Cape Verde 16°40' N, 22°03' W	FMNH 282337	R. Collin and E. Rolán
<i>Crepidula 'ustulatulina'</i>	Collin (2002)	Dzilam de Bravo, Yucatan, Mexico 21°20' N, 88°55' W	FMNH 282316	R. Collin and T. Griffin
<i>Crepidula</i> n. sp. pt		La Paz, Mexico 24°17' N, 110°17' W	FMNH 282195–282197	R. Collin
<i>Crucibulum Schumacher (1817)</i>				
<i>Crucibulum 'spinosum'</i> Peru	Sowerby (1824)	Santa Maria, Peru 12°20' S, 76°45' W	BM20010478 FMNH 282345	R. Collin and A. Indacochea
<i>Crucibulum 'spinosum'</i> Panama	Sowerby (1824)	Venado, Panama 8°55' N, 79°38' W	FMNH 299404	R. Collin and K. Zigler
<i>Crucibulum scutellatum</i>	Wood (1828)	Chumical, Pacific Coast, Panama 8°30' N, 79°40' W	FMNH 299405	R. Collin and K. Zigler

Table 2. Continued

Species	Author	Locality	Voucher numbers*	Collector(s)
<i>Crucibulum radiata</i>	Broderip (1834)	Venado, Pacific Coast, Panama 8°55' N, 79°38' W	FMNH 299399	R. Collin
<i>Crucibulum tenuis</i>	Broderip (1834)	Venado, Pacific Coast, Panama 8°55' N, 79°38' W	FMNH 299436	R. Collin
<i>Calyptraea Lamarck (1799)</i>				
<i>Calyptraea aspersa</i>	Adams (1852)	Islas de las Perlas, Panama 8°30' N, 79° 02' W	FMNH 282342	R. Collin
<i>Calyptraea chinensis</i>	Linneus (1758)	O'Grove Bay, Spain.	FMNH 299392	E. Rolán
<i>Calyptraea cf. conica</i>		Venado, Pacific Coast, Panama 8°55' N, 79°38' W	FMNH 299437	R. Collin
<i>Calyptraea fastigata</i>	Gould (1846)	Friday Harbor, Washington, USA 48°20' N, 123 01' W	FMNH 282221	R. Collin and B. Pernet
<i>Calyptraea cf. lichen</i>		Venado, Pacific Coast, Panama 8°55' N, 79°38' W	FMNH 282300	R. Collin
<i>Calyptraea mamillaris</i>	Broderip (1834)	Punta Charmé, Pacific Coast, Panama 08°30' N, 79°40' W	FMNH 282363	R. Collin
<i>Trochita Schumacher (1817)</i>				
<i>Trochita calyptraeformis</i> South	Born (1778)	Bahía de Herradura, Region IV, Chile 29°58' S, 71°21' W	ANSP A19737 BM20010476	R. Collin
<i>Trochita calyptraeformis</i> North	Born (1778)	Santa Maria, Peru 12°20' S, 76°45' W	BM20010475 FMNH 299424	R. Collin and A. Indocochea
<i>Bicatillus Swainson (1840)</i>				
<i>Bicatillus extinctorum</i>	Lamarck (1822)	Changi Point Beach, East of Singapore 1°15' N, 103°39' E	FMNH 299402	Tan Siong Kiat

<i>Sigapatella</i> Lesson (1830) <i>Sigapatella novaeselandiae</i>	Lesson (1831)	Portabello, South Island, New Zealand	FMNH 282186–282189 ANSP A19733 BM20010480	M. Barker C. Lambert
<i>Siphopatella</i> Lesson (1830) <i>Siphopatella walshi</i>	Reeve (1859)	Hong Kong 22°20' N, 114°0' W	FMNH 299401	B. Morton
<i>Zegalerus</i> Finlay (1926) <i>Zegalerus tenuis</i>	Gray (1867)	Omaha Bay, North Island, New Zealand 36°10' S, 174°30' E	FMNH 282309	R. Collin
<i>Capulidae</i> Montfort (1810) <i>Capulus ungaricus</i>	Linné (1767)	Koster, Sweden 58°52' N, 11°05' E	FMNH 299395	A. Warén
<i>Trichotropidae</i> Gray (1850) <i>Trichotropis cancellata</i>	Hinds (1843)	Friday Harbor, Washington, USA 48°20' N, 123 01' W	FMNH 282220, 285018	R. Collin
<i>Hipponicidae</i>, Troschel 1861 <i>Hipponix</i> sp. Australia		Lizard Island, Australia	UM-	T. Baumiller
' <i>Sabia conica</i> ' South Africa		Park Rynie, Kwazulu-natal, South Africa, 30°19' S, 30°44' E	FMNH 299397	R. Collin and R. Kilburn
' <i>Sabia conica</i> ' Australia		Edithburgh, Yorke Peninsula, South Australia 35°03' S, 137°26' E	FMNH 282246 ANSP A19750	W. Runball
<i>Cheilea equestris</i>	Linné (1758)	Louisiodes Archipelago, Papua New Guinea	FMNH 299396	G. Paulay
<i>Leptonetis perplexus</i>	Suter (1907)	New Zealand	FMNH 282289	R. Collin and S. O'Shea
<i>Vanikoro</i> sp.1		New Caledonia	SMNH 16892	A. Warén

*Abbreviations follow Leviton (1985) with SMNH for Swedish Museum of Natural History and ANM for Australian National Museum. Numerous additional lots from other localities have also been deposited at these institutions.

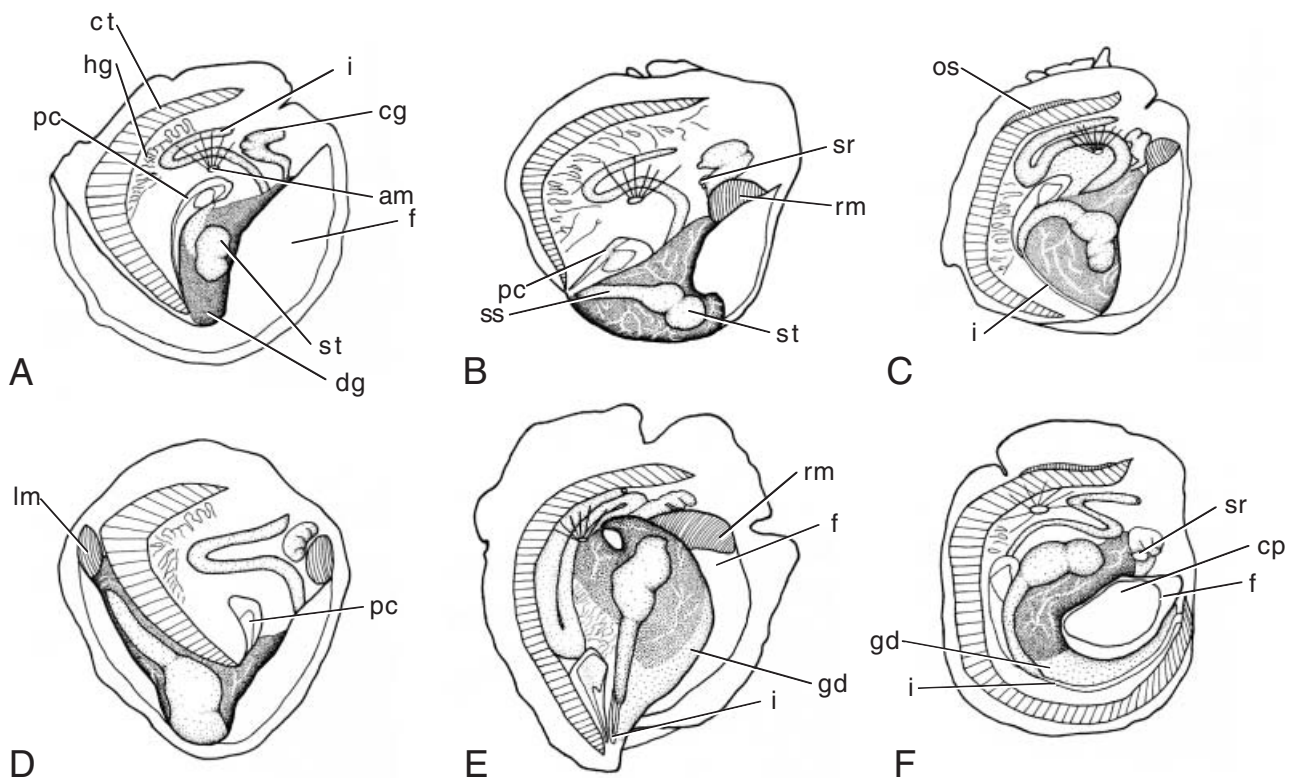


Figure 3. Illustration of the dorsal anatomy of calyptraeids (A) *Crepidula complanata*, (B) *Crepidula aculeata*, (C) *Crepipatella dilatata*, (D) *Crepidula monoxylla*, (E) *Calyptrea chinensis*, (F) *Crucibulum* cf. *personatum*. am = dorsal attachment muscle, cg = capsule gland, cp = connective tissue pad, ct = ctenidium, dg = digestive gland, f = foot, gd = gonad, hg = hypobranchial gland, i = intestine, lm = left shell muscle, os = osphradium, pc = pericardium, rm = right shell muscle, sr = seminal receptacle, ss = style sac, st = stomach.

was chosen because polarization using the earliest occurrence in fossils or ontogeny could not be applied equally to the molecular dataset.

Prior to phylogenetic analysis, I scored all morphological characters with respect to expected reliability and utility. Characters that represented large morphological differences and were easy to score unambiguously (e.g. presence/absence of a large shell muscle) were given a reliability score of 1, while characters that were more difficult to score, or showed more intraspecific variability, were given a score of 0 (e.g. differences in the shape of the subesophageal ganglion). Similarly, the anticipated phylogenetic utility of the characters, or the expected level of homoplasy was scored as 1 for characters that were not expected to be subject to high levels of homoplasy (e.g. presence/absence of large shell muscles) or 0 for characters for which high levels of homoplasy were expected (e.g. body colour). These scores reflect the likelihood that each character would be included in a morphological analysis in which characters deemed to be of low quality were subjectively excluded a priori.

TAXONOMY

Because the taxonomy of both the calyptraeids and hipponicids is highly uncertain, many of the species names listed in Table 2 are provisional. Where I am sure of the designation on the basis of examination of type material, the original type description and the original type locality, I have assigned the material examined to known species. However, in several cases where it was not clear to which species a particular population of animals belonged, I have indicated my uncertainty. Named species with which the material is most morphologically similar are indicated with 'cf.' (used here to imply morphological similarity only) or 'aff.' (used here to imply phylogenetic affinity and morphological similarity). Several of these species or species groups are currently being revised (Collin, 2002a; Véliz *et al.* 2001; R. Collin, unpubl. observ.). In some cases, two morphologically divergent populations of the same species may have been used as OTUs in this analysis (e.g. *Crucibulum lignarum* North and *Crucibulum lignarum* South, *Crepidula* aff. *williamsi*

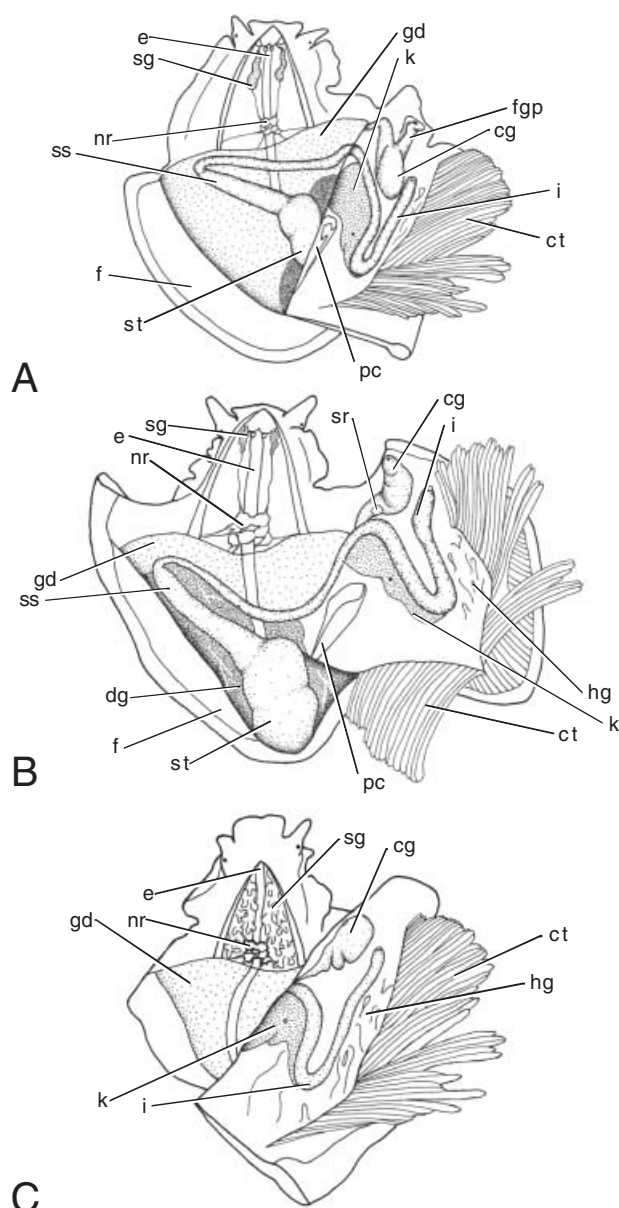


Figure 4. Illustration of the internal anatomy of calyptraeids. In this dorsal view the mantle is reflected to the left. (A) *Crepidula complanata*, (B) *Crepidula monoxyla*, (C) *Crepidula aculeata*. cg = capsule gland, ct = ctenidia, e = oesophagus, f = foot, fg = female genital papilla, gd = gonad, hg = hypobranchial gland, i = intestine, k = kidney, nr = nerve ring, pc = pericardium, sg = salivary gland, sr = seminal receptacle, ss = style sac, st = stomach.

Alaska and *Crepidula aff. williamsi* Washington) but adequate information is not currently available to assess their status as species. Vouchers from the same locality as the individuals used here have been deposited at the Field Museum, Chicago (FMNH), the Acad-

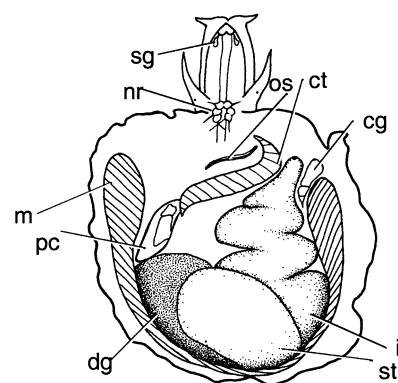


Figure 5. Illustration of hipponicid anatomy. cg = capsule gland, ct = ctenidium, dg = digestive gland, i = intestine, m = shell muscle, nr = nerve ring, os = osphradium, pc = pericardium, sg = salivary gland, st = stomach.

emy of Natural Sciences, Philadelphia (ANSP) and the Natural History Museum, London (BMNH).

PHYLOGENETIC ANALYSIS

The morphological dataset was concatenated with a molecular dataset composed of sequences from mitochondrial cytochrome oxidase I, 16S and nuclear 28S genes (Table 3). Taxa for which all datasets were not complete were deleted, creating a dataset of 77 taxa (including 69 calyptraeid operational taxonomic unit (OTUs), one trichotropid, one capulid, one vanikorid and five hipponicids). Details of DNA sequencing and alignment are given in Collin (2002b), and alignments can be obtained by the author.

Each of the four datasets (COI, 16S, 28S and morphology) were analysed separately. An unrooted, unordered, equal-weighted parsimony analysis was performed on each dataset using a heuristic search with tree-bisection-reconnection (TBR) branch-swapping, 1000 random additions, saving two trees at each step, and maxtrees set to 10 000. Gaps were treated as a fifth character state and areas of ambiguous alignment were excluded from the sequence data (Collin, 2002b). Bootstrap support for the resultant topologies was assessed based on 500 bootstrap replicates of a heuristic search, with TBR branch-swapping, 10 random additions saving two trees at each step, maxtrees set to 1000, and constant characters were excluded. The concatenated morphological and sequence dataset was analysed in the same way. Dataset combinability was assessed using the ILD-test as implemented in PAUP* version 4.0b8 (Swofford, 1998) with 100 replicates after excluding constant characters (Cunningham, 1997b).

Previous analysis of the DNA sequence data suggested that the hipponicids are a distant outgroup of

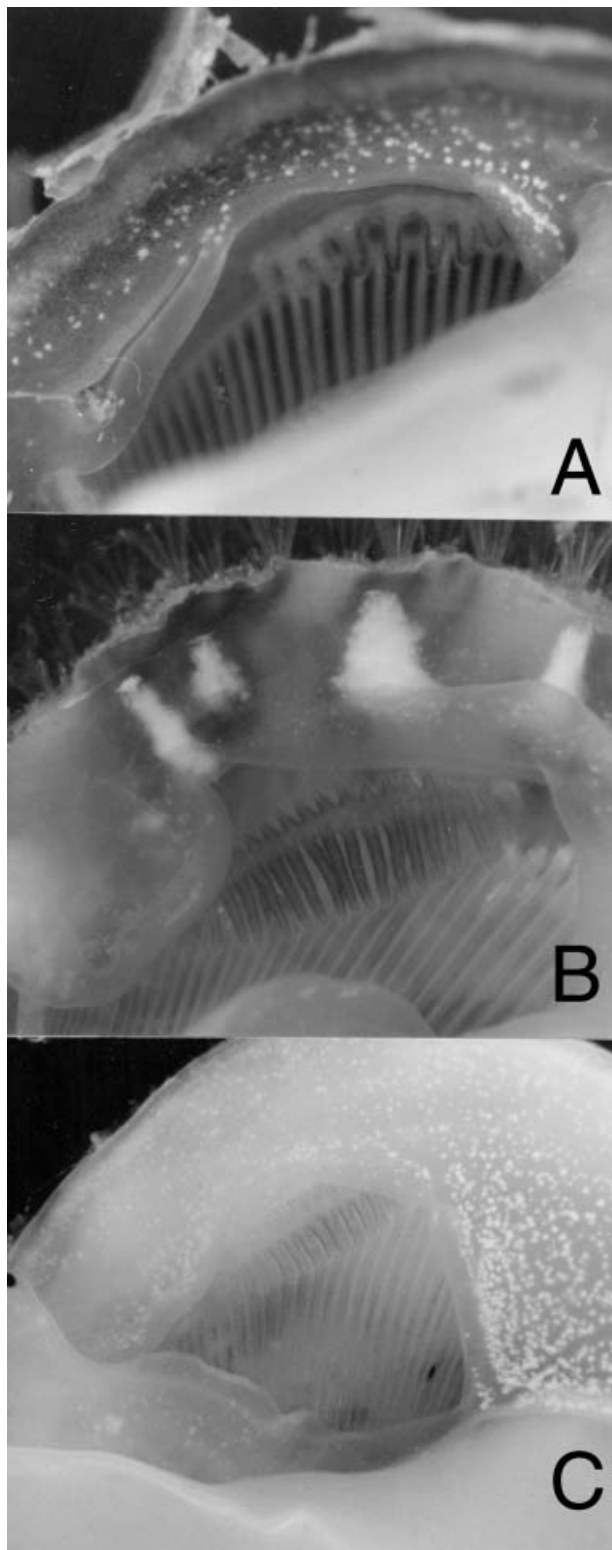


Figure 6. Photographs of calyptraeid osphradia. (A) *Crepidula adunca*, (B) *Crepipatella lingulata* and (C) *Calyptraea fastigata*.

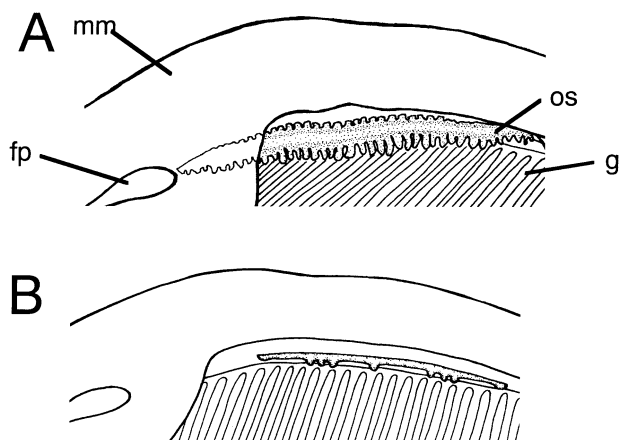


Figure 7. Illustrations of calyptraeid osphradia. (A) *Crepidula aculeata* and (B) *Crepidula norrisiarum*. fp = food pouch, g = gill, mm = mantle margin, os = osphradium.

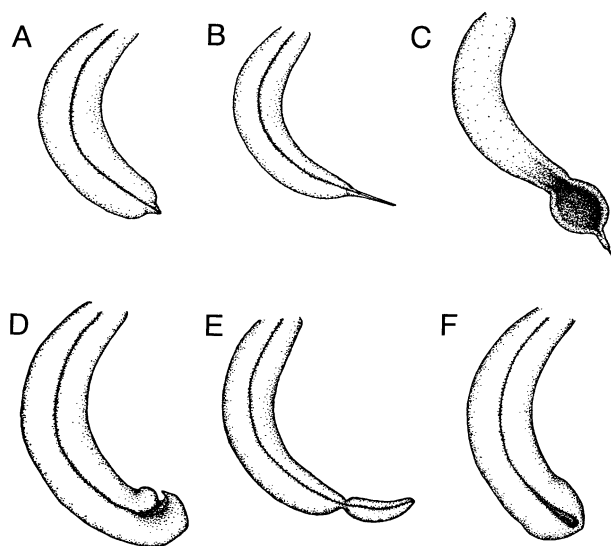


Figure 8. Illustration of calyptraeid penises. (A) *Crepidula aculeata*, (B) *Crepidula complanata*, (C) *Crepidula* n.sp. from La Paz, (D) *Calyptraea chinensis*, (E) *Crucibulum lignarum*, (F) *Calyptraea lichen*.

calyptraeids and may alter the ingroup relationships (Collin, 2002b). In addition, their limpet-like morphology that was most likely independently derived may mislead the morphological analysis. Therefore, the combined dataset was also analysed without the hipponicids and vanikorid. Exclusion of these taxa did not alter the results substantially (Collin, 2002b).

TAXONOMIC UTILITY OF DIFFERENT CHARACTER SETS

The taxonomic utility of different data sets was compared using a number of different metrics. The trees produced by analysis of the combined dataset were

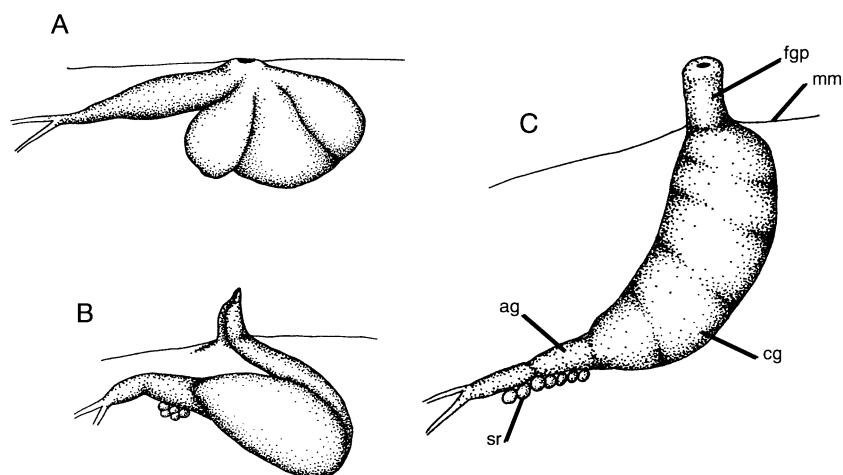


Figure 9. Illustration of calyptraeid female reproductive tracts. (A) *Crepidula aculeata*, (B) *Crepidula excavata* and (C) *Trochita calyptraeformis*. fgp = female genital papilla, mm = mantle margin, cg = capsule gland, ag = albumin gland and sr = seminal receptacles.

Table 3. Comparison of the four datasets and the trees they produce. GenBank numbers 28S: AF545871–AF545947; 16S: AF545948–AF546016, AY061765, AY061789, AY061770, AY061763, AY061764, AY061766, AY061767, AY061774; COI: AF546017–AF546076 AY061780, AY061789, AY061786, AY061780, AY061794, AY061783, AY061793, AY061792, AF178155, AF388698, AF178147, AF178120, AF178130, AF353129, AF388726, AF388700, AF353123

Datasets	No. characters	No. informative characters	No. taxa	MP tree length	No. MP trees	No. islands	No. times hit/1000	CI**	RI**	RCI**
Morphology	120	114	77	909	3 432	15	21/220	0.227	0.644	0.146
Shells	40	39	77	258	>100 000	–	–	0.292	0.739	0.216
Anatomy	80	75	77	553	104	3	168	0.237	0.669	0.159
DNA	1368	481	77	4728	6	2	187	0.223	0.520	0.116
28S	334	59	77	206	1 782	1	1000	0.617	0.755	0.465
16S	387	134	77	693	76	1	773*	0.404	0.702	0.284
COI	647	288	77	3749	18	4	337	0.173	0.478	0.083
Combined	1488	595	77	5773	16	1	277	0.219	0.531	0.116

* All random addition replicates that did not converge on the island of most parsimonious tree hit the maximum number of trees and therefore did not swap to completion. The 28S, COI and combined datasets never hit the maxtrees and the morphological dataset seldom did. ** Excluding uninformative characters.

considered to be the current 'best estimate' of calyptraeid phylogeny. The average consistency index [CI], Kluge and Farris (1969); and retention index [RI], Farris (1989) were calculated for parsimony informative characters from each dataset on the best estimate topologies. These indices reflect the levels of homoplasy and the retention of phylogenetic information for each data partition throughout the tree.

The power of each dataset to recover a topology, in which the nodes present in the 'best estimate' topologies are well resolved and well supported, was assessed by comparing the analyses of the individual datasets with the 'best estimate' topologies. The

resolving power of each dataset was assessed by counting the number of resolved nodes in the consensus of the most-parsimonious trees from each data set. The resolved nodes recovered by each data set were compared to the resolved nodes present in the consensus of the 'best estimate tree' to assess consistency of the dataset with the best estimate. The level of support each dataset provides for the recovered topology was assessed in a similar way by comparing nodes with >70% bootstrap support in the tree from each dataset to the nodes with >70% bootstrap consensus of the combined data (i.e. the bootstrap of the 'best estimate tree').

RESULTS

COMBINABILITY ANALYSIS

A total of 100 replicates of the ILD test demonstrated conflict among the datasets when all four datasets are included ($P = 0.01$), when the combined DNA dataset is compared to the morphological dataset ($P = 0.008$), and when the shell data were compared to the data from soft anatomy ($P = 0.007$). Because conflict among the three DNA datasets was not demonstrated by the ILD test (Collin, 2002b; R. Collin, unpubl. observ.) this result is almost certainly due to conflict between the morphological and DNA data. The ILD test has been demonstrated to be a conservative test for conflict among datasets (e.g. Sullivan, 1996; Cunningham, 1997a,b; Messenger & McGuire, 1998; Yoder *et al.*, 2001) and the small number of characters in the datasets for shell and soft anatomy may additionally weaken the test. However, the results of the ILD tests are also supported by the differences between the topologies produced by analysis of the DNA data and the morphological data (see below).

COMBINED ANALYSIS

Parsimony analysis of the total dataset was used to produce a topology that will be subsequently referred to as the 'best estimate topology'. This analysis resulted in a single island of 16 equally parsimonious trees with length 5773 (Table 3; Figs 10,11). About half (47) of the nodes had bootstrap support $>70\%$ (Fig. 10). Overall, the tree topology was well resolved (Fig. 11), well supported and in general agreement with the topologies supported by analysis of DNA data for 120 species (Collin, 2002b). Exclusion of the hipponicid and vanikorid outgroups did not significantly alter the best estimate topology (data not shown; Collin, 2002b).

There were different levels of average homoplasy

and phylogenetic retention for each of the different datasets on the best estimate topology (Table 4). The average CI, RI and rescaled consistency index [RCI] for the morphological characters, the DNA characters and all of the characters combined were more or less the same. However, 28S and 16S characters performed higher than average, both soft anatomy and shell characters had average scores and COI had substantially lower values for all three indices (Table 4). The lower values for COI sequences could reflect high levels of homoplasy resulting from saturation in these quickly evolving sequences (Collin, 2002b) or from constraints imposed by selection on amino acid sequence.

ANALYSIS OF INDIVIDUAL DATASETS

The unweighted parsimony analysis of the COI dataset produced a single island of the 18 most-parsimonious trees with length 3749 (Table 3; Figs 12,13). These trees are similar to the tree produced by the combined analysis. However, the combined analysis produced more nodes with high bootstrap support deep within the tree, while the COI dataset alone provides no support for the deep nodes (Fig. 12). Analysis of the 16S produces a single island of 78 trees similar to the topology produced by the analysis of COI (Table 3; Figs 14,15). The 16S has similar resolution as judged by the consensus of the 78 most-parsimonious trees (Fig. 15), but there are fewer nodes with high bootstrap support (Fig. 14). There is little support for the topology at the tips of the tree while deeper divisions within the calyptraeids are well supported. Finally, analysis of 28S sequences produced little resolution and few well supported nodes (Figs 16,17). The low levels of differentiation and the large number of trees in the island of most parsimonious trees contributed to the low number of resolved nodes (Table 3; Figs 16,17). Analysis of all the DNA data combined

Table 4. Consistency of characters on the 'best estimate' tree including all taxa

Character groups	Number of informative characters	Tree length*	CI*	RI*	RCI*
Total data	595	5605	0.195	0.531	0.104
Total morphology	114	1020–1030	0.198–0.200	0.582–0.587	0.115–0.117
Anatomy	75	654–658	0.196–0.197	0.585–0.589	0.115–0.116
Shell	39	366–372	0.202–0.205	0.574–0.583	0.116–0.119
Total DNA	481	4575–4585	0.194–0.195	0.517–0.519	0.100–0.101
28S	59	183–184	0.418–0.421	0.668–0.671	0.279–0.282
16S	134	660–666	0.330–0.333	0.678–0.683	0.224–0.228
COI	288	3729–3737	0.159	0.471–0.472	0.075

*Excluding uninformative characters.

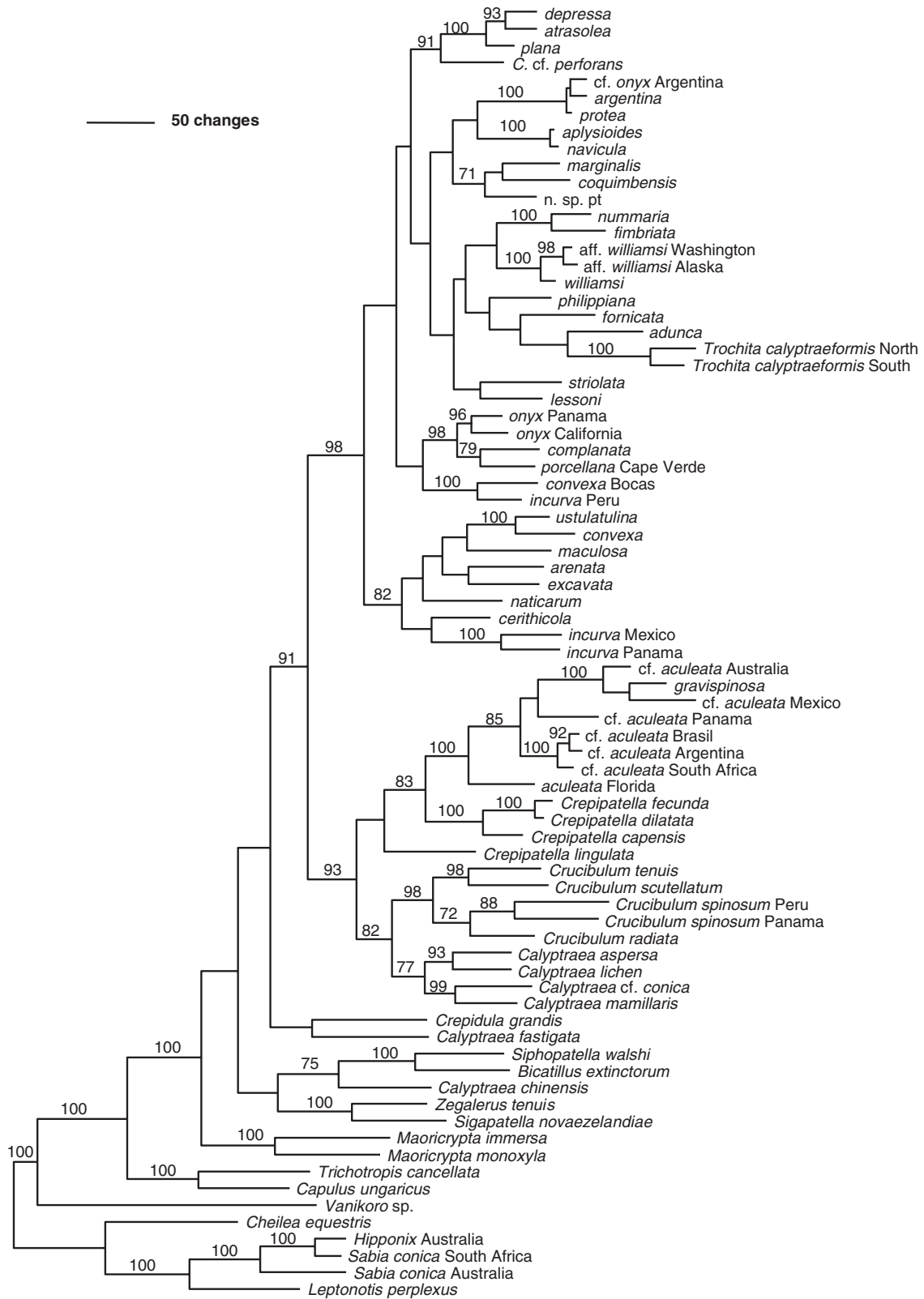


Figure 10. One of the 16 'best estimate trees'. A phylogram of a most parsimonious tree from the analysis of all the data combined. Bootstrap supports of >70% are above the branches. Species without genus names are *Crepidula* species.

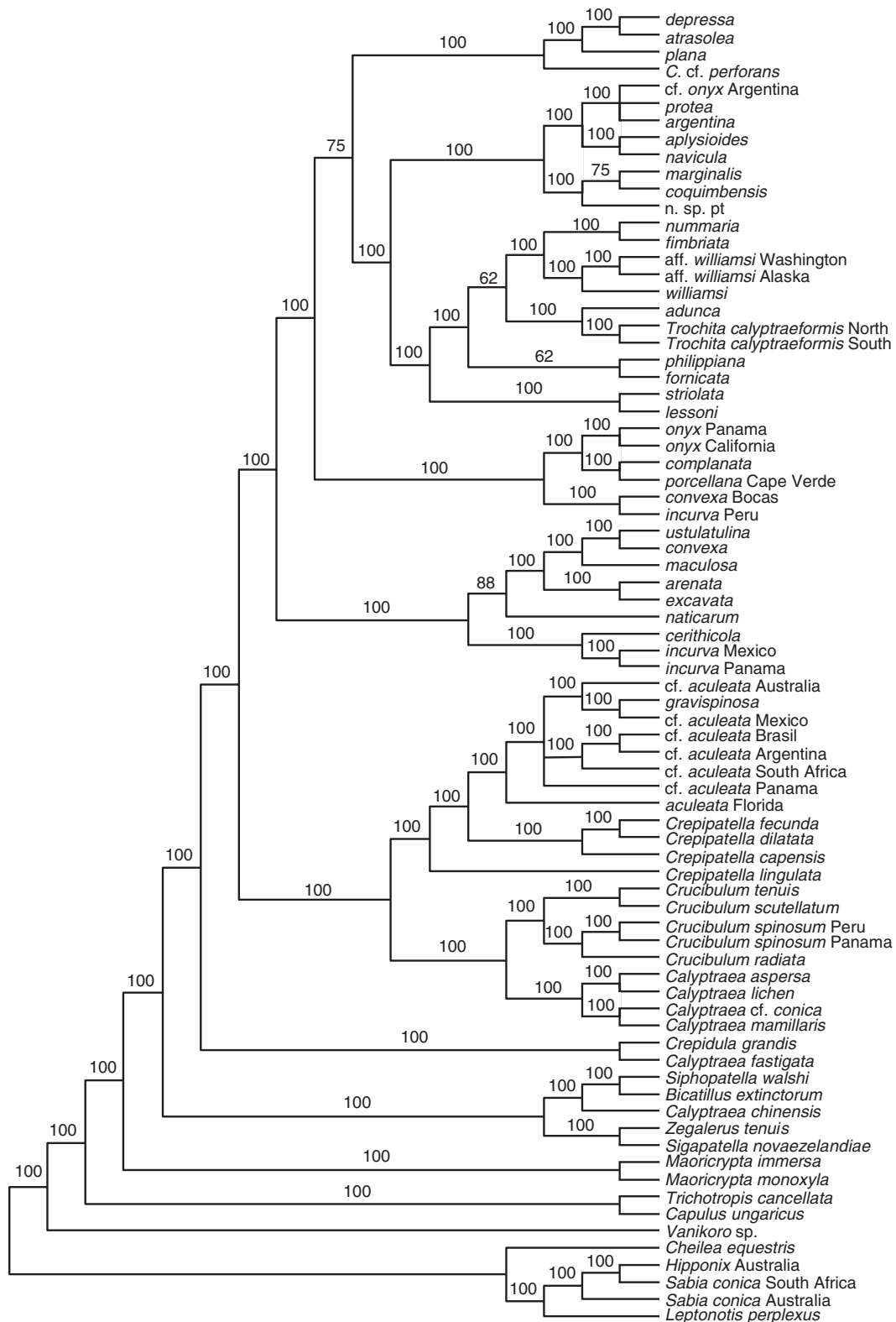


Figure 11. Consensus of the 'best estimate trees'. The consensus of most parsimonious trees from the analysis of all data combined. Proportion of parsimonious trees with the branch given above the branch. Species without genus names are *Crepidula* species.

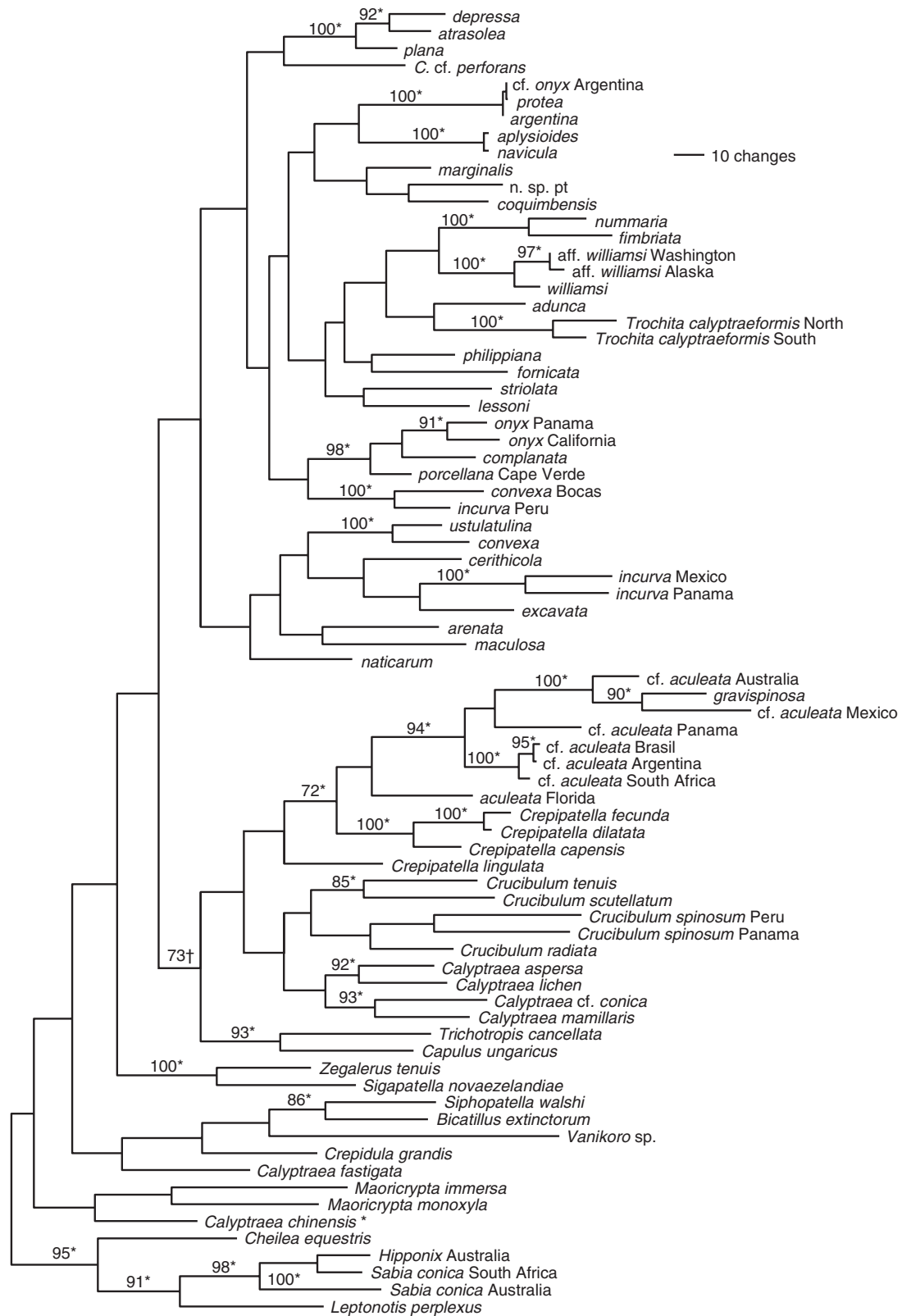


Figure 12. A single most parsimonious tree from the analysis of COI DNA sequence data. Bootstrap supports of >70% are above the branches. *Branches supported with >70% bootstrap in the 'best estimate tree'. †Branches conflicting with >70% bootstrap supported branches in the 'best estimate tree'. Species without genus names are *Crepidula* species.

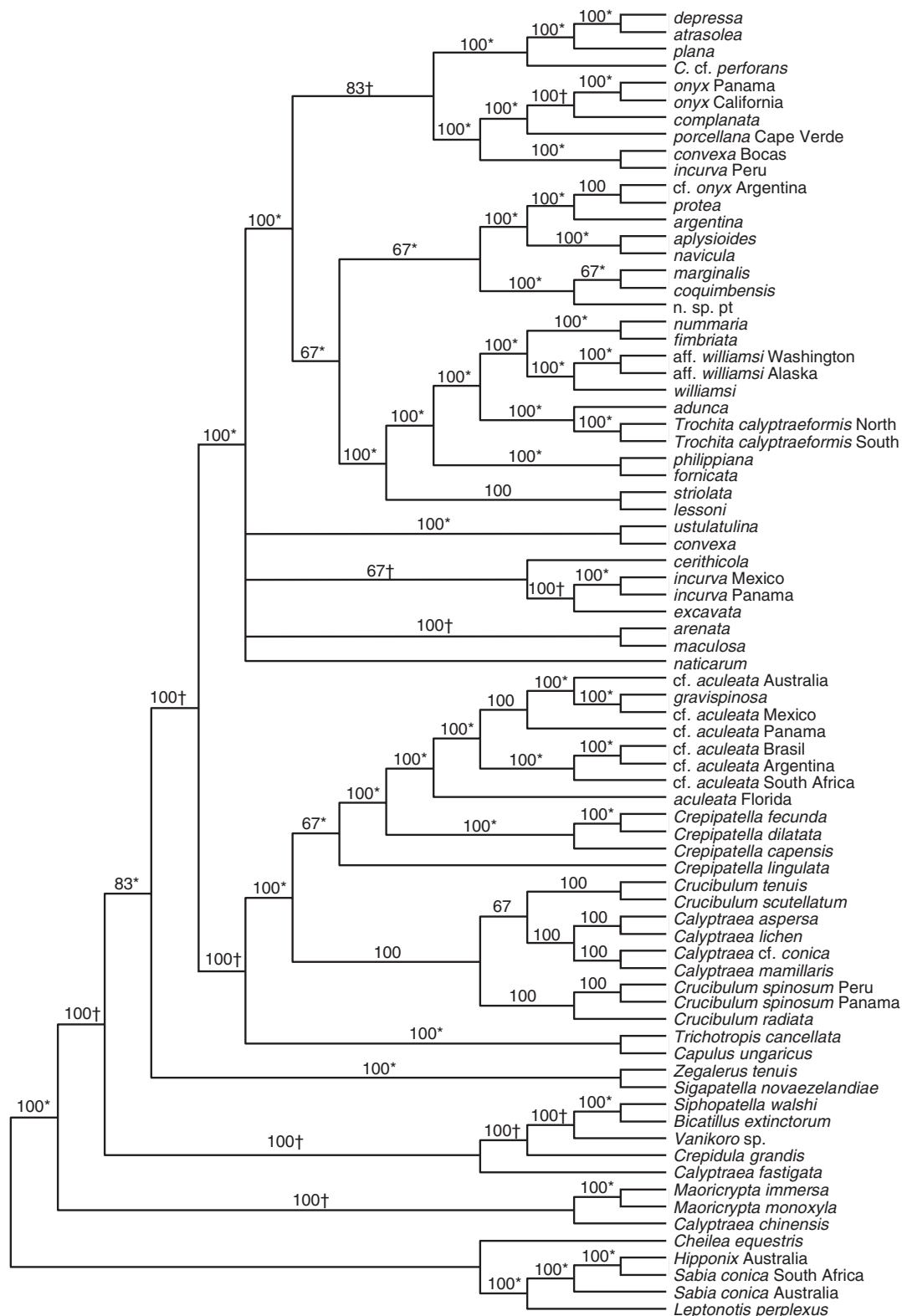


Figure 13. The consensus of most parsimonious trees from the analysis of COI DNA sequence data. Proportion of parsimonious trees with the branch given above the branch. *Branches that also occur in the consensus of the 'best estimate trees'. †Branches conflicting the consensus of the 'best estimate trees'. Species without genus names are *Crepidula* species.

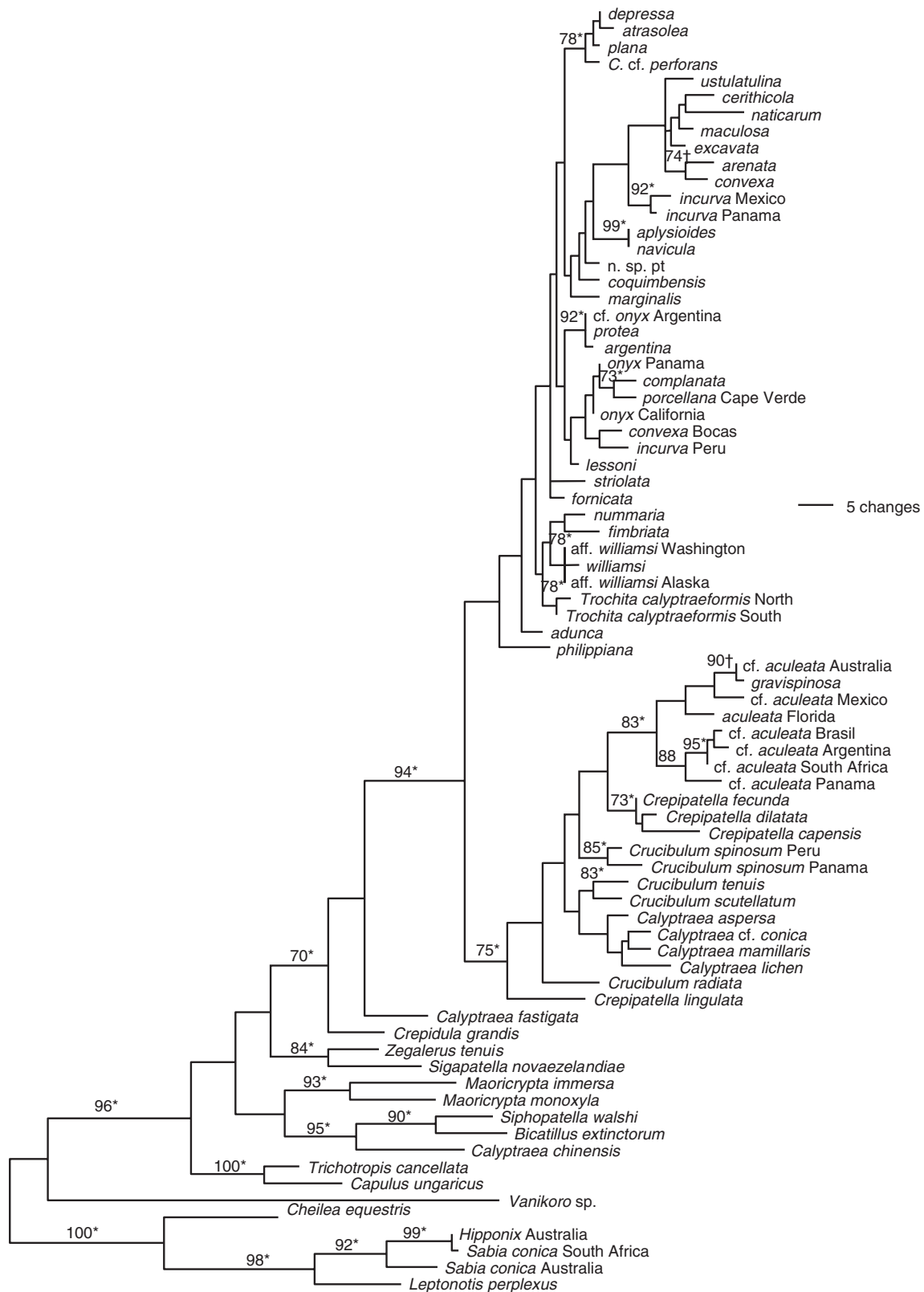


Figure 14. A single most parsimonious tree from the analysis of 16S DNA sequence data. Bootstrap support of >70% are above the branches. *Branches supported with >70% bootstrap in the 'best estimate tree'. †Branches conflicting with >70% bootstrap supported branches in the 'best estimate tree'. Species without genus names are *Crepidula* species.

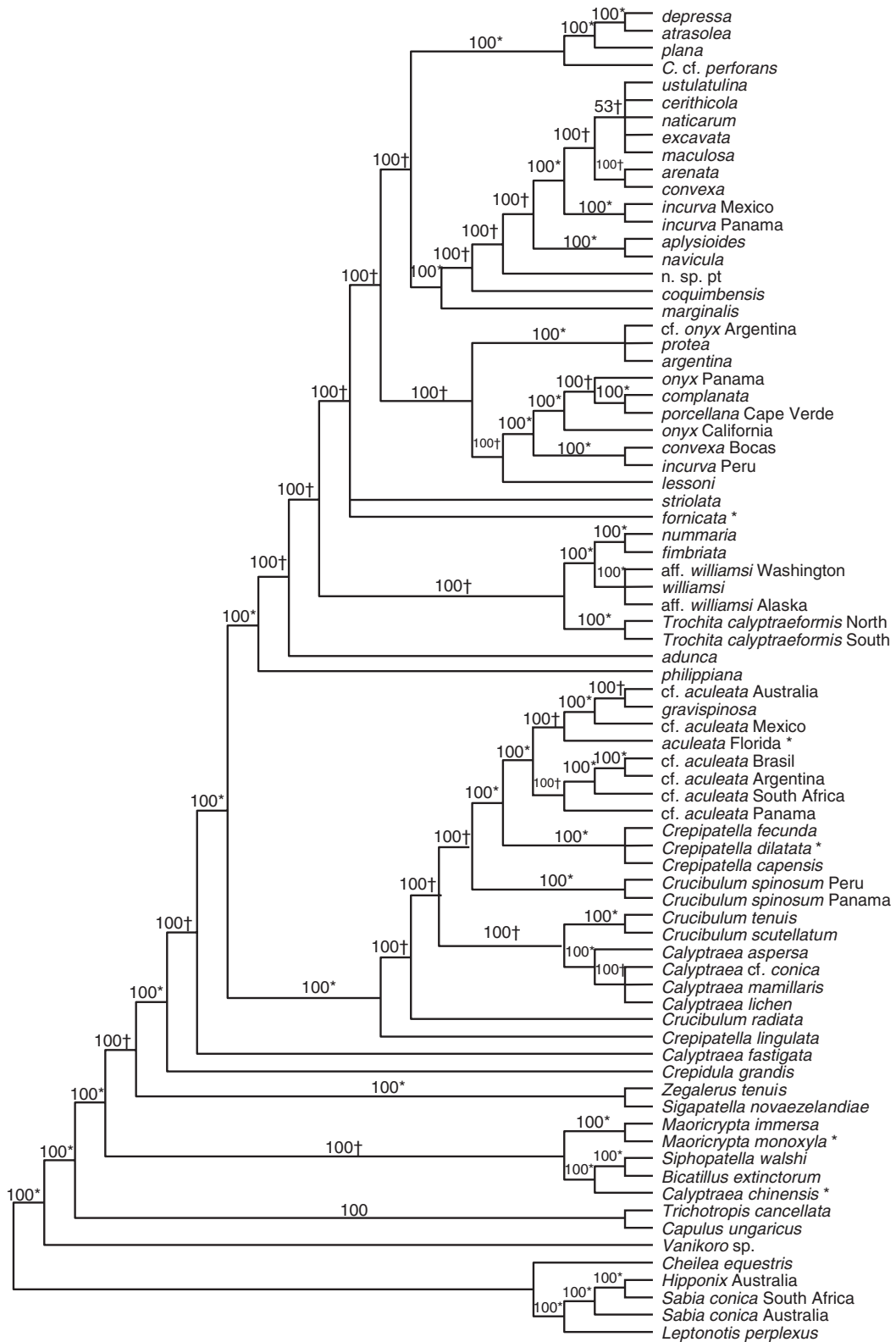


Figure 15. The consensus of most parsimonious trees from the analysis of 16S DNA sequence data. Proportion of parsimonious trees with the branch given above the branch. *Branches that also occur in the consensus of the 'best estimate trees'. †Branches conflicting the consensus of the 'best estimate trees'. Species without genus names are *Crepidula* species.

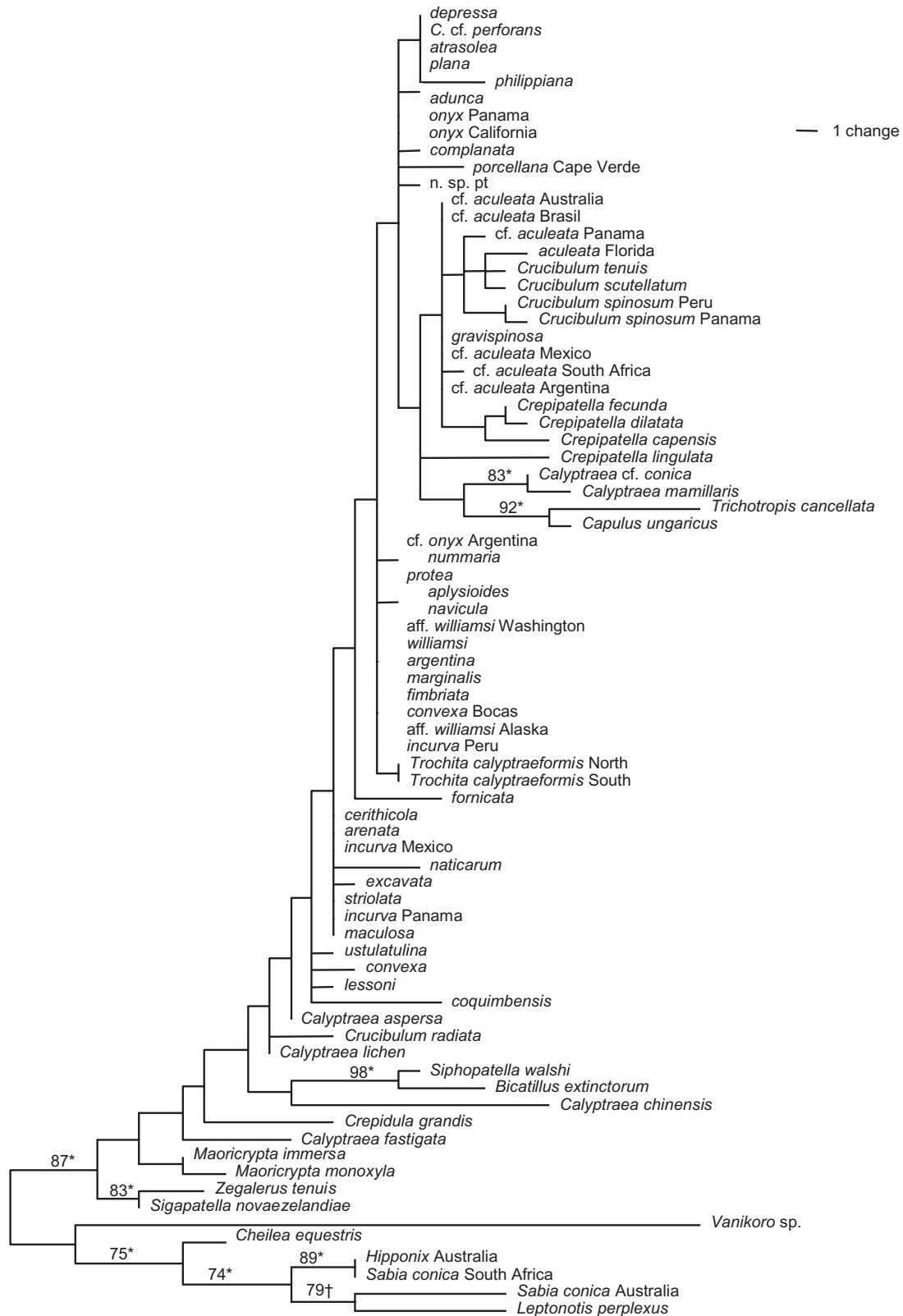


Figure 16. A single most parsimonious tree from the analysis of 28S DNA sequence data. Bootstrap support of >70% are above the branches. *Branches supported with >70% bootstrap in the 'best estimate tree'. †Branches conflicting with >70% bootstrap supported branches in the 'best estimate tree'. Species without genus names are *Crepidula* species.

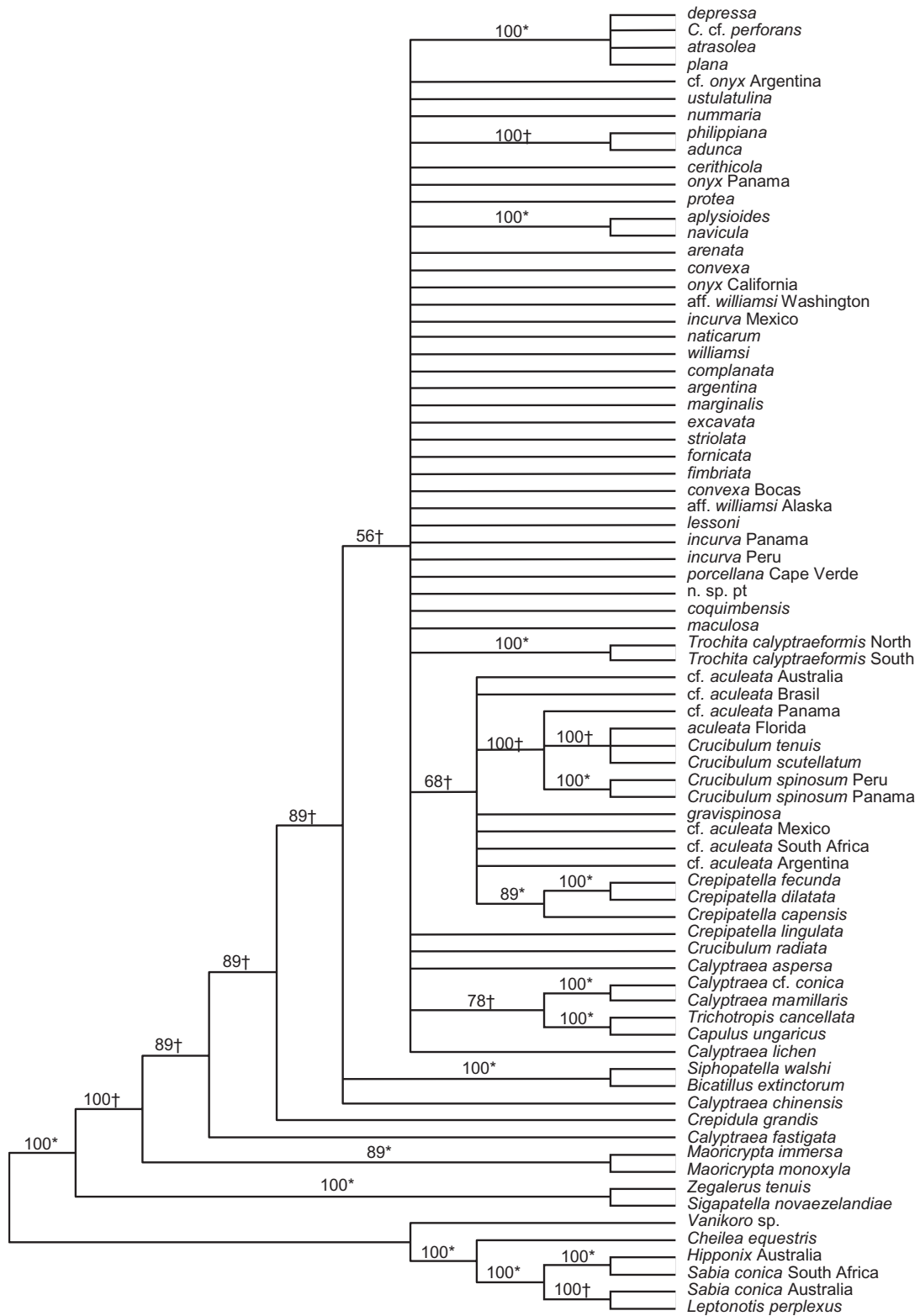


Figure 17. The consensus of most parsimonious trees from the analysis of 28S DNA sequence data. Proportion of parsimonious trees with the branch given above the branch. *Branches that also occur in the consensus of the 'best estimate trees'. †Branches conflicting the consensus of the 'best estimate trees'. Species without genus names are *Crepidula* species.

resulted in a tree with high resolution and support (Table 3; Figs 18,19).

Parsimony analysis of the morphological data produced numerous islands of equally parsimonious trees, each of which was reached only a few times, and numerous islands of slightly longer trees (Figs 20,21). Despite the fact that many of the nodes were resolved on the consensus of the parsimonious trees (Fig. 21), very few of the nodes were well supported in the bootstrap analysis (Fig. 20). Some of the aspects of the anatomical tree reflect the topologies produced by the 16S, COI and combined analysis (Figs 10–19). For example, the south-west Pacific species, *C. monoxyla* and *C. immersa*, appear at the base of the calyptraeids, and the calyptraeids are divided into two major groups, one comprised of *Crepidula s.s.* and the other including *Crucibulum*, *Calyptraea*, *Bostrycapulus* and *Crepidatella* (Figs 20,21). However, there are striking differences in the details of the topologies. In all except the morphological analyses, *C. grandis* is not placed within the true *Crepidula* clade while both samples of *Trochita* species are in this clade. In addition, the morphological analyses support the monophyly of *Crucibulum* and the paraphyly of the *Calyptraea*-morphs, whereas the other analyses show *Crucibulum* as paraphyletic and the *Calyptraea*-morphs as polyphyletic. Finally, in all other analyses the western Pacific species appear in a basal polytomy with *C. immersa* and *C. monoxyla*, while the morphological data places them well within the *Crucibulum*–*Calyptraea* clade.

Separate analysis of the characters from shells and soft anatomy produce somewhat different tree topologies (Figs 22–24). The topologies supported by anatomical characters are similar to the topology produced by analysis of all of the morphological data: Monophyletic calyptraeids and hipponicids + vaniko-

rid clades are well supported, *C. immersa* and *C. monoxyla* are basal to the two major calyptraeid clades, and *Crepidula s.s.* is sister to a clade comprised of the other calyptraeids. The shell data, on the other hand, produce a topology (Fig. 24) even further removed from the best estimate topology. In addition to placing *C. grandis* within the *Crepidula s.s.* clade (as in the total morphology), the western Pacific species *C. immersa* and *C. monoxyla* are also nested within the *Crepidula s.s.* clade. Finally, neither the calyptraeids nor hipponicids appear as monophyletic. This is most likely due to the large number of characters that are based on the internal shelly septum which is present in *Cheilea* and calyptraeids but not other hipponicids. Unfortunately, the low number of characters in each of these datasets makes it difficult to determine how robust these topologies would be to the addition of more characters.

RESOLUTION AND SUPPORT

Comparisons of the resolution and support for each node on the topologies obtained by analysis of each dataset with the best estimate topologies illustrated interesting patterns. The resolution, as measured by the number of nodes recovered in the consensus of all most parsimonious trees, was generally similar among datasets (Table 5; with the exception of the 28S dataset, which recovered few nodes). However the number of resolved nodes that agreed with the best estimate tree differed strikingly among datasets (Table 5): Morphological data produced trees in which 9–28% of the resolved nodes appeared in the best estimate tree, while 53–96% of the nodes resolved by the DNA datasets occurred in the best estimate tree. In contrast, high levels of bootstrap support for a node in the analysis of a single dataset did indicate that this

Table 5. Comparisons of the number of resolved nodes recovered by each dataset compared to the resolved nodes in the 'best estimate' tree

Character groups	No. resolved nodes in the consensus tree majority rule/strict	No. nodes resolved correctly in consensus majority rule/strict	No. nodes resolved incorrectly in consensus majority rule/strict
Total data	72/67	–	–
Total morphology	56/11	12/1 (21/9%)	43/9
Anatomy	69/54	15/15 (21/28%)	54/39
Shell	63/38	7/6 (11/16%)	55/31
Total DNA	72/57	58/55 (80/96%)	12/4
28S	26/18	14/12 (53/66%)	12/6
16S	67/66	41/41 (61/62%)	26/25
COI	69/61	55/51 (79/83%)	14/10

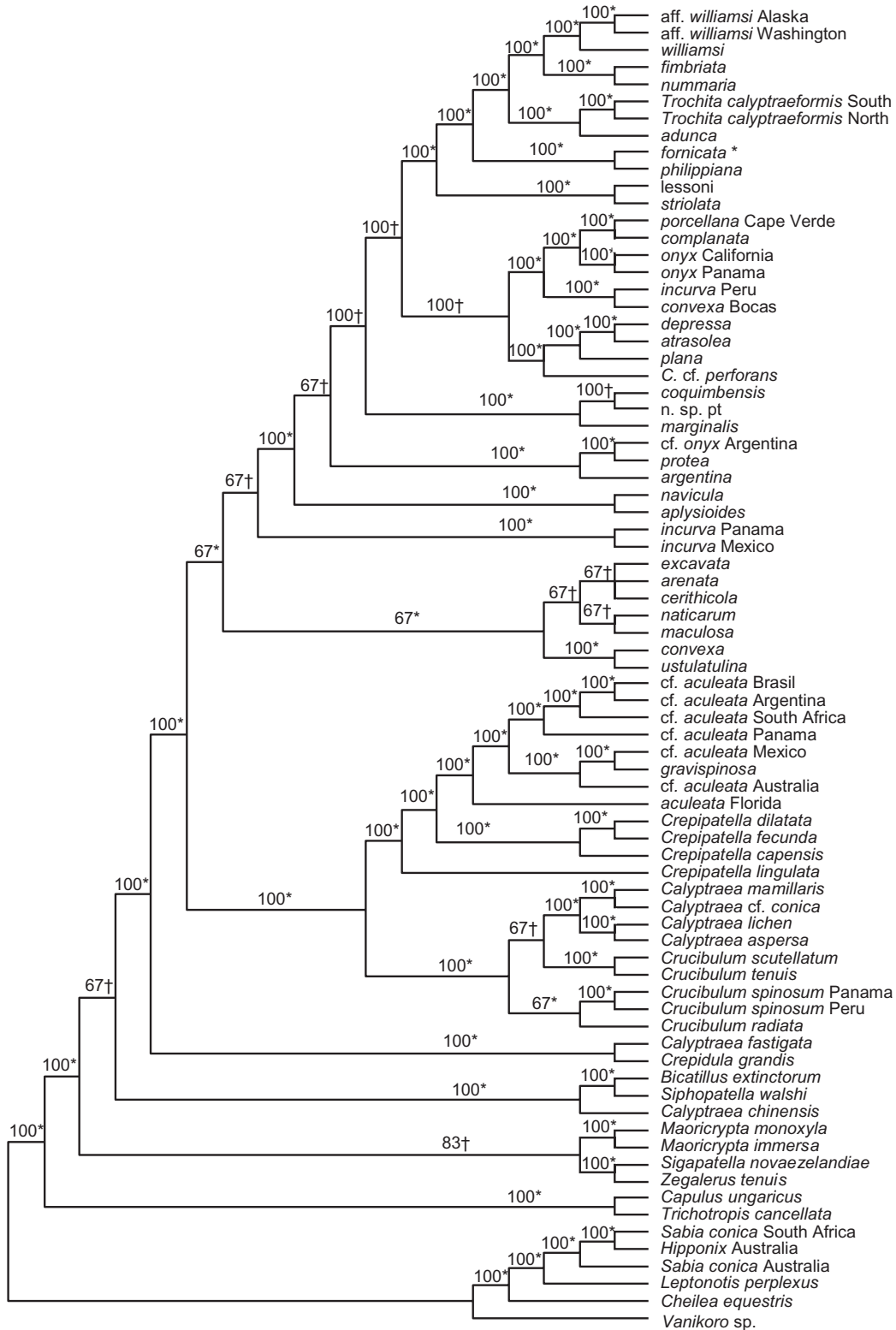


Figure 19. The consensus of all most parsimonious trees from the analysis of all the DNA data. Proportion of parsimonious trees with the branch given above the branch. *Branches that also occur in the consensus of the ‘best estimate trees’. †Branches conflicting the consensus of the ‘best estimate trees’. Species without genus names are *Crepidula* species.

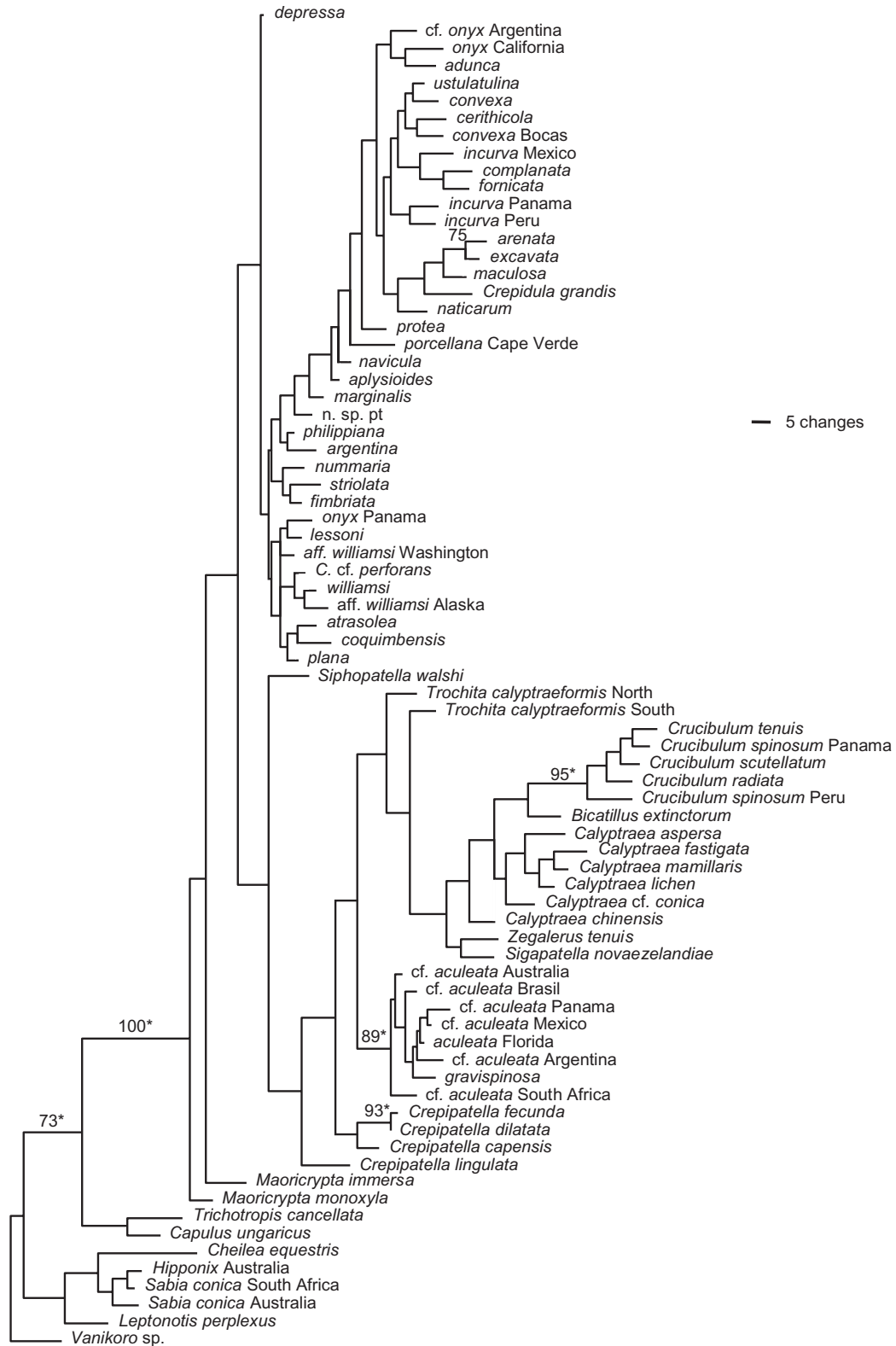


Figure 20. A single most parsimonious tree from the analysis of all the morphological data. Bootstrap support of >70% are above the branches. *Branches supported with >70% bootstrap in the 'best estimate tree'. †Branches conflicting with >70% bootstrap supported branches in the 'best estimate tree'. Species without genus names are *Crepidula* species.

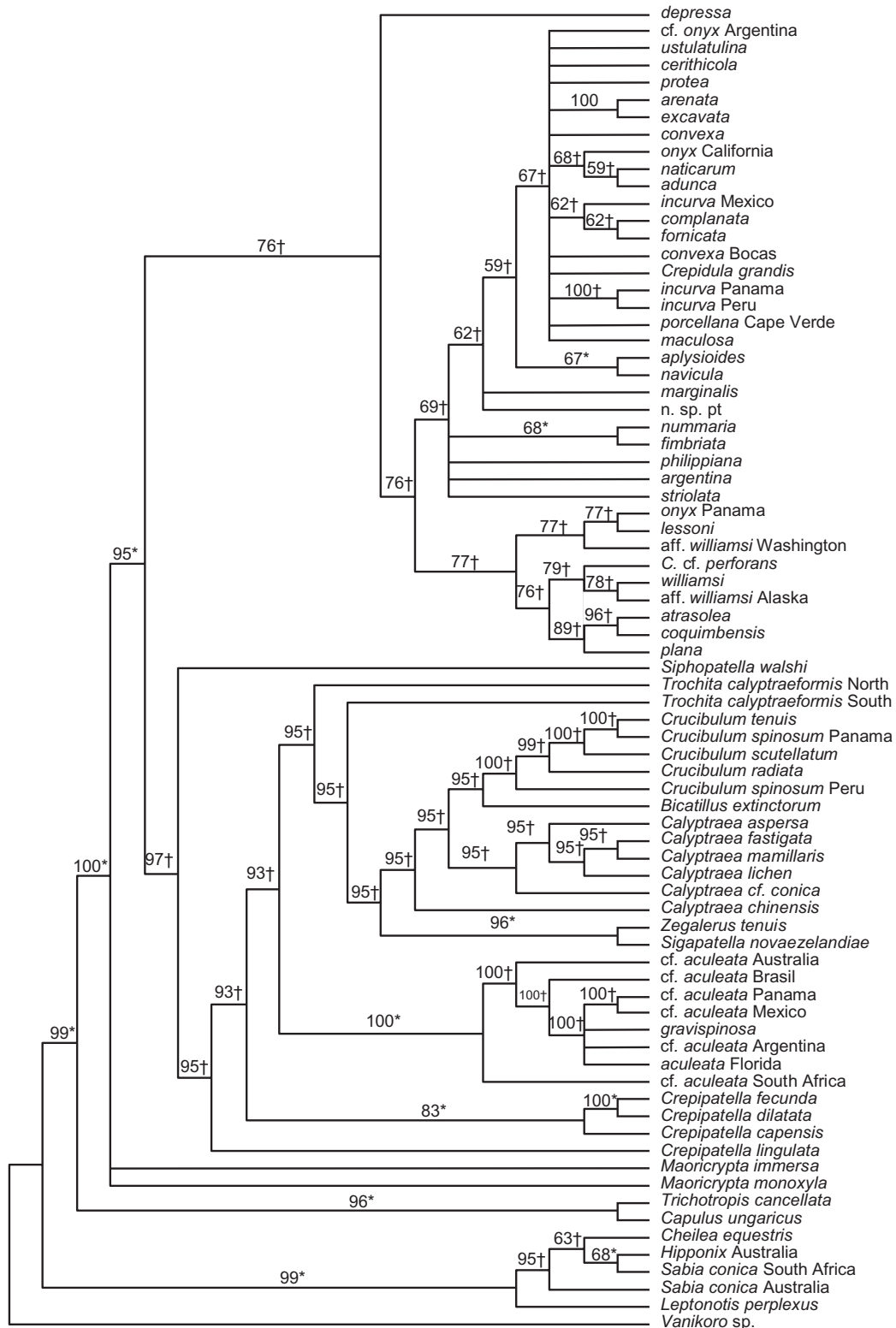


Figure 21. The consensus of most parsimonious trees from the analysis of all the morphological data. Proportion of parsimonious trees with the branch given above the branch. *Branches that also occur in the consensus of the 'best estimate trees'. †Branches conflicting the consensus of the 'best estimate trees'. Species without genus names are *Crepidula* species.

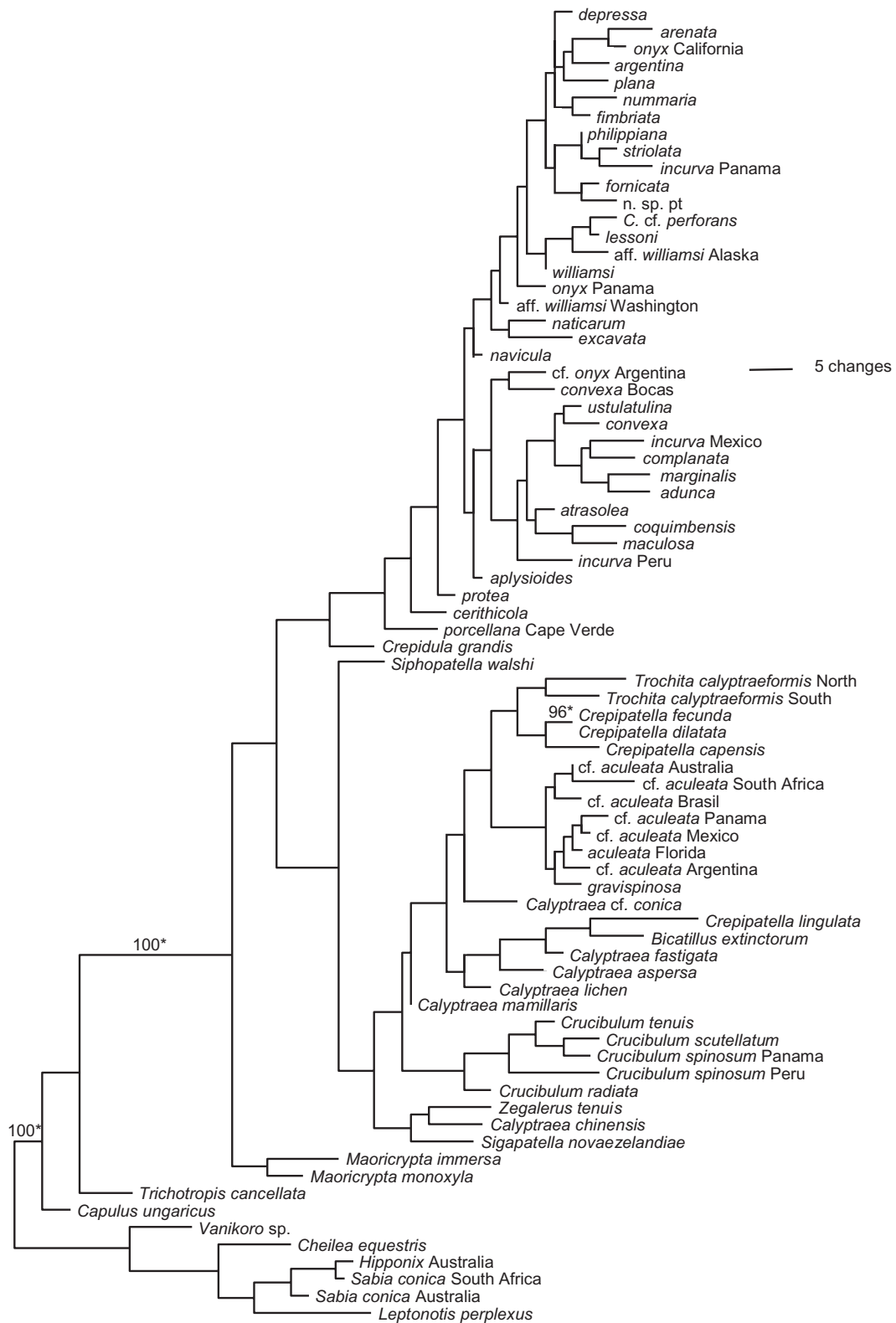


Figure 22. A single most parsimonious tree from the analysis of characters from soft morphology. Bootstrap supports of >70% are above the branches. *Branches supported with >70% bootstrap in the 'best estimate tree'. †Branches conflicting with >70% bootstrap supported branches in the 'best estimate tree'. Species without genus names are *Crepidula* species.

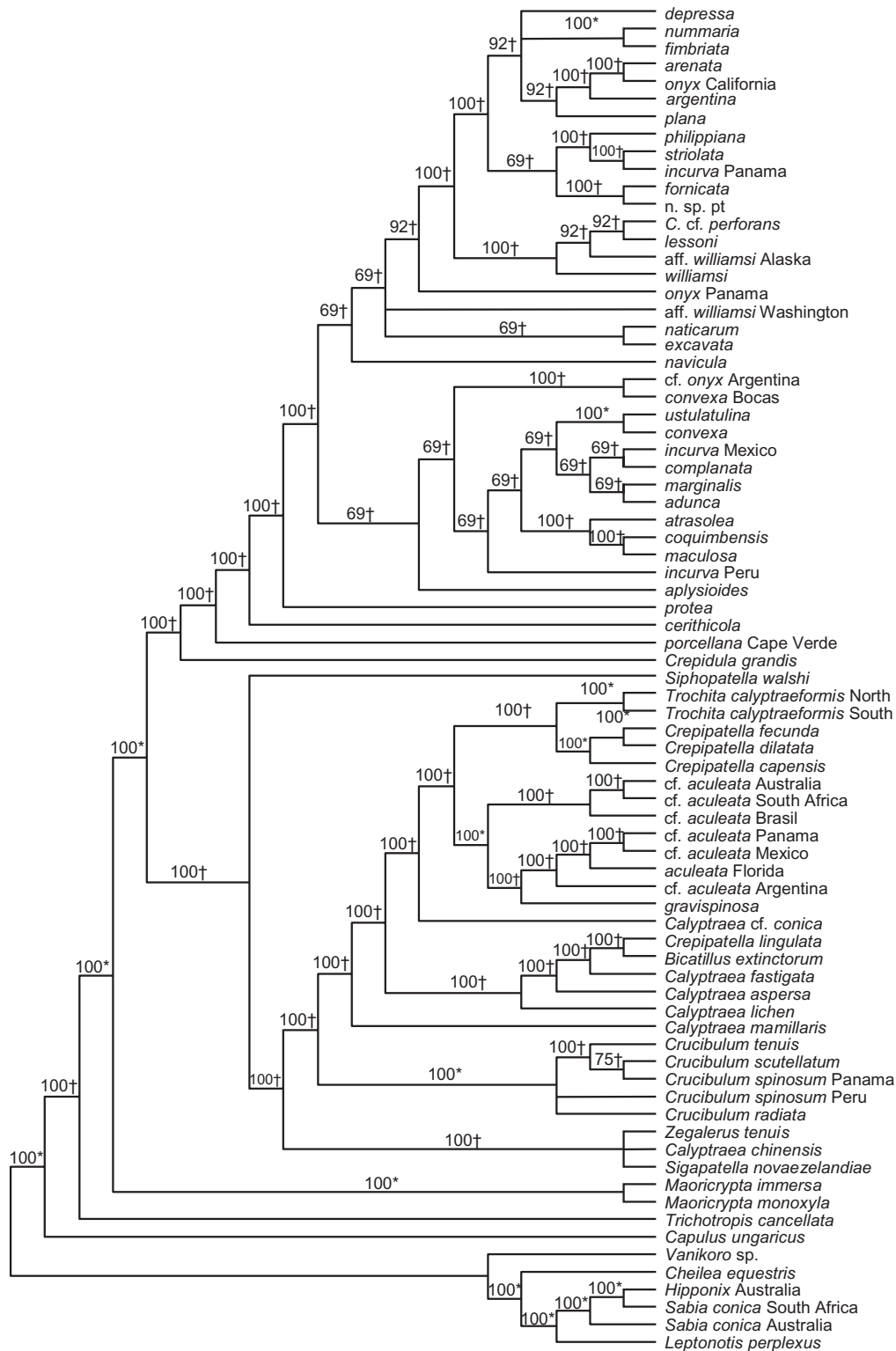


Figure 23. The consensus of all most parsimonious trees from the analysis of characters from soft morphology. Proportion of parsimonious trees with the branch given above the branch. *Branches that also occur in the consensus of the 'best estimate trees'. †Branches conflicting the consensus of the 'best estimate trees'. Species without genus names are *Crepidula* species.

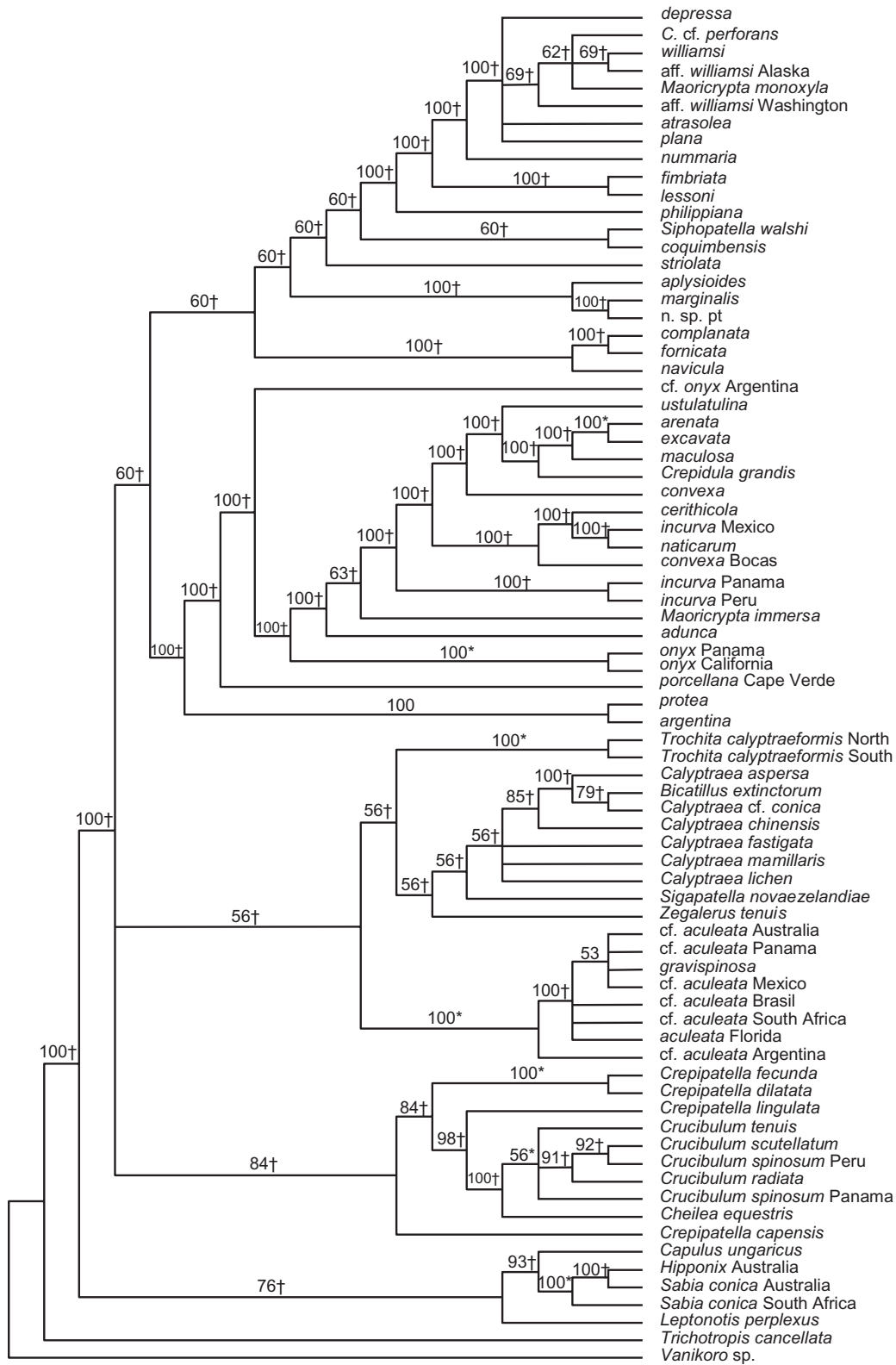


Figure 24. The consensus of all most parsimonious trees from the analysis of shell characters. Proportion of parsimonious trees with the branch given above the branch. *Branches that also occur in the consensus of the 'best estimate trees'. †Branches conflicting the consensus of the 'best estimate trees'. Species without genus names are *Crepidula* species.

Table 6. Comparisons of the number of supported nodes recovered by each dataset compared to the supported nodes in the 'best estimate' tree

Character Groups	No. nodes with >70% bootstrap support	No. correct nodes with >70% bootstrap support	No. incorrect nodes with >70% bootstrap support
Total data	47	–	–
Total morphology	6	5	0
Anatomy	3	3	0
Shell	–	–	–
Total DNA	39	39	0
28S	9	8	1
16S	28	26	2
COI	32	30	1

node would also have support in the best estimate tree (Table 4). Almost all of the nodes that occurred in the analysis of any dataset with >70% bootstrap support also received bootstrap support in the best estimate tree.

The number of both resolved and supported nodes increased when the different datasets were combined. The combined DNA dataset produced more resolution and support than 16S, 28S or COI alone. Despite the general weak performance of the morphological data alone, when the morphological characters were combined with the DNA dataset there was an additional increase in resolution and support (Tables 5,6).

PREDICTED QUALITY OF ANATOMICAL CHARACTERS

A compound index of predicted character quality was obtained by adding the expected reliability and expected utility. This index was correlated with the length, CI and RI of each anatomical character on the best estimate tree (Fig. 25). However the CIs and RIs varied greatly both in characters that were and were not expected to be useful. This demonstrates that, although the characters chosen a priori as subjectively 'better' perform better on average than the characters identified as 'poor', the phylogenetic quality of any specific character cannot be well predicted a priori.

DISCUSSION

The utility of shell and anatomical characters in the recovery of molluscan relationships has been the subject of recent discussion (e.g. Schander & Sundberg, 2001; Wagner, 2001). Previous studies of muricids (Kool, 1993; Vermeij & Carlson, 2000) have suggested that shell characters may be misleading at deep nodes due to pervasive convergences associated with adaptations for predation (e.g. apertural teeth) or defenses

(e.g. ribs). On the other hand, anatomical data have been considered too conservative to construct well-resolved species-level phylogenies (Kool, 1993; Vermeij & Carlson, 2000). However, in a review of 28 morphological studies, Schander & Sundberg (2001) found that the CIs and RIs of shell characters did not differ noticeably from the CIs and RIs of anatomical characters. They concluded that there is no a priori reason to exclude shell characters as phylogenetically misleading. Similarly, the results presented here showed that the average CIs and RIs of shell characters and anatomical characters did not differ on the best estimate topology of calyptraeid relationships. In addition the overall average CI and RI of morphological data did not differ from the values of the DNA data, although the values varied among genes.

The results reported here do offer support for the previous conclusions that shell characters may be subject to convergences that are difficult to detect. For example, the shells of *C. immersa* and *C. monoxyla* are indistinguishable from shells of species in the *Crepidula s.s.* clade. However, the arrangement of the visceral mass in these two species is significantly different from the arrangement of the visceral mass in other *Crepidula* species. In *C. immersa* and *C. monoxyla* the mantle cavity runs obliquely across the viscera, not along the left margin of the visceral mass, the style sac is lateral to the mantle cavity as opposed to below it, and finally the dorsal attachment muscle is fused with the right shell muscle. I believe that this anatomical data in combination with the DNA data provides compelling evidence for the convergent evolution of shell shape in *Crepidula s.s.* and *Maoricrypta*. A similar situation occurs in *Bostrycapulus*. *Bostrycapulus* shells differ from the shells of the *Crepidula s.s.* clade only in that they are slightly more coiled and that they have spines. However, they are anatomically quite different; *Bostrycapulus* species

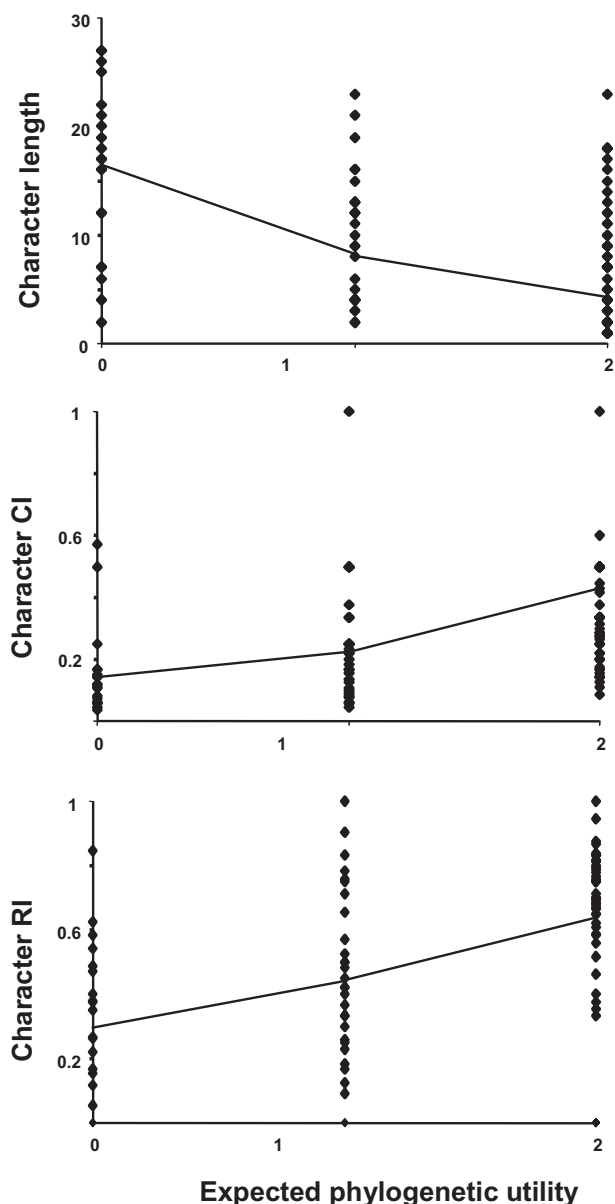


Figure 25. Expected phylogenetic utility vs. realized utility. The relationship between expected phylogenetic utility of the morphological characters and character length, consistency index and retention index. Lines join the means of each category.

differ from all species of *Crepidula s.s.* because they have large branched salivary glands, a laterally directed style sac that is posterior to the mantle cavity, the capsule gland and albumin gland converge, and the female genital papilla is absent. Again it is apparent from both anatomical and DNA sequence data that the shells of *Bostrycapulus* and *Crepidula s.s.* are convergent. The occurrence of such divergent anatomy

combined with very similar shells suggests that the arrangement of the internal anatomy is independent of the shell morphology in these groups.

Other cases of convergences in shell morphology supported by DNA data receive little or no support from anatomical data. For example, the species of *Trochita*, *Calyptreaea*, *Zegalerus* and *Sigapatella* all have similar shells and do not differ in any major anatomical arrangements, but they are widely separated on the best estimate phylogeny. There are what appear to be minor anatomical differences among these taxa. For example, *Trochita* species do not have a dorsal attachment muscle, the tentacles of the Panamanian *Calyptreaea* species are particularly thick, in some species the style sac is orientated more laterally than posteriorly, and there is considerable variation in penis morphology. Because they share such similar shells, none of these anatomical differences would have been convincing evidence for polyphyly of these groups in the absence of DNA data. The apparent independence of shell and anatomical characters in other clades of calyptraeids suggests that the similarity of morphology in these groups is not due to constraints imposed by the shell shape.

Despite the fact that analyses can be misled by these convergences if morphological characters are used alone, these characters contribute significantly to the combined dataset. The CIs and RIs of morphological characters on the best estimate tree are no worse than they are for the DNA data. When the morphological characters are added to the DNA dataset the resolution and bootstrap support is significantly increased. However the evidence of pervasive convergences in shell morphology demonstrated here, warn against the use of morphological characters alone.

OTHER POTENTIAL CHARACTERS IN CALYPTRAEID SYSTEMATICS

The characters used here were identified during a preliminary survey of 30 species of calyptraeids. Additional taxon sampling and the work of other researchers have suggested some other areas of calyptraeid anatomy that may provide useful characters for subsequent morphological analyses. For example, the number of seminal receptacles in the female reproductive system appears to vary among species. It was not used as a character here because there appeared to be some within-species variation and it was difficult to consistently dissect all of the receptacles. However, it should be noted that the *Crucibulum* species and some of the *Calyptreaea* species have only a single large seminal receptacle, so this may be a fruitful source of additional characters. There also appears to be some variation in the size and shape of the food pouch and

the orientation and arrangement of the gonad and digestive gland in the visceral mass which were not coded in the present study. Finally, a few characters of the radula may be useful for calyptraeid systematics. The radula was not used here due to the high level of within-species variation in the number of denticles on each tooth (Collin, 2000b). However, a preliminary survey of 20 species suggests that there are some qualitative differences in the overall shape of the cusps between members of the *Crepidula* s.s. clade and the other calyptraeids. Radula characters certainly vary significantly between hipponicids, capulids and calyptraeids, but these higher-level relationships were not the focus of this study. Finally, L. Simone (pers. comm.) has found that the buccal musculature may be a rich source of systematic characters in the calyptraeids. These features were not considered here.

A PRIORI CHARACTER SELECTION

In order to explore the effectiveness of subjective a priori character selection as a way to weed highly homoplasious characters out from a morphological dataset, I scored each character for expected phylogenetic utility before conducting the analysis. Subsequent comparisons of my subjective predictions of the phylogenetic utility of each character with its length, CI and RI on the best estimate tree shows that my ability to predict phylogenetic utility a priori (despite taking all the data and coding all the characters myself) was not good. Although the characters predicted to have high utility had a shorter length and higher CIs and RIs overall, there was considerable scatter (Fig. 25). This demonstrates that if I had a priori excluded all characters judged to have low phylogenetic utility, I would have excluded a number of useful characters while making little difference to the average length, CI or RI of the morphological characters. This suggests that the commonly held assumption that a researcher familiar with the morphological characters and taxa can always accurately select the phylogenetically most useful characters for inclusion in an analysis, while excluding homoplasious or misleading characters, may not hold.

GEOGRAPHIC PATTERNS IN CALYPTRAEID EVOLUTION

The best estimate phylogeny from this analysis and the combined molecular phylogeny of 94 calyptraeids (Collin, 2002b; R. Collin, unpub. observ.) demonstrate some biogeographical patterns that are worth further discussion. Most noteworthy is the observation that patterns of coincidence between molecular and morphological divergence differ regionally (see below).

Unlike many groups of molluscs and other marine

invertebrates, calyptraeids are not particularly diverse in the Indo-Pacific. In fact, *Crepidula* and *Crucibulum* appear to be unknown from the islands of the Indo-Pacific (with the possible exception of a very old, and almost certainly incorrect record of *C. dilatata* from Tahiti) and *Calyptraea* species are not as abundant or diverse as in the New World. The species of *Crepidula* from areas bordering the Indo-Pacific included in this study, *C. immersa* (Australia), *C. monoxyla* (New Zealand) and *C. grandis* (Japan) all fall outside of the *Crepidula* s.s. clade. Additionally, *C. costata* and an undescribed deep-water species from New Zealand also group with *C. monoxyla*. This means that no members of the *Crepidula* s.s. clade occur in the Indo-Pacific. *Crepidula complanata* from South Africa does range east around the south coast of Africa north to Durban and could be considered to range slightly into the Indian Ocean. Of the east Pacific taxa, *Crepidula* aff. *williamsi* extends as far west as Kodiak Island and *C. excavata* extends west to the Galapagos. Judging from the shell morphology, it is possible that the extraordinarily rare Japanese *C. isabellae* (Taki, 1938) does belong to the *Crepidula* s.s. clade. However, the presence of this species in Japan awaits verification (Hoagland, 1977), as does its phylogenetic affinity. It is unclear why a clade that is so successful along both coasts of the Americas and which occurs in Europe and Africa does not occur in the Indo-Pacific. The recent rapid invasion of *C. onyx* throughout Japan, Korea and Hong Kong suggests that lack of appropriate habitats or presence of superior competitors or predators may not be the reason.

In the two major clades of calyptraeids there appears to be very little biogeographical structure among closely related species. In several cases, closely related species occur sympatrically or have adjoining ranges. For example, *C. depressa*, *C. atrasolea* and *C. plana* all occur along the east coast of North America, *C. cf. onyx* Argentina, *C. argentina* and *C. protea* all occur along the south Atlantic coast of South America and *Calyptraea adspersa*, *Cal. lichen*, *Cal. conica* and *Cal. mamillaris* all occur along the Pacific coast of Panama. However, in other cases close relatives are separated by oceans or even continents. For example, *C. cf. perforans* from California is sister to the *C. plana* clade from the east coast of North America, *C. complanata* from South Africa and *C. procellana* from Cape Verde are sister to *C. onyx* from California and Panama, and *C. aculeata* from South Africa is sister to similar animals from Brazil and Argentina. These patterns suggest that either dispersal and extinction are far more prevalent than might be expected or that taxon sampling is not adequate to address biogeographical questions at a low

taxonomic level. As calyptraeids are most diverse in areas of upwelling, changes in ocean circulation are likely to have been important in driving patterns of extinction and speciation.

Finally, there is a striking difference in morphological versus genetic differentiation between taxa from the two coasts of Latin America. Samples of species in the *Crepidula s.s.* clade from the south Atlantic fall into two clades. One clade is comprised of *C. argentina*, *C. protea* and *C. cf. onyx* from Argentina and Brazil, and the second clade is comprised of *C. aplysioides* and *C. navicula* from Venezuela. In both clades, the species can be clearly differentiated on the basis of morphology (Simone *et al.*, 2000; R. Collin, pers. observ.) but are more or less indistinguishable on the basis of the DNA sequence data obtain here. Species from the Pacific coast of Latin America show a different pattern. There are several groups of species that are morphologically difficult or impossible to distinguish. For example the species referred to here as *C. excavata* and *C. arenata* are often considered to be conspecific (e.g. Keen, 1971; Hoagland, 1977) and this species is also thought to include *C. excavata* Peru (Collin, 2002b). Another morphospecies, *C. incurva*, usually includes the species referred to here as *C. incurva* Mexico, *C. incurva* Panama and *C. incurva* Peru. Unlike the situation in the south Atlantic where morphologically distinct species are genetically identical, these morphologically similar or indistinguishable species show very high levels of genetic divergence and in some cases do not even appear to be close relatives. This curious pattern is unlikely to be the result of different taxonomic practices in the two regions, as the taxonomy of the calyptraeid fauna of both regions was originally described by the same authors in the 1800s and was revised by Hoagland in 1977. Subsequent to this, there has been little taxonomic work on *Crepidula s.s.* from either region with the exception of the description of *C. argentina* (Simone *et al.*, 2000) in the South Atlantic and the description of *C. coquimbensis* (Brown & Olivares, 1996) in the South Pacific. At present, it is not clear what is responsible for this apparent difference in the relationship between the rates of morphological and genetic evolution between the two coasts.

ACKNOWLEDGEMENTS

I thank Maria Byrne (University of Sydney, Australia) Oscar Chaparro (Universidad Austral, Valdivia, Chile), Nestor Ciocco (Centro Nacional Patagonico, Argentina), Bob Creese (Leigh Marine Laboratory, University of Auckland, New Zealand), Steve Gaines (University of California, Santa Barbara, CA, USA), Carlos Gallardo (Universidad Austral, Valdivia, Chile), Jose Leal (Bailey–Matthews Shell Museum,

Florida), Tim Collins (Florida International University, FL, USA), Haris Lessios (Smithsonian Tropical Research Institute, Panama), Mary Rice (Smithsonian Research Station at Fort Pierce, FL, USA), Richard Strathmann (Friday Harbor Laboratories), George Branch (University of Cape Town, South Africa), Dick Kilburn (The Natal Museum), Carlos Caceres (Universidad Autonoma Baja California Sur, Mexico), Sonia Valle (Universidad San Carlos, Lima, Peru), Federico Winkler (Universidad Catolica Norte, Coquimbo, Chile), and the faculty and staff of Friday Harbor Laboratories for generously allowing me to use their lab space and equipment, without which this study would not have been possible. I would also like to thank A. Indocochea, O. Chaparro, A. Reiderman, T. Ridgeway, K. Ruck, D. Véliz, K. Zigler, E. Rolán, P. Selvakumaraswami, T. Griffin, S. Anderson and B. Pernet for helping me collect animals and those people listed in Table 2 for providing preserved animals. I am grateful to the curators and collections managers of the CAS, FMNH, BMNH, LACM, ANSP and NMNH, and especially K. Way and J. Jones for helping me track down type material, processing loans, and allowing me to deposit vouchers at their institutions. Finally, I am indebted to fellow calyptraeid workers L. Simone and D. Véliz for sharing their knowledge with me. Comments by B. Chernoff, J. Bates, R. Bieler, M. Foote, F. Lutzoni and L. Van Valen improved the manuscript. This research was supported by grants from the Conchologists of America, the University of Chicago Women's Board and National Geographic Society (#6335-89), and an NSF dissertation improvement grant (DEB#9972555). During completion of this manuscript I was supported by a dissertation fellowship from the American Association of University Women and a Lester Armour Fellowship from the Field Museum of Natural History.

REFERENCES

- Abbott RT.** 1974. *American seashells*, 2nd edn. New York: Van Nostrand Reinhold Co.
- Bandel K, Riedel F.** 1994. Classification of fossil and recent Calyptraeidea (Caenogastropoda) with a discussion of neomesogastropod phylogeny. *Berliner Geowiss Abhand E* **13**: 329–367.
- Broderip WJ.** 1834. Characters of new genera and species of Mollusca and Conchifera, collected by Mr. Cuming. Descriptions of new species of Calyptraeidae. *Proceedings of the Zoological Society of London* **2**: 35–40.
- Brown DI, Olivares CA.** 1996. A new species of *Crepidula* (Mollusca: Mesogastropoda: Calyptraeidae) from Chile: additional characters for the identification of the eastern Pacific planar *Crepidula* group. *Journal of Natural History* **30**: 1443–1458.
- Carlton JT.** 1979. History, biogeography, and ecology of the

- introduced marine and estuarine invertebrates of the Pacific coast of North America. PhD Dissertation. Davis, CA, USA: University of California.
- Coe WR. 1938.** Sexual phases in the gastropod *Crucibulum spinosa*. *Journal of Morphology* **63**: 345–361.
- Coe WR. 1942a.** The reproductive organs of the prosobranch mollusk *Crepidula onyx* and their transformation during the change from male to female phase. *Journal of Morphology* **70**: 501–512.
- Coe WR. 1942b.** Influence of natural and experimental conditions in determining shape of shell and rate of growth in gastropods of the genus *Crepidula*. *Journal of Morphology* **71**: 35–47.
- Coe WR. 1949.** Divergent methods of development in morphologically similar species of prosobranch gastropods. *Journal of Morphology* **84**: 383–400.
- Collin R. 1995.** Sex, size, and position: a test of models predicting the size at sex change in the protandrous gastropod *Crepidula fornicata*. *American Naturalist* **146**: 815–831.
- Collin R. 2000a.** Life history, reproduction and development of *Crepidula adunca* and *C. lingulata*. *Veliger* **43**: 24–33.
- Collin R. 2000b.** *C. plana* cryptic species complex in North America. *Canadian Journal of Zoology* **78**: 1500–1514.
- Collin R. 2002a.** Another last word on *Crepidula convexa* and a description of *C. ustulatulina* sp. nov. (Gastropoda: Calyptraeidae) from the Gulf of Mexico. *Bulletin of Marine Science*, **70**(1): 177–184.
- Collin R. 2002b.** Evolution of mode of development in *Crepidula*. Gastropoda: Calyptraeidae: causes and consequences. PhD Dissertation. Chicago, IL, USA: University of Chicago.
- Conklin EG. 1897.** The embryology of *Crepidula*. *Journal of Morphology* **13**: 3–226.
- Cunningham CW. 1997a.** Is congruence between data partitions a reliable predictor of phylogenetic accuracy? Empirically testing an iterative procedure for choosing among phylogenetic methods. *Systematic Biology* **46**: 464–478.
- Cunningham CW. 1997b.** Can three incongruence tests predict when data should be combined? *Molecular Biology and Evolution* **14**: 733–740.
- Deslous-Paoli JM. 1985.** *Crepidula fornicata* L. (gastéropode) dans le bassin de Marennes-Oléron: structure, dynamique et production d'une population. *Oceanologica Acta* **8**: 453–460.
- Dickinson AJG, Nason J, Croll RP. 1999.** Histochemical localization of FMRF amide, serotonin and catecholamines in embryonic *Crepidula fornicata* (Gastropoda, Prosobranchia). *Zoomorphology* **119**: 49–62.
- Farris JS. 1989.** The retention index and the rescaled consistency index. *Cladistics* **5**: 417–419.
- Finlay HJ. 1924.** The recent Mollusca of the Chatham Islands. *Transactions of the New Zealand Institute* **57**: 320–485.
- Fischer P. 1880–87.** 13694. In: *Manuel de Conchyliologie*. Paris: Savy, 1.
- Gallardo CS. 1979.** Especies gemelas del género *Crepidula* (Gastropoda, Calyptraeidae) en la costa de Chile: una redescubrimiento de *C dilatata* Lamarck y descripción de *C. fecunda* n. sp. *Studies of Neotropical Fauna Environment* **14**: 215–226.
- Gallardo CS. 1977.** *Crepidula philippiana* n. sp. nuevo gastropodo Calyptraeidae de Chile con especial referencia al patron de desarrollo. *Studies of Neotropical Fauna and Environment* **12**: 177–185.
- Gould AA. 1846.** Descriptions of shells of the exploring expedition. *Proceedings of the Boston Society of Natural History* **2**: 159–162.
- Graham A. 1954.** The anatomy of the prosobranch *Trichotropis borealis* Broderip and Sowerby, and the systematic position of the Capulidae. *Journal of the Marine Biology Association of the United Kingdom* **33**: 129–144.
- Hoagland KE. 1977.** Systematic review of fossil and recent *Crepidula*. *Malacologia* **16**: 363–420.
- Hoagland KE. 1978.** Protandry and the evolution of environmentally-mediated sex change: a study of the mollusca. *Malacologia* **17**: 365–391.
- Hoagland KE. 1986.** Patterns of encapsulation and brooding in the *Calyptraeidae* (Prosobranchia: Mesogastropoda). *American Malacological Bulletin* **4**: 173–183.
- Keen AM. 1971.** *Sea shells of tropical west America*, 2nd edn. Stanford, USA: Stanford University Press, 1064.
- Kleinstuber H. 1913.** Die Anatomie von *Trochita*, *Calyptraea* und *Janacus*. *Zoologisches Jahrbuchsupplement* **13**: 385–476.
- Kluge AG, Farris JS. 1969.** Quantitative phyletics and the evolution of anurans. *Systematic Zoology* **18**: 1–32.
- Kool SP. 1993.** Phylogenetic analysis of the *Rapaninae* (Neogastropoda: Muricidae). *Malacologia* **35**: 155–259.
- Lesson RP. 1830.** Mollusques. In: Dupery LJ, ed. *Voyage autour du monde exécuté par ordre du roi, sur la corvette de S. M. La coquille pendant les années 1822–25*. *Zoologie* **2**(1). Paris: Bertrand, 239–488.
- Leviton AE, Gibbs RH, Heal E, Dawson CE. 1985.** Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* **1985**: 802–832.
- Lima GM, Pechenik JA. 1985.** The influence of temperature on growth rate and length of larval life of the gastropod *Crepidula plana* Say. *Journal of Experimental Marine Biology and Ecology* **90**: 55–71.
- Loomis SH, VanNieuwenhuyze W. 1985.** Sediment correlates to density of *Crepidula fornicata* Linnaeus in the Pataganset River, Connecticut. *Veliger* **27**: 266–272.
- Matusiak JP, Fell PE. 1982.** Reproductive cycle of *Crepidula convexa* (Say) within a New England eelgrass community. *International Journal of Invertebrate Reproduction* **5**: 253–260.
- McGee BL, Targett NM. 1989.** Larval and habitat selection in *Crepidula* (L.) and its effect on adult distribution patterns. *Journal of Experimental Marine Biology and Ecology* **131**: 195–214.
- Menke KT. 1851.** Conchylien von Mazatlan, mit kritischen Anmerkungen. *Zeitschrift für Malakozoologie* **8**: 33–38.
- Mörch OAL. 1877.** Synopsis molluscorum marinorum Indiarum occidentaliū imprimis insularum danicarum. *Malakozoological Blätt* **24**: 93–123.
- Moritz CE. 1938.** The anatomy of the gastropod *Crepidula adunca* Sowerby. *University of California Publications in Zoology* **43**: 83–91.

- Olson AA, Harbison A. 1953.** Pliocene mollusca of southern Florida. *Academy of Natural Sciences of Philadelphia Monograph* **8**: 1–457.
- Owen R. 1834.** On the anatomy of Calyptraeidae. *Transactions of the Zoological Society of London* **1**: 207–212.
- Pechenik JA. 1980.** Growth and energy balance during the larval lives of three prosobranch gastropods. *Journal of Experimental Marine Biology and Ecology* **44**: 1–28.
- Pechenik JA, Hilbish TJ, Eyster LS, Marshall D. 1996.** Relationship between larval and juvenile growth rates in two marine gastropods, *Crepidula plana* and *C. fornicata*. *Marine Biology* **125**: 119–127.
- Sauriau P-G, Pichocki-Seyfried C, Walker P, de Montaudouin X, Palud C, Héral M. 1998.** *Crepidula fornicata* L. (mollusque, gastéropode) en baie de Marennes-Oléron: cartographie des fonds par sonar à balayage latéral et estimation du stock. *Océanologica Acta* **21**: 1–10.
- Schander C, Sundberg P. 2001.** Useful characters in gastropod phylogeny: soft information or hard facts? *Systematic Biology* **50**: 136–141.
- Shenk MA, Karlson RH. 1986.** Colonization of a shell resource by calyptraeid gastropods: tests of habitat selection and preemption models. *Journal of Experimental Marine Biology and Ecology* **99**: 79–89.
- Simone LRL. 2002.** Comparative morphological study and phylogeny of representatives of the superfamilies Calyptraeoidae (including Hipponicoidea) (Mollusca, Caenogastropoda). *Biotaneotropica* **2**(2). Accessed online at <http://www.biotaneotropica.org.br>.
- Simone LRL, Pastorino G, Penchaszadeh PE. 2000.** *Crepidula argentina* (Gastropoda: Calyptraeidae), a new species from the littoral of Argentina. *Nautilus* **114**: 127–141.
- Sullivan J. 1996.** Combining data with different distribution of among-site variation. *Systematic Biology* **45**: 375–380.
- Swofford DL. 1998.** *PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods)*, Version 4. Sunderland, MA USA: Sinauer Associates.
- Taylor JD, Miller JA. 1989.** The morphology of the osphradium in relation to feeding habits in Meso- and Neogastropods. *Journal of Molluscan Studies* **55**: 227–237.
- Thiele J. 1929.** Handbuch der systematischen Weichtierkunde. *Fischer Jena* **1**: 376.
- Thorson G. 1965.** A neotenous dwarf-form of *Capulus ungaricus* (L.) (Gastropoda, Prosobranchia) commensalistic on *Turritella communis* Risso. *Ophelia* **2** (1): 175–210.
- Véliz D, Guisado C, Winkler FM. 2001.** Morphological, reproductive, and genetic variability among three populations of *Crucibulum quiriquinae* (Gastropoda: Calyptraeidae) in Northern Chile. *Marine Biology* **139**: 527–534.
- Vermeij GJ, Carlson SJ. 2000.** The muricid gastropod subfamily Rapaninae: phylogeny and ecological history. *Paleobiology* **26**: 19–46.
- Vermeij GJ, Lowell RB, Walters LJ, Marks JA. 1987.** Good hosts and their guests: relations between trochid gastropods and the epizoic limpet *Crepidula adunca*. *Nautilus* **101**: 69–74.
- Wagner PJ. 2001.** Gastropod phylogenetics: progress, problems and implications. *Journal of Paleontology* **75**: 1128–1140.
- Warner RR, Fitch DL, Standish JD. 1996.** Social control of sex change in the shelf limpet, *Crepidula norrisiarum*: size-specific responses to local group composition. *Journal of Experimental Marine Biology and Ecology* **204**: 155–167.
- Wenz W. 1940.** Gastropoda, Prosobranchia. In: Schindewolf OH, ed. *Handbuch der Paläozoologie*, Berlin: Borntraeger, 721–960.
- Werner B. 1955.** Über die Anatomie, die Entwicklung, und Biologie des Veligers und der Veliconcha von *Crepidula fornicata* L. (Gastropoda: Prosobranchia). *Helgoländer Wissenschaftliche Meeresuntersuchungen* **5**: 169–217.
- Werner B, Grell KG. 1950.** *Die amerikanische Pantoffelschnecke Crepidula fornicata L Eine Anleitung zur Präparation*. Jena: Verlag von Gustav Fischer, 24.
- Woodruff DS, McMeekin LL, Mulvey M, Carpenter MP. 1986.** Population genetics of *Crepidula onyx*: variation in a Californian slipper snail recently established in China. *Veliger* **29**: 53–63.
- Yipp MW. 1983.** The anatomy of the organs of reproduction of *Crepidula walshi* (Mollusca: Gastropoda). In: Morton B, Dudgeon D, eds. *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China*. Hong Kong: Malacofauna of Hong Kong and Southern China, 243–256.
- Yoder AD, Irwin JA, Payseur BA. 2001.** Failure of the ILD to determine data combinability for slow loris phylogeny. *Systematic Biology* **50**: 408–424.
- Young CM. 1938.** Evolution of ciliary feeding in the Prosobranchia, with an account of feeding in *Capulus ungaricus*. *Journal of Marine Biology Association of the United Kingdom* **22**: 453–468.

APPENDIX 1

MORPHOLOGICAL CHARACTER DESCRIPTIONS

Morphological data were coded from dissections of live, formalin- or ethanol-preserved material for all calyptraeids, *Hipponix* and *Trichotropis*. *Capulus* was coded from my observations of the single female provided by A. Warén (Table 2), male reproductive characters were obtained from Young (1938), Graham (1954) and Simone (2002) which were in general agreement with each other.

SHELL CHARACTERS

Calyptraeid species have been described almost exclusively from shells (Figs 1,2). In most species the shells are very plastic and shell morphology varies with substrate and from site to site. However, there are also shell features that are found consistently in a species. I have endeavored to code the shell characters with the least intraspecific variation as well as the characters that are often used for species-level taxonomy. The fol-

lowing shell characters are all based on a ventral view of the shell (i.e. right on the shell is actually the animal's left).

Muscle scars

Calyptraeid gastropods are characterized by zero, one or two large muscle scars on the shell just anterior to the shell septum. These muscles are thought to be homologous to the columella muscle of coiled gastropods. However it is unclear if the presence of the right, left or both calyptraeid muscle(s) is a homologous state to the presence of the columellar muscle. *Calyptraea* shells are the most coiled calyptraeids and often retain a fold and thickening on the left side of the septum, towards the centre of the shell. This appears to be homologous to the columella. There is a muscle scar in this fold, which suggests that the animal's right shell muscle is homologous to the columellar muscle of other gastropods. The outgroups, *Capulus* and *Hipponix*, have horseshoe-shaped muscle scars that are not obviously homologous to the condition in either calyptraeids or coiled gastropods. These two characters are listed here as shell characters because the presence of a muscle scar on the shell is often used in calyptraeid taxonomy, but the characters were coded from the soft bodies because muscle scars are often difficult to distinguish in *Calyptraea* species and are not always clearly visible in live-collected shells.

S1. Right muscle/scar

- 0 = absent (e.g. *C. fornicata*, *Calyptraea* spp., *Crucibulum* spp.)
- 1 = present (e.g. *C. norisarium*, *C. costata*)
- 2 = horseshoe-shaped (e.g. *Hipponix* spp.).

S2. Left muscle/scar

- 0 = absent (e.g. *C. fornicata*, *Crucibulum* spp.)
- 1 = present (e.g. *C. maculosa*, *Calyptraea* spp.)
- 2 = horseshoe-shaped (e.g. *Hipponix* spp.)
- 3 = on columella

Shelf shape

The internal shell septum in calyptraeid shells is thought to be homologous to the columella of coiled gastropods. Ontogenetically it is an extension of the columella of the larval shell. The cup-shaped septum of *Crucibulum*, and the flat septa of *Calyptraea* and *Crepidula* are homologous. In newly metamorphosed *Crepidula* juveniles the shelf margin is more or less straight and angled forward on the right. This is a consequence of the shape of the larval shell. There is no clearly homologous feature in the shells of *Hipponix* or *Capulus* and the columella of coiled gastropods does not display any of the shape states listed here. The internal prong of shell in *Cheilea* is similar to half of the cup-shaped septum in *Crucibulum* species but it is not likely to be homologous. Many of the septum characters listed here can be inapplicable or uncodable in two different ways: The septum may not be present, making septum shape characters inapplicable (state 8 here) or the septum may be present, but its form may be such that it is not possible to code the shape character (state 7 here).

S3. Septum

- 0 = absent (e.g. *Hipponix*, capulids, trichotropids)
- 1 = present (e.g. calyptraeids, *Cheilea*)

S4. Septum length/shell length (this character was excluded due to high intraspecific variability) gap coded

- 7 = present but uncodable
- 8 = inapplicable

S5. Septum shape

- 0 = convex (e.g. *Crepidula coquimbensis*, *C. monoxylo* Fig. 1C)
- 1 = flat (e.g. *Crepidula fornicata*, *C. costata* Fig. 1G)
- 2 = concave (e.g. *Crucibulum* Fig. 2D)
- 3 = prong (e.g. *Cheilea* sp.)
- 8 = inapplicable (e.g. outgroups)

S6. Longitudinal ridge on septum

- 0 = absent (e.g. *Crepidula depressa* Fig. 1B)
- 1 = present (e.g. *Crepidula aculeata* Fig. 2B)
- 7 = septum present but uncodable (e.g. *Crucibulum*)
- 8 = inapplicable

S7. Bipartite septum

- 0 = absent (e.g. *Crepidula*)
- 1 = present (e.g. *Siphopatella walshi* Fig. 1H)
- 8 = inapplicable

S8. Left side of septum

- 0 = free (e.g. *Cheilea*)
- 1 = attached parallel to shell margin (e.g. *Crepidula*)
- 2 = attached vertically to shell wall (e.g. *Crucibulum*)
- 3 = attaches to central columella (e.g. *Calyptraea*)
- 8 = inapplicable

S9. Right side of septum

- 0 = free (e.g. *Crucibulum*)
- 1 = attached parallel to margin (e.g. *Crepidula*, *Calyptraea*)
- 8 = inapplicable

S10. Septum margin

- 0 = sinuous (e.g. *Crepidula depressa* Fig. 1B)
- 1 = straight (e.g. *Crepidula costata* Fig. 1G)
- 2 = parabolic (e.g. *Crepidula norrisiarum*)
- 3 = tongue-like (e.g. *Crepidatella* Fig. 2F)
- 7 = present but this character uncodable (e.g. *Crucibulum*)
- 8 = inapplicable

S11. Septum margin

0 = angled forward on right (e.g. *Crepidula maculosa* Fig. 2A)

- 1 = transverse (e.g. *Crepidula costata* Fig. 1G)
- 2 = angled forward on left (slightly in *C. incurva*)
- 7 = septum present but this character uncodable (e.g. *Crucibulum*)
- 8 = inapplicable

S12. Fold in septum

- 0 = absent (e.g. *Crepidula* spp.)
- 1 = present (e.g. *Siphopatella walshi* Fig. 1H)
- 7 = septum present but this character uncodable (e.g. *Crucibulum*)
- 8 = inapplicable

S13. Notch on right side of septum

- 0 = absent (e.g. *Crepidula costata* Fig. 1G)
- 1 = present (e.g. *Crepidula depressa* Fig. 1B)
- 7 = septum present but this character uncodable (e.g. *Crucibulum*)
- 8 = inapplicable

External shell shape

The external limpet-like shell shape of *Crepidula* species shows some considerable variation in the extent of coiling, and shape of the apex. The apex is coded as ros-

trate if it is free and hooked, appressed if it is distinct and pressed against the body of the shell, and neither if it is indistinct. Shell symmetry was coded by following the dorsal curve of the shell from the midpoint of the anterior shell margin to the apex. Outgroups with coiled shells were not coded for apex characters because their apex morphology is not comparable to the conditions in limpet-shaped shells.

- S14. Shell shape
0 = coiled with small aperture (e.g. *Trichotropis*)
1 = limpet-like with large aperture (e.g. *Calyptraeids*, *Capulus*)
- S15. Shell shape
0 = not conical (e.g. *Crepidula*, *Bostrycapulus*)
1 = conical with central apex (e.g. *Crucibulum*, *Calyptraea*)
- S16. Operculum
0 = absent in adult
1 = present in adult
- S17. Apex
0 = rostrate (e.g. *Crepidula adunca*)
1 = appressed (e.g. *Bostrycapulus*)
2 = indistinct (e.g. *Crepidula plana*)
8 = inapplicable
- S18. Apex
0 = on the same level as the shell aperture (e.g. *Crepidula plana*)
1 = dorsal to shell aperture (e.g. *Crepidula incurva*)
8 = inapplicable
- S19 Apex
0 = above shell aperture
1 = extending posterior or posterior lateral to aperture
8 = inapplicable
- S20. Apex
0 = not excavated below shelf (e.g. *Crepidula plana*)
1 = excavated below shelf (e.g. *Crepidula excavata*)
8 = inapplicable
- S21. Lateral shell symmetry
0 = coiled (e.g. *Bostrycapulus*)
1 = curved (e.g. *Crepidula fornicata*)
2 = straight (e.g. *Crepidula adunca*, *Crepidula plana*)

Shell colour and periostracum

Shell colour and development of periostracum varies substantially among species. There is also considerable colour variation within a species. However, species are generally consistently white, light or dark and the general colour patterns are consistently present within a species.

- S22. Periostracum
0 = not visible (e.g. *C. plana*)
1 = thin (e.g. *C. excavata*)
2 = thick (e.g. *C. grandis*)
3 = shaggy (e.g. *C. striolata*)
- S23. Ventral shelly plate
0 = absent (e.g. *calyptraeids*)
1 = present (e.g. *Cheilea*)
- S24. Brown external shell pigment
0 = absent
1 = present (e.g. *C. dilatata*)

- S25. Tan external shell pigment
0 = absent
1 = present (e.g. *C. norisarum*)
- S26. Black external shell pigment
0 = absent
1 = present (e.g. *C. onyx*)
- S27. Pink external shell pigment
0 = absent
1 = present (e.g. apex of *C. norisarum*)
- S28. White areas on shell
0 = absent
1 = present
- S29. Purple external shell pigment
0 = absent
1 = present (e.g. *B. extinctorum*)
- S30. External shell pattern
0 = solid (e.g. *C. plana*)
1 = striped (e.g. *C. costata*)
2 = spotty/speckled (e.g. *C. incurva*)
3 = blotchy (e.g. *C. maculosa*)
- S31. Internal shell material
0 = same colour as external shell colour
1 = different colour from external shell colour
- S32. Shelf colour
0 = white
1 = dark
8 = inapplicable

Shell sculpture

Crepidula and *Calyptraea* species generally have very little shell sculpture, however, numerous *Crucibulum* species have distinctive sculpture. It is difficult to assess the levels of homology among the various spines or ribs, as considerable variation in the development of these features occurs within many species.

- S33. Spines
0 = absent
1 = present (e.g. *Calyptraea chinensis*, *Bostrycapulus*)
- S34. Fine radial ribs
0 = absent
1 = present (e.g. *Crucibulum quiriquinae*)
- S35. Laminated shell
0 = absent
1 = present externally (e.g. *C. lessoni*)
2 = present internally only (e.g. *C. immersa*)
- S36. Radial corrugations
0 = absent
1 = present (e.g. *C. costata*)
- S37. Lateral ribs
0 = absent
1 = present (e.g. *Trochita*)

Protoconch

The protoconch is usually corroded or eroded in adult calyptraeids. However when small shells are available or when the animals have been raised from larvae differences in shell sculpture are visible. The consistency of coding the protoconch sculpture may be low because in some cases sculpture was observed in live juveniles, in some cases in larvae or embryos and in some cases from SEMs of juvenile or adult shells.

- S38. Juvenile shell colour
 0 = same as adult shell
 1 = darker than adult shell (e.g. *C. williamsi*)
- S39. Protoconch sculpture
 0 = smooth (e.g. *C. plana* (Collin, 2000b))
 1 = granular (e.g. *B. gravispinosa*)
 2 = beaten (e.g. *Crepidula fimbriata*)
 3 = ribbed (e.g. *Crucibulum spinosum* Peru)
 4 = striated (e.g. *Calyptraea chinensis*)
 5 = echinospira (e.g. *Trichotropis cancellata*)

Other shell features

- S40. Convexity
 0 = flat (e.g. *C. plana*)
 1 = convex (e.g. *C. adunca*)
- S41. Lateral shell slope
 0 = equal (e.g. *C. fornicata*)
 1 = steeper on the animal's left side (e.g. *C. excavata*)

ANATOMICAL CHARACTERS

The anatomy of some calyptraeid species have been described in detail [*Crepidula fornicata* (Werner & Grell, 1950); *Trochita calyptraeformis* Kleinstuber (1913); *Crepidula adunca* (Moritz, 1938), *Crepidula argentina* (Simone *et al.*, 2000), and *Crepidula aculeata*, *C. cf. plana*, *C. protea*, *Calyptraea centralis*, *Crucibulum auricula*, *Crucibulum quiriquinae*, *Trochita trochiformis*, and *Sigapatella calyptraeformis* (Simone, 2002)]. In general, the gross anatomy of these groups is very similar and has been interpreted as evidence that *Calyptraea*, *Crepidula* and *Crucibulum* should be combined into a single genus (Broderip, 1834; Owen, 1834). However, Simone's (2002) comparative analysis of 11 calyptraeids demonstrated that major clades of calyptraeids can be distinguished with morphological characters. The characters described here are viewed from the animal's point of view (i.e. 'right' refers to the animal's right).

External morphology

There are various modifications of the calyptraeid and hipponicid foot that reflect their sedentary life-styles. *Crepidula* have a relatively well-developed flexible propodium and mesopodium, while other calyptraeids have a more rectangular and less flexible foot. *Hipponix* and *Sabia* have extremely reduced feet which are little more than thin flaps of epithelial tissue. Calyptraeids have well developed eyes at the base of the somewhat stubby (when fixed) tentacles. Hipponicids have evenly tapering conical tentacles and the eye is often extremely reduced or absent.

- A1. Lips
 0 = symmetrical
 1 = left larger
 2 = right larger
- A2. Mesopodium
 0 = indistinct (e.g. *Crucibulum*)
 1 = laterally extended flaps (e.g. *Crepidula plana*)
- A3. Propodium
 0 = rectangular (e.g. *Crucibulum*)
 1 = laterally extended (e.g. *Crepidula plana*)

- A4. Pseudopropodium
 0 = absent (e.g. calyptraeids)
 1 = present (e.g. hipponicids)
- A5. Tentacle shape
 0 = stubby (e.g. calyptraeids)
 1 = evenly tapered (e.g. *Hipponix*)
 2 = distally inflated (e.g. *Vanikoro* sp.)
- A6. Eyes
 0 = well developed (e.g. calyptraeids)
 1 = greatly reduced or absent (e.g. hipponicids)
- A7. Foot
 0 = muscular (e.g. calyptraeids)
 1 = thin epithelium (e.g. *Hipponix*)

Pigmentation

All calyptraeids have small white granules across the mantle, neck and head (Fig. 6) and many of them have a general dark cast. However some have a very distinctive marbled black pigment limited to the side of the foot, and large yellow or creamish pigment blotches are also common. These characteristics, and the pigmentation coded here may be subject to preservation artefacts and I have coded most of these on the basis of my observations of live animals. The dark pigmentation appears to be retained in preserved material but the yellow pigment blotches are lost in both formalin- and ethanol-preserved animals.

- A8. Black pigment on sides of the foot
 0 = absent
 1 = marbled (e.g. *Bostrycapulus*, *Crucibulum*)
 2 = solid (e.g. *Crepidula incurva*)
- A9. Yellow pigment blotches
 0 = absent
 1 = present on mantle and neck (e.g. *Bostrycapulus*)
- A10. Dark stripes on edge of mantle
 0 = absent
 1 = present (e.g. *Crepidula onyx*)
- A11. Dark body pigment
 0 = absent
 1 = present

Mantle cavity and visceral mass

The mantle cavity runs along the dorsal left side of the visceral mass in calyptraeids. In *Calyptraea* and *Crepidula* it extends simply to the posterior edge of the visceral mass, while in *Crucibulum* it extends around to the right side of the animal. The characters listed here pertain to the general arrangement of visceral mass. Finally, note that character A13 is sensitive to fixation: live animals and ethanol preserved animals retain this feature, while it is always absent in formalin-fixed animals.

- A12. Visceral mass orientation
 0 = anterior-posterior (Fig. 3)
 1 = dorsal-ventrally (Fig. 5)
- A13. White vessels in viscera
 0 = absent (Fig. 3A)
 1 = present (Fig. 3B–F)
- A14. Mantle cavity extends
 0 = half-way to distal end of gonad and digestive gland (e.g. Fig. 3B–E)

- 1 = to distal end of gonad and digestive gland (e.g. Fig. 3A,C)
 2 = u-shaped, encircling body past end of digestive gland (e.g. Fig. 3F)
 3 = very shallow cavity (e.g. Fig. 8)
- A15. Mantle cavity
 0 = does not extend to posterior shell margin (e.g. Fig. 3B,D)
 1 = extends to posterior shell margin and ends (e.g. Fig. 3A,C)
 2 = extend to posterior shell margin and continues laterally (e.g. Fig. 3F)
 3 = very shallow cavity (e.g. Fig. 5)
- A16. Gills
 0 = large triangular base more than half the length of the filament.
 1 = primarily filamentous
- A17. Mantle cavity
 0 = extends posterior along left edge of visceral mass (e.g. Fig. 3A–C,E)
 1 = curves posteriorly lateral across visceral mass (e.g. Fig. 3D)
 2 = extends posteriorly, encircling body (e.g. Fig. 3F)
 3 = shallow rounded cavity
- A18. Visceral mass
 0 = straight (Fig. 3A,D)
 1 = curved (Fig. 3B)
 2 = orientated laterally
 3 = coiled
- A19. Dorsal attachment muscle
 0 = absent
 1 = present

Osphradium

The osphradium, the chemosensory organ, anterior to the gill in the mantle cavity, shows considerable variation among caenogastropods (Taylor & Miller, 1989). The calyptraeid osphradium is either a mono- or bipectinate row of simple leaflets. The number of these leaflets varies within species with body-size. Many species (e.g. *C. plana*, *C. atrasolea*, *C. adunca*) have osphradia that seldom have more than 12 leaflets in the largest animals, while other species (e.g. *C. aculeata*, *C. fornicata*) usually have 25–40 leaflets in adult animals. In species with a large number of leaflets the osphradium usually extends across the entire mantle opening from the food pouch to the mantle connection to the foot. In species with few leaflets the osphradium may be a small cluster of leaflets that takes up a small portion of the mantle opening, or the leaflets may be widely spaced and cover the entire mantle opening.

- A20. Osphradium
 0 = simple ridge
 1 = monopectinate (Figs 6A,7B)
 2 = bipectinate (Figs 6B,C, 7A)
 3 = row of ridges
- A21. Osphradium cross section
 0 = ridge
 1 = triangular
 2 = rectangular
 3 = row of ridges

- A22. Osphradial spacing
 0 = even (Fig. 7A)
 1 = uneven (Figs 6A,7B)
- A23. Osphradial spacing
 0 = closely packed (Fig. 7A)
 1 = distantly spaced (Figs 6A,7B)
- A24. Osphradium size
 0 = less than 60% of the mantle opening
 1 = 100% of the mantle opening.

Reproductive organs

Calyptraeids, trichotropids and capulids are protandrous hermaphrodites. The morphological transformation between males and females has been described in detail for *C. onyx* (Coe, 1942a) and the reproductive systems have been described in detail for *Cruc. spinosum* (Coe, 1938) and *S. walshi* (Yipp, 1983). Sex change of individuals maintained in captivity has been observed in *Crepipatella lingulata* (Collin, 2000a) and *C. norri-siarum* (Warner *et al.*, 1996). In many other species it has been noted that males are usually smaller than females and it is on the basis of this that all calyptraeids are assumed to be protandrous.

The possible utility of the reproductive organs in calyptraeid systematics was first discussed by Hoagland (1986). There is considerable variation in the morphology of both the penis (Fig. 8) and the pallial oviduct (Fig. 9). The terminology and homologies of caenogastropod reproductive systems are confused and unclear. Here I follow the terminology of Hoagland (1986). This terminology should not be assumed to reflect homologies with structures of the same name in other caenogastropod families but are consistent with Hoagland (1986) and L. Simone (pers. comm.).

- A25. Penis
 0 = evenly tapered
 1 = somewhat tapered with a long thin papilla (Fig. 8B)
 2 = blunt with a very short papilla (Fig. 8A)
 3 = somewhat tapered with a cup-like mid-piece (Fig. 8C)
 4 = evenly tapered with inflated papilla (Fig. 8E)
 5 = hooked cup shape with papilla into the cup (Fig. 8D)
 6 = blunt ended with a very open groove at the distal end (Fig. 8F)
- A26. Penis
 0 = cylindrical
 1 = dorsal-ventrally flattened (e.g. calyptraeids)
 2 = laterally flattened (e.g. some hipponicids)
- A27. Seminal groove
 0 = open
 1 = closed
- A28. Seminal groove
 0 = extends to end of penis
 1 = does not extend to end of penis
- A29. Seminal groove
 0 = ventral side of penis
 1 = posterior edge of penis
 2 = anterior edge of penis
 3 = changes sides of penis

- A30. Vas deferens
0 = open
1 = closed
- A31. Female genital papilla
1 = absent (Fig. 9A)
2 = extending into mantle cavity with one side attached to mantle
3 = extending into mantle cavity with both sides free (Fig. 9B,C)
- A32. Female genital papilla
0 = absent (Fig. 9A)
1 = with a groove (Fig. 9B)
2 = without a groove (Fig. 9C)
- A33. Distal end of female genital papilla
0 = blunt (Fig. 9C)
1 = pointed (Fig. 9B)
2 = bulbous
3 = extraordinarily long and thin (e.g. *C. walshi*)
- A34. Arrangement of female reproductive tract
0 = albumin gland and capsule gland linear (Fig. 9B,C)
1 = albumin gland and capsule gland converge (Fig. 9A)
- A35. Distal end of female reproductive tract
0 = capsule gland opens directly into mantle cavity (Fig. 9A)
1 = capsule gland connects to narrow tube in mantle before opening (either in female genital papilla or from mantle) (Fig. 9B)
2 = capsule gland connects to a narrow tube not embedded in the mantle (Fig. 9C)
- A36. Large bursa copulatrix
0 = absent (e.g. calyptraeids)
1 = present (e.g. hipponicids)
- Egg capsules and reproductive behaviour*
The morphology of calyptraeid egg capsules is fairly conservative. The triangular thin-walled capsules are transparent and the lower corner tapers into a thread-like stalk. The base of the stalk is somewhat wider and the capsules are attached to each other and to the substrate with this plaque. Hipponicid capsules are similar in morphology but are usually attached to the pseudopodium. In both groups the capsules are brooded below the neck. Vanikorid egg capsules are deposited on the rocks around the sedentary adults (A. Warén, pers. comm.) and the egg mass of capulids are held in the propodium (Thorson, 1965).
The planktotrophic veliger larvae of calyptraeids have been described in some detail for *Crepidula fornicata* (Werner, 1955), and *Crepidatella lingulata* (Collin, 2000b) and intracapsular development has been described for a number of other species (reviewed in Collin, 2002b). *Capulus* and *Trichotropis* have been described as having a echinospira larva, however, the thickened larval shell does not appear to be homologous to the 'true' echinospira of lamellarids (A. Warén pers. comm., B. Pernet, pers. comm.). The thickened and elaborate larval shell of these groups is, however, clearly different from the simple larval shell of calyptraeids and is therefore coded as a separate state here.
- A37. Capsule stalks
0 = thin
1 = thick
- 2 = absent
3 = evenly tapered
- A38. Egg masses
0 = gel mass
1 = thin capsules
2 = thick unstalked capsules
- A39. Egg capsule
0 = attached to substrate (e.g. calyptraeids)
1 = attached to pseudopodium (e.g. hipponicids)
2 = free
- A40. Brooding
0 = absent
1 = externally (e.g. trichotropids)
2 = below neck, under shell (e.g. calyptraeids)
- A41. 'Echinospira' larvae
0 = absent (e.g. calyptraeids)
1 = present (e.g. *Trichotropis*)
- Alimentary system*
The alimentary system reflects the general suspension-feeding lifestyle of calyptraeids. Particulate food is concentrated in a mucus thread that travels along the neck lappets to the mouth and is sometimes collected in the food pouch. The small jaws and radula draw the food into the mouth. Much of the variation in the overall calyptraeid bodyplan is due to differences in the orientation of the stomach and style sac in relation to the mantle cavity (Figs 6,7,8). In most *Crepidula* species the stomach is positioned at the posterior end of the viscera and the style sac extends anteriorly below the mantle cavity. In *Calyptrea* the stomach is positioned farther forward and the style sac is short and directed laterally, along the posterior margin of the mantle cavity. In *Crucibulum* the style sac is very long and extends posteriorly around the shell septum. Capulids, trichotropids and hipponicids also have a distinct style sac although it is considerable shorter than in calyptraeids, and it is missing in *Leptonotis perplexus*. Many of the other alimentary characters coded here reflect the complex and bizarre alimentary system of most hipponicids in which faecal pellets retained in the distal intestine take up 20–30% of the visceral mass.
- A42. Proboscis
0 = absent (e.g. Fig. 4)
1 = extension of ventral lip (e.g. capulids and trichotropids)
- A43. Snout
0 = short (e.g. Fig. 4)
1 = extended muscular (Fig. 5)
- A44. Obligate filter feeders
0 = absent
1 = present
- A45. Food pouch
0 = absent
1 = present (Figs 6,7)
- A46. Oesophagus
0 = does not extend to end of viscera
1 = extends to end of viscera
- A47. Oesophageal pouch
0 = absent (e.g. calyptraeids)
1 = present
- A48. Oesophagus posterior to nerve ring
0 = straight
1 = curves to dorsal right

- 2 = curves left
3 = looped in foot
- A49. Salivary glands
0 = around buccal mass
1 = extending along neck about half-way
2 = extending along neck past nerve ring
3 = around nerve ring but not extending along neck
4 = extends half-way down nerve ring
- A50. Salivary glands
0 = tubular (e.g. *Crepidula*)
1 = branched (e.g. *Bostrycapulus*)
2 = round
3 = flattened and indistinct (e.g. *Cheilea*)
- A51. Salivary glands
0 = equal in length
1 = asymmetrical
- A52. Caecum
0 = absent (e.g. calyptraeids)
1 = present
- A53. Style sac
0 = short
1 = longer than stomach (e.g. *Crepidula fornicata*)
2 = absent
- A54. Style sac
0 = ventral to mantle cavity (e.g. *Crepidula*)
1 = in dorsal viscera (e.g. *Bostrycapulus*, *Maoricrypta*)
2 = absent
- A54b. Style sac
0 = ventral to mantle cavity (e.g. *Crepidula*)
1 = lateral (e.g. *Maoricrypta*)
2 = posterior (e.g. *Bostrycapulus*)
3 = absent
- A55. Loop in distal intestine
0 = absent
1 = shallow
2 = deep
3 = coiled
- A56. Proximal dip in intestine
0 = absent
1 = present
2 = coiled
- A57. Style sac
0 = runs anteriorly (e.g. *Crepidula*)
1 = laterally (e.g. *Bostrycapulus*)
2 = runs posterior (e.g. *Crucibulum*)
3 = absent
- A58. Style sac thickness
0 = thin walled
1 = thick walled
2 = absent
- A59. Distal intestine
0 = narrow (e.g. calyptraeids)
1 = distended (e.g. hipponicids)
- A60. Faecal pellets
0 = soft (e.g. calyptraeids)
1 = calcium carbonate (e.g. hipponicids)
- A61. Shell muscles attach
0 = in the foot (e.g. calyptraeids)
1 = attached to substrate (e.g. *Hipponix* sp.)
- A62. Pericardium
0 = lateral to gill (Fig. 3A,C–F)
1 = posterior to gill (Fig. 3B)

Nervous system

The esophageal nerve ring of calyptraeids shows a high degree of concentration of the ganglia from both the esophageal and visceral regions: The cerebral, pleural, parietal and pedal ganglia are all more or less fused into a concentrated nerve ring around the oesophagus. There is little variation in the general arrangement of the ganglia or their connections within the Calyptraeidae. There is some variation in the overall shape of each ganglia, however, this variation is continuous and subtle and it was difficult to code this variation satisfactorily for phylogenetic analysis.

- A63. Nerve ring
0 = near tentacles (Fig. 5)
1 = posterior to tentacles (Fig. 4)
- A64. Suboesophageal ganglion
0 = right of oesophagus
1 = left of oesophagus
2 = below oesophagus
- A65. Supraoesophageal ganglion
0 = directly above oesophagus
1 = right of oesophagus
2 = left of oesophagus
- A66. Suboesophageal ganglion
0 = closely connected to right pleural ganglion
1 = not closely connected to right pleural ganglion
- A67. Pedal ganglia
0 = fused with nerve ring
1 = separate from nerve ring
- A68. Suboesophageal ganglion
0 = on level with pleural and cerebral ganglia
1 = below pleural ganglia
- A69. Suboesophageal ganglion
0 = not connected laterally to the right pleural ganglion
1 = connected laterally to the right pleural ganglion
- A70. Suboesophageal ganglion
0 = not connected posterior to the right pleural ganglion
1 = connected posterior the right pleural ganglion
- A70c. Suboesophageal ganglion
0 = not connected below to the right pleural ganglion
1 = connected below to the right pleural ganglion
- A71. Suboesophageal ganglion
0 = round
1 = bifurcate
2 = elongate
- A72. Supraoesophageal ganglion
0 = fused to right pleural ganglion
1 = connected but not fused to right pleural ganglion
2 = connected with long connective
3 = not connected to right pleural ganglion
- A73. Supraoesophageal ganglion
0 = round
1 = elongate
2 = triangular
- A74. Cerebral ganglion
0 = rounded
1 = kidney-shaped
2 = flattened
3 = elongate

Miscellaneous

A75. Neck lappets

0 = absent

1 = present (Fig. 4)

A76. Ganglia in nerve ring

0 = unpigmented

1 = pigmented

A77. Oesophagus

0 = pale

1 = black

A78. Eyes

0 = raised from tentacles

1 = embedded in tentacle

A79. Style sac

0 = does not bulge into mantle cavity anteriorly

1 = bulges into mantle cavity anteriorly

APPENDIX 2

Morphological character consistency on the best estimate tree

Character	Number of states	Expected quality	Length on the best tree	CI on the best tree	RI on the best tree
COI	1–4	–	1–26	0.048–1.00	0–1.00
16S	1–4	–	1–18	0.071–1.00	0–1.00
28S	1–4	–	1–14	0.09–1.00	0–1.00
S1 [1641]	3	2	7	0.286	0.375
S2 [1642]	4	2	11	0.273	0.795
S3 [1643]	2	2	2	0.500	0.833
S4 [1644]	Many	0	Excluded	Excluded	Excluded
S5 [1645]	5	2	12	0.333	0.619
S6 [1646]	4	1	11–12	0.182–0.167	0.655–0.690
S7 [1647]	3	2	4	0.500	0.833
S8 [1648]	5	2	9	0.444	0.750
S9 [1649]	3	2	6	0.333	0.750
S10 [1650]	6	2	12	0.417	0.816
S11 [1651]	5	2	15	0.267	0.607
S12 [1652]	4	2	7	0.286	0.667
S13 [1653]	4	2	16–17	0.176–0.188	0.650–0.675
S14 [1654]	2	2	2	0.500	0
S15 [1655]	2	2	7	0.143	0.684
S16 [1656]	2	2	2	0.500	0
S17 [1657]	4	2	17–18	0.111–0.118	0.568–0.595
S18 [1658]	3	0	6	0.167	0.844
S19 [1659]	3	2	9	0.222	0.759
S20 [1660]	3	2	14	0.143	0.586
S21 [1661]	3	2	23	0.087	0.462
S22 [1662]	4	1	21–22	0.136–0.143	0.367–0.400
S23 [1663]	2	2	3	0.333	0
S24 [1664]	2	1	16	0.062	0.571
S25 [1665]	2	1	23–24	0.043	0.258–0.290
S26 [1666]	2	1	4	0.250	0.250
S27 [1667]	2	1	3	0.333	0
S28 [1668]	2	1	11	0.091	0.091
S29 [1669]	2	1	6	0.167	0.167
S30 [1670]	4	0	21	0.143	0.379
S31 [1671]	2	1	10	0.100	0.182
S32 [1672]	3	1	2	0.500	0.833
S33 [1673]	2	2	4	0.250	0.700
S34 [1674]	2	1	12	0.083	0.421
S35 [1675]	3	1	4	0.500	0
S36 [1676]	2	2	1	1.00	0/0
S37 [1677]	2	2	4	0.250	0

Appendix 2 *Continued*

Character	Number of states	Expected quality	Length on the best tree	CI on the best tree	RI on the best tree
S38 [1678]	2	1	4	0.250	0
S39 [1679]	6	0	6–7	0.571–0.667	0.625–0.750
S40 [1680]	2	1	11–13	0.154–0.182	0.421–0.526
S41 [1681]	2	1	9	0.222	0.125
A1 [1682]	3	0	7	0.143	0
A2 [1683]	2	2	8	0.125	0.788
A3 [1684]	2	2	7	0.143	0.838
A4 [1685]	2	2	1	1.00	1.00
A5 [1686]	3	1	2	1.00	1.00
A6 [1687]	2	2	3	0.333	0
A7 [1688]	2	2	1	1.00	1.00
A8 [1689]	3	1	11–12	0.167–182	0.524–0.571
A9 [1690]	2	0	12	0.083	0.542
A10 [1691]	2	1	3	0.333	0.333
A11 [1692]	2	1	15–17	0.059–0.067	0.484–0.548
A12 [1693]	2	2	3	0.333	0.714
A13 [1694]	2	1	4	0.250	0.903
A14 [1695]	4	2	18	0.278	0.698
A15 [1696]	4	2	18	0.167	0.583
A16 [1697]	2	2	4	0.250	0.4
A17 [1698]	4	2	10	0.300	0.650
A18 [1699]	4	2	11	0.273	0.692
A19 [1700]	2	2	5	0.200	0.765
A20 [1701]	4	2	7	0.429	0.867
A21 [1702]	4	2	3	1.00	1.00
A22 [1703]	2	1	4	0.500	0.75
A23 [1704]	2	1	4	0.500	0.714
A24 [1705]	2	0	17–18	0.056–0.059	0.469–0.500
A25 [1706]	7	2	18–19	0.316–0.333	0.675–0.700
A26 [1707]	3	2	5	0.200	0
A27 [1708]	2	1	4	0.250	0.4
A28 [1709]	2	0	Uninformative	Uninformative	Uninformative
A29 [1710]	4	2	5	0.600	0.778
A30 [1711]	2	0	2	0.500	0
A31 [1712]	3	2	18	0.167	0.516
A32 [1713]	3	0	19	0.105	0.585
A33 [1714]	4	1	12–13	0.231–0.250	0.231–0.308
A34 [1715]	2	2	7	0.143	0.700
A35 [1716]	3	1	19	0.105	0.452
A36 [1717]	2	2	2	0.500	0.833
A37 [1718]	4	1	Excluded	Excluded	Excluded
A38 [1719]	3	2	1	1.00	0/0
A39 [1720]	3	2	2	1.00	1.0
A40 [1721]	3	2	1	1.00	0/0
A41 [1722]	2	1	Uninformative	Uninformative	Uninformative
A42 [1723]	2	2	1	1.00	1.00
A43 [1724]	2	2	1	1.00	1.00
A44 [1725]	2	2	1	1.00	1.00
A45 [1726]	2	2	1	1.00	1.00
A46 [1727]	2	0	16	0.062	0.400
A47 [1728]	2	2	Uninformative	Uninformative	Uninformative
A48 [1729]	4	1	8	0.375	0.783
A49 [1730]	5	0	25	0.120	0.488

Appendix 2 *Continued*

Character	Number of states	Expected quality	Length on the best tree	CI on the best tree	RI on the best tree
A50 [1731]	4	2	9	0.333	0.684
A51 [1732]	2	0	4	0.250	0
A52 [1733]	2	2	2	0.500	0
A53 [1734]	3	2	10	0.200	0.667
A54 [1735]	3	2	4	0.500	0.946
A54b [1736]	4	2	9	0.222	0.811
A55 [1737]	4	0	27	0.111	0.351
A56 [1738]	3	1	9	0.222	0.759
A57 [1739]	4	2	8	0.375	0.815
A58 [1740]	2	2	13	0.154	0.353
A59 [1741]	2	2	3	0.333	0.333
A60 [1742]	2	2	2	0.500	0.750
A61 [1743]	2	2	1	1.00	1.00
A62 [1744]	2	2	2	0.500	0.875
A63 [1745]	2	2	2	0.500	0.800
A64 [1746]	3	2	2	1.00	1.00
A65 [1747]	3	0	12	0.167	0.167
A66 [1748]	2	2	2	0.500	0.833
A67 [1749]	2	2	2	0.500	0.833
A68 [1750]	2	0	18	0.056	0.056
A69 [1751]	2	0	22–23	0.043–0.045	0.154–0.192
A70 [1752]	2	0	16	0.062	0.375
A70b [1753]	2	0	26	0.038	0.219
A71 [1754]	3	0	17	0.118	0.118
A72 [1755]	4	1	16	0.125	0.300
A73 [1756]	3	0	27	0.074	0.265
A74 [1757]	4	0	20	0.150	0.261
A75 [1758]	2	2	1	1.00	1.00
A76 [1759]	2	1	12–13	0.077–0.83	0.500–0.542
A77 [1760]	2	1	5	0.200	0.333
A78 [1761]	2	2	1	1.00	1.00
A79 [1762]	2	1	4	0.250	0.500

APPENDIX 3

Data matrix

	s1	s2	s3	s4	s5	s6	s7	s8	s9	s10	s11	s12	s13	s14	s15	s16	s17	s18	s19	s20
<i>depressa</i>	0	0	1	?	0/1	0	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>cf. onyx</i>	0	0	1	?	1	0	0	1	1	0	1	0	1	1	0	0	0	0/1	1	1
<i>ustulatulina</i>	0	1	1	?	1	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1
<i>nummaria</i>	0	0	1	?	0	0	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>philippiana</i>	0	0	1	?	1	0	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>cerithicola</i>	1	1	1	?	1	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1
<i>aff. onyx</i>	0	0	1	?	1	0	0	1	1	0	1	0	0	1	0	0	2	0	1	0
<i>protea</i>	0	0	1	?	0/1	0	0	1	1	0	1	0	0	1	0	0	0	0	1	0
<i>cf. aplysioides</i>	0	0	1	?	1	1	0	1	1	0	1	0	1	1	0	0	0/2	0	1	0
<i>arenata</i>	0	1	1	?	1	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1
<i>immersa</i>	0	1	1	?	0/1	0	0	1	1	1	1	0	0	1	0	0	0	0	1	0
<i>cf. perforans</i>	0	0	1	?	0	0	0	1	1	0	1	0	0	1	0	0	2	0	1	0
<i>convexa</i>	0	1	1	?	1	1	0	1	1	1	0	0	0	1	0	0	0	1	1	1
<i>onyx</i>	0	0	1	?	1	0	0	1	1	0	1	0	0	1	0	0	0	1	1	1
<i>aff. williamsi</i> Washington	0	0	1	?	0/1	0	0	1	1	1	1	0	1	1	0	0	2	0	1	0
<i>walshi</i>	0	0	1	?	1	1	1	1	0	3	8	1	1	1	0	0	2	0	1	0
<i>incurva</i>	1	1	1	?	1	0	0	1	1	1	1	0	0	1	0	0	0	0/1	1	1
<i>naticarum</i>	1	1	1	?	2	0	0	1	1	1	1	0	0	1	0	0	0	0/1	1	1
<i>atrasolea</i>	0	0	1	?	0/1	0	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>williamsi</i>	0	0	1	?	0/1	0	0	1	1	0	1	0	0	1	0	0	2	0	1	0
<i>complanata</i>	0	0	1	?	1	1	0	1	1	0	1	0	0	1	0	0	1	0	1	0/1
<i>argentina</i>	0	0	1	?	1	0	0	1	1	0	2	0	1	1	0	0	1	0	1	0
<i>marginalis</i>	0	0	1	?	1	1	0	1	1	0	0/1	0	1	1	0	0	2	0	1	0
<i>excavata</i>	0	1	1	?	1	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1
<i>striolata</i>	0	0	1	?	1	1	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>fornicata</i>	0	0	1	?	1	0/1	0	1	1	0	1	0	0	1	0	0	1	0	1	0
<i>fimbriata</i>	0	0	1	?	1	0	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>cf. convexa</i>	0	0	1	?	0/1	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1
<i>grandis</i>	0	1	1	?	1	0	0	1	1	1/2	0	0	0	1	0	0	0	1	0	1
<i>aff. williamsi</i> Alaska	0	0	1	?	0	0	0	1	1	1	1	0	0	1	0	0	2	0	1	0
<i>monoxyla</i>	1	1	1	?	0	0	0	1	1	1	1	0	0	1	0	0	2	0	1	0
<i>plana</i>	0	0	1	?	0	0/1	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>navicula</i>	0	0	1	?	0/1	1	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>lessoni</i>	0	0	1	?	1	1	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>incurva</i> Panama	0	1	1	?	1	0	0	1	1	1	2	0	0	1	0	0	0	0	1	0/1
<i>incurva</i> Peru	0	1	1	?	1	0	0	1	1	1	2	0	0	1	0	0	0	0	1	1
<i>porcellana</i>	0	0	1	?	1	0	0	1	1	0	1	0	1	1	0	0	1	0	1	0
<i>Crep. n. sp. pt.</i>	0	0	1	?	1	0	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>coquimbensis</i>	0	0	1	?	0/1	1	0	1	1	0	1	0	1	1	0	0	2	0	1	0
<i>adunca</i>	1	1	1	?	1	0	0	1	1	2	1	0	0	1	0	0	0	1	1	1
<i>maculosa</i>	0	1	1	?	1	0	0	1	1	1	0	0	0	1	0	0	0/1	0/1	1	1
<i>T. calyptraeformis</i> North	0	1	1	?	1	0	0	3	1	0	0/1	0	0	1	1	0	2	1	0	0
<i>T. calyptraeformis</i> South	0	1	1	?	1	0	0	3	1	0	0	0	0	1	1	0	0	1	0	0
<i>cf. aculeata</i> Australia	0	1	1	?	1	1	0	1	1	0	0	0	0	1	0	0	1	1	0	0
<i>cf. aculeata</i> Brazil	0	1	1	?	0/1	1	0	1	1	0	0	0	1	1	0	0	1	1	0	0
<i>cf. aculeata</i> Panama	0	1	1	?	1	1	0	1	1	0	1	0	0	1	0	0	1	0/1	0	0
<i>gravispinosa</i>	0	1	1	?	1	1	0	1	1	0	1	0	1	1	0	0	1	1	0	0
<i>cf. aculeata</i> Mexico	0	1	1	?	1	1	0	1	1	0	0	0	1	1	0	0	1	1	0	0
<i>cf. aculeata</i> South Africa	0	1	1	?	1	1	0	1	1	0	0/1	0	0	1	0	0	1	1	0	0
<i>cf. aculeata</i> Argentina	0	1	1	?	1	1	0	1	1	0	0	0	1	1	0	0	1	1	0	0
<i>aculeata</i> Florida	0	1	1	?	1	1	0	1	1	0	0	0	1	1	0	0	1	1	0	0
<i>fecunda</i>	0	1	1	?	2	0	0	1	0	3	1	0	1	1	0	0	2	1	1	0
<i>dilatata</i>	0	1	1	?	2	0	0	1	0	3	1	0	1	1	0	0	2	1	1	0
<i>capensis</i>	0	1	1	?	2	1	0	1	0	0	1	0	1	1	0	0	0	1	0	0
<i>dorsata</i>	0	0	1	?	2	1	0	1	0	3	0	0	1	1	0	0	0/2	1	0	1
<i>Cruc. tenuis</i>	0	0	1	?	2	1	1	2	0	7	7	0	7	1	1	0	0	1	0	1
<i>Cruc. scutellatum</i>	0	0	1	?	2	1	1	2	0	7	7	0	7	1	1	0	0	1	0	1
<i>Cruc. spinosum</i> Peru	0	0	1	?	2	1	1	2	0	7	7	1	7	1	1	0	2	1	0	1
<i>Cruc. spinosum</i> Panama	0	0	1	?	2	1	1	2	0	7	7	0	7	1	1	0	0	1	0	1
<i>Cruc. radiata</i>	0	0	1	?	2	1	1	2	0	7	7	0	7	1	1	0	0	1	0	1
<i>Cal. aspersa</i>	0	0	1	?	1	0	0	3	1	3	1	1	1	1	1	0	2	1	0	1
<i>B. extinctorum</i>	0	1	1	?	2	0	1	0	1	3	1	1	1	1	1	0	0	1	0	1
<i>Z. tenuis</i>	0	1	1	?	1	0	0	3	1	1	0	0	0	1	1	0	0	1	0	0
<i>Cal. cf. conica</i>	0	1	1	?	0	0	0	3	1	3	1	1	1	1	1	0	0	1	0	1
<i>Cal. chinensis</i>	0	1	1	?	1	0	0	3	1	3	1	1	1	1	1	0	0	1	0	1
<i>Cal. fastigata</i>	0	1	1	?	1	0	0	3	1	3	1	1	1	1	1	0	0	1	0	0
<i>Cal. mamallaris</i>	0	1	1	?	1	0	0	3	1	3	1	1	1	1	1	0	0	1	0	0
<i>Cal. cf. lichen</i>	0	1	1	?	1	0	0	3	1	3	1	1	1	1	1	0	0	1	0	0
<i>S. novaezealandiae</i>	0	1	1	?	1	0	0	3	1	1	0	1	0	1	1	0	0	1	0	0
<i>T. cancellata</i>	0	3	0	8	8	8	8	8	8	8	8	8	8	8	0	0	1	0	1	8
<i>Cap. ungaricus</i>	2	2	0	8	8	8	8	8	8	8	8	8	8	8	1	0	0	1	1	8
<i>Vanikoro</i> sp.	0	3	0	8	8	8	8	8	8	8	8	8	8	8	0	0	1	1	1	8
<i>Cheilea equestris</i>	0	0	1	?	3	0	0	0	0	7	7	0	7	1	1	0	0	1	0	0
<i>Hipponix</i> Australia	2	2	0	8	8	8	8	8	8	8	8	8	8	8	1	1	0	0	1	8
<i>Sabia conica</i> Australia	2	2	0	8	8	8	8	8	8	8	8	8	8	8	1	1	0	0	1	8
<i>Leptonetis perplexus</i>	2	2	0	8	8	8	8	8	8	8	8	8	8	8	1	0	0	2	1	8
<i>Hipponix</i> South Africa	2	2	0	8	8	8	8	8	8	8	8	8	8	8	1	1	0	0	1	8

s21	s22	s23	s24	s25	s26	s27	s28	s29	s30	s31	s32	s33	s34	s35	s36	s37	s38	s39	s40	s41	a1
2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	0	1	1	0	0	0	0	2	1	0	0	0	0	0	0	0	0	1	0	0
1	1	0	1	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0
1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0
1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0
2	0	0	1	1	0	0	1	0	1/2	0	0	0	0	0	0	0	0	0	1	0	1
2	3	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
1/2	1	0	0	1	0	1	1	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0
1	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
1	2	0	0	1	0	0	1	0	2	1	0	0	0	0	0	0	0	?	1	1	0
2	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0	0	0
2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1/2	0	1	1	0	0	1	1	0/2	0	0	0	0	0	0	0	0	0	1	0	0
1/2	3	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0
2	0	0	1	0	1	0	1	0	2	1	0	0	0	0	0	0	0	0	1	0	0
2	1	0	1	1	1	0	1	0	3	0	0	0	0	0	0	0	0	0	1	0	1
2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
1	2	0	1	1	0	0	1	0	0/2	1	0	0	0	0	0	0	1	0	1	0	0
0/1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
1	2	0	0	1	0	0	1	0	2	1	0	0	0	0	0	0	0	?	1	1	1
1	3	0	0	1	0	0	1	0	0/1	0	0	0	0	0	0	0	0	?	0	0	0
1	1	0	0	1	0	0	1	0	1/2/3	1	0	0	0	0	0	0	0	0	1	0	0
0/1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2	1	0	0
2	0	0	1	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	1	1	0
1	2/3	0	1	1	0	0	1	0	0/1	0	0	0	0	0	0	0	0	?	1	1	1
2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0	0	?	1	0	0
1/2	0	0	0	0	0	0	1	0	0	0	0/1	0	0	1	0	0	0	0	1	0	0
2	1	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	?	1	1	0
2	1	0	1	1	1	0	0	0	2	0	0	0	0	0	0	0	0	?	1	0	0
2	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1
1	0	0	1	1	0	0	1	0	1	0	0/1	0	0	0	0	0	0	0	0	0	0
2	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
1	2	0	1	1	0	0	1	0	1/2	1	0	0	0	0	0	0	0	?	1	1	1
0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	?	1	0	0
0	2	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	0	?	1	0	0
0	0	0	1	1	0	0	1	0	2	0	0	1	1	0	0	0	0	1	1	0	0
0	0	0	1	1	0	0	1	0	3	0	0	1	1	0	0	0	0	0	1	0	0
0	0	0	1	0	0	0	1	0	3	0	0	1	1	0	0	0	0	1	1	0	0
1	0	0	1	1	0	0	1	0	1/3	0	0	1	1	0	0	0	0	1	1	0	0
0	0	0	1	1	0	0	1	0	3	0	0	1	1	0	0	0	0	1	1	0	0
0	0	0	0	1	0	0	1	0	0/3	0	0	1	1	0	0	0	0	0	1	0	0
0	0	0	1	1	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	1	1	0
0	0	0	1	1	0	0	1	0	1/2/3	0	0	1	1	0	0	0	0	0	1	0	0
1	0/2	0	1	1	0	0	1	0	1/3	1	0	0	0	0	0	0	0	0	1	0	0
1	0	0	1	0	0	0	1	1	0/1/2	1	0	0	0	0	0	0	0	0	1	0	0
1	0	0	1	0	0	0	1	1	0/3	0	0	0	0	0	0	0	0	?	1	0	0
1	0	0	0	0/1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0
2	0	0	1	1	0	0	1	0	0/3	0	0	0	0	0	1	0	0	?	1	0	0
2	0	0	1	1	0	0	1	0	0/3	1	0	1	0	0	0	0	0	1	1	0	0
1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0
2	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0
0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	?	1	0	1
1	0	0	1	1	0	0	1	0	1/2	0	0	0	1	0	0	0	0	?	1	0	0
0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0/1	0	1	0	0
0	1	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	?	1	0	0
0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	4	1	0	0
2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	?	1	0	0
2	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0
0	3	0	0	1	0	0	1	1	0/3	0	0	0	0	0	0	0	0	?	1	0	0
0	3	0	0	1	0	0	1	0	0	0	8	1	1	0	0	1	0	5	2	2	0
1	3	0	0	0	0	0	1	0	0	0	8	0	1	0	0	0	0	?	1	0	0
0	0	0	0	0	0	0	1	0	0	0	8	0	0	0	1	0	0	?	2	2	0
2	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	?	1	0	0
2	0	1	1	0	0	0	0	0	0	0	8	0	1	0	0	0	0	0	1	0	0
2	2	0	1	1	0	0	1	0	3	1	8	0	1	0	0	0	0	0	1	0	0
2	1	0	0	0	0	0	1	0	0	0	8	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	1	0	0	0	8	0	1	0	0	0	0	?	1	0	0

Appendix 3 Continued

	a2	a3	a4	a5	a6	a7	a8	a9	a10	a11	a12	a13	a14	a15	a16	a17	a18	a19	a20	a21	a22
<i>depressa</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
cf. <i>onyx</i>	1	1	0	0	0	0	0	0	0	0	0	0	4	0	1	0	0	1	1	2	0
<i>ustulatulina</i>	1	1	0	0	0	0	2	1	0	1	0	0	4	0	1	0	0	1	1	2	0
<i>nummaria</i>	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
<i>philippiana</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
<i>cerithicola</i>	1	1	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	1	1	2	0
aff. <i>onyx</i>	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	1	1	2	0
<i>protea</i>	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	2	0
cf. <i>aplysioides</i>	1	1	0	0	0	0	2	?	0	1	0	0	0	0	1	0	0	1	1	2	0
<i>arenata</i>	1	1	0	0	0	0	2	0	1	1	0	0	1	1	1	0	0	0	1	2	0
<i>immersa</i>	1	1	0	0	0	0	?	0	0	0	0	1	0	0	1	1	0	0	1	2	0
cf. <i>perforans</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	2	2	0
<i>convexa</i>	1	1	0	0	0	0	2	1	0	1	0	0	4	0	1	0	0	1	1	2	0
<i>onyx</i>	1	1	0	0	0	0	?	1	1	0	0	1	1	1	1	0	0	1	1	2	0
aff. <i>williamsi</i> Washington	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
<i>ualshi</i>	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	2	0	1	2	0
<i>incurva</i>	1	1	0	0	0	0	2	1	0	1	0	0	1	1	1	0	0	1	1	2	1
<i>naticarum</i>	?	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	1	2	0
<i>atrasolea</i>	1	1	0	0	0	0	0	1	0	1	0	0	4	0	1	0	0	1	1	2	0
<i>williamsi</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
<i>complanata</i>	1	1	0	0	0	0	2	1	1	1	1	0	1	1	1	0	0	1	1	2	0
<i>argentina</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
<i>marginalis</i>	1	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	1	2	0
<i>excavata</i>	1	1	0	0	0	0	2	0	0	1	0	1	1	1	1	0	0	1	1	2	0
<i>striolata</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
<i>fornicata</i>	1	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	1	2	0
<i>fimbriata</i>	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
cf. <i>convexa</i>	1	1	0	0	0	0	2	0	0	1	0	0	4	0	1	0	0	1	1	2	0
<i>grandis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	2	2	0
aff. <i>williamsi</i> Alaska	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	2	0
<i>monoxyla</i>	?	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	2	1
<i>plana</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	2	0
<i>navicula</i>	1	1	0	0	0	0	?	0	1	0	0	0	0	0	1	0	0	1	1	2	0
<i>lessoni</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	0
<i>incurva</i> Panama	1	1	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	1	1	2	1
<i>incurva</i> Peru	1	0	0	0	0	0	?	0	1	0	0	3	0	1	0	0	0	1	1	2	0
<i>porcellana</i>	0	1	0	0	0	0	0	1	0	1	0	0	3	0	1	0	0	1	1	2	0
<i>Crep. n. sp. pt.</i>	1	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	1	2	0
<i>coquimbensis</i>	1	1	0	0	0	0	0	0	0	0	0	0	4	0	1	0	0	1	1	2	0
<i>adunca</i>	1	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	1	2	1
<i>maculosa</i>	1	1	0	0	0	0	0	1	0	0	0	0	4	0	1	0	0	1	1	2	0
<i>T. calyptraeformis</i> North	0	0	0	0	0	0	?	0	1	0	0	0	0	0	1	0	1	0	1	2	0
<i>T. calyptraeformis</i> South	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	1	0	1	0	2	0
cf. <i>aculeata</i> Australia	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	2	2	0
cf. <i>aculeata</i> Brazil	0/1	0	0	0	0	0	1	?	0	1	0	1	0	0	1	0	1	1	2	2	0
cf. <i>aculeata</i> Panama	0	0	0	0	0	0	1	1	0	1	0	1	0	1	1	0	1	1	2	2	0
<i>gravispinosa</i>	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	2	2	0
cf. <i>aculeata</i> Mexico	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	2	2	0
cf. <i>aculeata</i> South Africa	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	2	2	0
cf. <i>aculeata</i> Argentina	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	2	2	0
<i>aculeata</i> Florida	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	2	2	0
<i>fecunda</i>	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	2	0
<i>dilatata</i>	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	2	0
<i>capensis</i>	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	0	1	1/2	2	0
<i>dorsata</i>	0	0	0	0	0	0	0	1	0	0	0	1	5	1	1	0	2	1	2	2	0
<i>Cruc. tenuis</i>	0	0	0	0	0	0	1	0	0	1	0	1	2	2	1	2	0	1	2	2	0
<i>Cruc. scutellatum</i>	0	0	0	0	0	0	1	0	0	0	0	1	2	2	1	2	0	1	2	2	0
<i>Cruc. spinosum</i> Peru	1	0	0	0	0	0	1	1	0	1	0	1	2	2	1	2	2	1	2	2	0
<i>Cruc. spinosum</i> Panama	0	0	0	0	0	0	1	1	0	1	0	1	2	2	1	2	1	1	2	2	0
<i>Cruc. radiata</i>	0	0	0	0	0	0	1	0	0	0	1	1	2	2	1	2	1	1	2	2	0
<i>Cal. aspersa</i>	0	1	0	0	0	0	?	0	0	0	1	0	1	1	0	3	1	2	2	2	0
<i>B. extinctorum</i>	0	0	0	0	0	0	1	1	0	1	0	1	0	1	1	1	2	1	2	1	0
<i>Z. tenuis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	2	2	0
<i>Cal. cf. conica</i>	0	0	0	0	0	0	?	0	0	0	1	0	1	1	1	1	1	1	2	2	0
<i>Cal. chinensis</i>	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	1	1	0	2	2	0
<i>Cal. fastigata</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	2	2	0
<i>Cal. mamallaris</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	?	2	2	0
<i>Cal. cf. lichen</i>	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	1	2	2	0
<i>S. novaezelandiae</i>	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	0	2	2	0
<i>T. cancellata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	3	0
<i>Cap. ungaricus</i>	0	0	0	0	0	0	?	0	0	0	0	3	3	0	3	0	3	0	3	3	0
<i>Vanikoro</i> sp.	1	0	1	2	0	0	?	?	?	?	1	0	3	3	0	3	3	0	0	0	2
<i>Cheilea equestris</i>	0	0	1	1	1	0	0	0	0	0	1	0	3	3	1	3	0	0	0	0	2
<i>Hipponix</i> Australia	0	0	1	1	0	1	0	0	0	1	1	0	3	3	0	3	0	0	0	0	2
<i>Sabia conica</i> Australia	0	0	1	1	0	1	?	0	1	1	0	3	3	1	3	0	0	0	0	0	2
<i>Leptonetis perplexus</i>	0	0	1	1	1	1	0	0	0	1	0	3	3	1	3	0	0	0	0	0	2
<i>Hipponix</i> South Africa	0	0	1	1	1	1	0	0	0	1	1	0	3	3	0	3	0	0	0	0	2

a23	a24	a25	a26	a27	a28	a29	a30	a31	a32	a33	a34	a35	a36	a37	a38	a39	a40	a41	a42	a43
0	0	1	1	0	0	0	0	3	1	0	0	0	0	?	1	0	2	0	0	0
0	1	1	1	0	0	0	0	3	1	1	0	0	0	0	1	0	2	0	0	0
0	1	0	1	0	0	0	0	3	1	0	0	1	0	0	1	0	2	0	0	0
0	0	0	1	0	0	0	?	1	0	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	2	1	0	0	?	0	0	1	0	2	0	0	0
0	1	1	1	1	0	0	0	3	2	0	0	?	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	1	0	0	1	0	0	1	0	2	0	0	0
0	1	1	1	0	0	0	0	3	0	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	?	3	1	0	0	1	0	1	1	0	2	0	0	0
0	0	?	?	?	?	?	?	3	1	0	0	1	0	?	1	0	2	0	0	0
0	1	?	?	?	?	?	?	1	0	0	1	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	2	0	0	1	0	0	1	0	2	0	0	0
0	1	0	1	0	0	0	0	3	1	1	0	1	0	0	1	0	2	0	0	0
0	1	1	1	0	0	0	0	3	2	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	1	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	1	0	0	1	0	?	1	0	2	0	0	0
0	0	6	1	0	0	0	0	3	0	3	0	0	0	0	1	0	2	0	0	0
1	1	0	1	0	0	0	0	3	1	1	0	1	0	0	1	0	2	0	0	0
0	1	1	1	0	0	0	0	3	1	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	1	1	0	1	0	0	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	2	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	1	1	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	2	0	0	1	0	0	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	1	1	0	1	0	?	1	0	2	0	0	0
0	0	?	?	?	?	?	?	3	1	1	0	0	0	?	1	0	2	0	0	0
0	0	?	?	?	?	?	?	2	1	0	0	1	0	?	1	0	2	0	0	0
0	0/1	0	1	0	0	0	0	3	1	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	1	0	0	1	0	?	1	0	2	0	0	0
0	1	0	0	0	0	0	0	3	1	1	0	1	0	?	1	0	2	0	0	0
0	1	6	1	0	0	0	0	3	2	0	0	0	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	2	0	0	1	0	1	1	0	2	0	0	0
1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	1	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	?	3	1	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	2	0	0	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	1	1	0	1	1	0	?	1	0	2	0	0	0
0	0	1	1	0	0	0	0	3	2	1	0	0	?	1	0	2	0	0	0	0
0	0	1	1	0	0	0	0	3	2	0	0	1	0	?	1	0	2	0	0	0
0	0	3	1	1	0	0	0	3	1	0	0	1	0	?	1	0	2	0	0	0
0	0	0	1	1	0	0	1	3	2	1	0	1	1	0	1	0	2	0	0	0
1	1	2	1	0	0	0	0	3	2	1	0	0	0	1	1	0	2	0	0	0
0	1	1	1	1	0	0	0	3	1	1	0	0	0	?	1	0	2	0	0	0
0	1	0	1	0	0	0	0	3	2	1	0	0	0	?	1	0	2	0	0	0
0	1	0	0	0	0	0	0	3	0	0	0	0	0	1	1	0	2	0	0	0
0	1	2	1	0	0	0	0	0	0	0	1	0	?	1	1	0	2	0	0	0
0	0	2	1	0	0	0	0	1	0	0	1	1	0	?	1	0	2	0	0	0
0	1	2	1	0	0	0	0	1	0	0	1	1	0	1	1	0	2	0	0	0
0	1	2	1	0	0	0	0	1	0	0	1	0	0	?	1	0	2	0	0	0
0	1	2	1	0	0	0	0	1	0	0	1	1	0	1	1	0	2	0	0	0
0	1	2	1	0	0	0	0	0	0	0	1	0	0	1	1	0	2	0	0	0
0	1	2	1	0	0	0	0	1	0	0	1	0	0	1	1	0	2	0	0	0
0	1	0	1	0	0	0	0	3	1	2	0	0	0	1	1	0	2	0	0	0
0	1	0	1	0	0	0	0	3	1	2	0	0	0	1	1	0	2	0	0	0
0	1	0	1	0	0	0	0	3	1	0	0	2	0	1	1	0	2	0	0	0
0	0	0	0	0	0	0	0	3	2	0	0	1	0	1	1	0	2	0	0	0
0	0	4	1	0	0	3	0	?	?	?	?	?	0	?	1	0	2	0	0	0
0	1	4	1	0	0	3	0	1	0	0	1	?	0	?	1	0	2	0	0	0
0	0	4	1	0	0	0	1	1	0	0	1	0	0	?	1	0	2	0	0	0
0	1	4	0	0	0	3	0	1	0	0	1	0	0	?	1	0	2	0	0	0
0	1	4	?	?	?	3	?	0	0	0	1	1	0	1	1	0	2	0	0	0
0	1	1	1	0	0	0	0	1	0	0	0	0	0	?	1	0	2	0	0	0
0	1	6	1	0	0	0	0	3	2	3	0	1	0	1	1	0	2	0	0	0
0	1	5	1	0	0	0	0	1	0	0	0	1	0	1	1	0	2	0	0	0
0	0	6	0	0	0	0	0	1	0	0	1	0	0	?	1	0	2	0	0	0
0	0	5	1	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0
0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0
0	1	5	1	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0
0	1	0	1	0	0	1	0	0	0	0	0	0	?	2	2	0	1	?	1	0
0	1	0	1	0	0	1	0	0	0	0	0	1	?	?	?	0	2	?	1	0
2	1	?	?	?	?	?	?	1	0	0	1	0	1	?	?	?	?	?	0	1
2	1	1	1	1	0	?	0	0	0	0	1	1	1	?	1	1	2	?	0	1
2	1	0	1	0	0	2	0	1	0	0	0	0	1	3	1	1	2	0	0	1
2	1	0	1	0	0	2	?	1	0	0	1	0	1	1	1	1	2	?	0	1
2	0	0	1	0	0	1	0	1	0	0	1	0	1	2	1	2	2	0	0	1
2	1	0	1	0	0	2	?	1	0	0	0	0	1	3	1	1	2	0	0	1

Appendix 3 Continued

	a44	a45	a46	a47	a48	a49	a50	a51	a52	a53	a54	a54b	a55	a56	a57	a58	a59	a60
<i>depressa</i>	1	1	1	0	0	0/1	0	0	0	1	0	0	1	1	0	0	0	0
<i>cf. onyx</i>	1	1	1	0	0	4	0	0	0	1	0	0	2	1	0	0	0	0
<i>ustulatulina</i>	1	1	1	0	0	0	0	0	0	1	0	0	2	1	0	0	0	0
<i>nummaria</i>	1	1	1	0	0	4	1	0	0	1	0	0	1	1	0	0	0	0
<i>philippiana</i>	1	1	1	0	0	4	0	0	0	1	0	0	2	1	0	0	0	0
<i>cerithicola</i>	1	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
<i>aff. onyx</i>	1	1	1	0	0	4	0	0	0	1	0	0	2	1	0	0	0	0
<i>protea</i>	1	1	1	0	0	4	0	0	0	1	0	0	1	1	0	0	0	0
<i>cf. aplysioides</i>	1	1	1	0	0	1	0	0	0	1	0	0	2	1	0	0	0	0
<i>arenata</i>	1	1	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0
<i>immersa</i>	1	1	1	0	0	0	0/2	0	0	1	1	1	2	1	0	0	0	0
<i>cf. perforans</i>	1	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
<i>convexa</i>	1	1	1	0	0	1/4	0	1	0	1	0	0	2	1	0	0	0	0
<i>onyx</i>	1	1	1	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0
<i>aff. williamsi</i> Washington	1	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
<i>walshi</i>	1	1	0	0	1	0	2	0	0	1	1	1	2	0	2	0	0	0
<i>incurva</i>	1	1	1	0	0	1	0	0	0	1	0	0	2	1	0	0	0	0
<i>naticarum</i>	1	1	1	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0
<i>atrasolea</i>	1	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
<i>williamsi</i>	1	1	1	0	0	4	0	0	0	1	0	0	1	1	0	0	0	0
<i>complanata</i>	1	1	1	0	0	1	0	0	0	1	0	0	2	1	0	0	0	0
<i>argentina</i>	1	1	1	0	1	4	0	0	0	1	0	0	1	1	0	1	0	0
<i>marginalis</i>	1	1	1	0	0	4	0	1	0	1	0	0	2	1	0	0	0	0
<i>excavata</i>	1	1	1	0	0	4	0	0	0	1	0	0	1	1	0	0	0	0
<i>striolata</i>	1	1	0	0	0	2	1	0	0	1	0	0	2	1	0	1	0	0
<i>fornicata</i>	1	1	1	0	0	4	0	0/1	0	1	0	0	1	1	0	0	0	0
<i>fimbriata</i>	1	1	1	0	0	2	1	0	0	1	0	0	2	1	0	0	0	0
<i>cf. convexa</i>	1	1	1	0	0	?	0	0	0	1	0	0	2	1	0	0	0	0
<i>grandis</i>	1	1	0	0	0	?	0	0	0	1	0	0	1	1	0	0	0	0
<i>aff. williamsi</i> Alaska	1	1	1	0	0	4	0	0	0	1	0	0	1	1	0	0	0	0
<i>monoxyla</i>	1	1	1	0	0	0	2	0	0	1	1	1	1	1	0	0	0	0
<i>plana</i>	1	1	0	0	0	4	0	0	0	1	0	0	1	1	0	0	0	0
<i>navicula</i>	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
<i>lessoni</i>	1	1	1	0	0	4	0	0	0	1	0	0	2	1	0/1	0	0	0
<i>incurva</i> Panama	1	1	1	0	0	2	0	0	0	1	0	0	2	1	0	1	0	0
<i>incurva</i> Peru	1	1	1	0	0	2	0	0	0	1	0	0	2	1	0	1	0	0
<i>porcellana</i>	1	1	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0
<i>Crep. n. sp. pt.</i>	1	1	1	0	0	4	0	0	0	1	0	0	1	1	0	0	0	0
<i>coquimbensis</i>	1	1	0	0	0	0/1	0	0	0	1	0	0	1	1	0	0	0	0
<i>adunca</i>	1	1	1	0	0	1	0	0	0	1	0	0	2	1	0	0	0	0
<i>maculosa</i>	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
<i>T. calyptraeformis</i> North	1	1	1	0	1	4	0	0	0	0	1	2	1	0	1	1	0	0
<i>T. calyptraeformis</i> South	1	1	0	0	1	4	0	0	0	0	1	1	1	0	2	0	0	0
<i>cf. aculeata</i> Australia	1	1	1	0	0	2	1	0	0	0	1	2	1	0	1	0	0	0
<i>cf. aculeata</i> Brazil	1	1	1	0	0	2	1	0	0	0	1	2	2	0	1	0	0	0
<i>cf. aculeata</i> Panama	1	1	1	0	0	4	1	0	0	0	1	2	2	0	1	0	0	0
<i>gravispinosa</i>	1	1	1	0	0	4	1	0	0	0	1	2	1	0	1	1	0	0
<i>cf. aculeata</i> Mexico	1	1	1	0	0	4	1	0	0	0	1	2	2	0	1	0	0	0
<i>cf. aculeata</i> South Africa	1	1	0	0	0	2	1	0	0	0	1	2	1	1	1	0	0	0
<i>cf. aculeata</i> Argentina	1	1	0	0	0	2/4	1	0	0	0	1	2	2	1	1	0	0	0
<i>aculeata</i> Florida	1	1	1	0	0	4	1	0	0	0	1	2	2	0	1	0	0	0
<i>fecunda</i>	1	1	1	0	1	2	0	0	0	0	1	1	2	0	1	0	0	0
<i>dilatata</i>	1	1	1	0	1	2	0	0	0	0	1	1	2	0	1	0	0	0
<i>capensis</i>	1	1	1	0	0	2	0	0	0	0	1	2	2	0	1	0	0	0
<i>dorsata</i>	1	1	1	0	0	2	0	0	0	1	1	1	1	0	1	0	0	0
<i>Cruc. tenuis</i>	1	1	0	0	1	4	0	0	0	1	1	1	2	0	2	0	0	0
<i>Cruc. scutellatum</i>	1	1	0	0	1	2	0	0	0	1	1	1	2	0	2	0	0	0
<i>Cruc. spinosum</i> Peru	1	1	0	0	1	4	1	0	0	1	1	1	1	0	2	1	0	0
<i>Cruc. spinosum</i> Panama	1	1	0	0	1	1	0	0	0	1	1	1	2	0	2	0	0	0
<i>Cruc. radiata</i>	1	1	0	0	1	4	0	0	0	1	1	1	2	0	2	0	0	0
<i>Cal. aspersa</i>	1	1	1	0	1	4	0	0	0	0	1	1	1	0	2	1	0	0
<i>B. extinctorum</i>	1	1	0	0	1	1	0	0	0	0	1	1	2	0	2	0	0	0
<i>Z. tenuis</i>	1	1	0	0	1	0	0	0	0	1	1	2	1	0	2	0	0	0
<i>Cal. cf. conica</i>	1	1	1	0	1	1	0	1	0	0	1	1	2	0	2	0	0	0
<i>Cal. chinensis</i>	1	1	0	0	1	1	0	0	0	1	1	2	2	0	2	0	0	0
<i>Cal. fastigata</i>	1	1	0	0	1	1	0	0	0	0	1	1	0	0	2	0	0	0
<i>Cal. mamallaris</i>	1	1	0	0	1	4	0	0	0	0	1	1	2	0	2	0	0	0
<i>Cal. cf. lichen</i>	1	1	1	0	1	4	0	0	0	1	1	1	2	0	2	0	0	0
<i>S. novaezelandiae</i>	1	1	0	0	1	0	0/2	0	0	0	1	2	2	0	1	0	0	0
<i>T. cancellata</i>	0	0	0	0	0	0	2	0	0	1	1	2	0	1	0	1	0	0
<i>Cap. ungaricus</i>	0	0	1	0	0	0	3	0	0	1	1	2	0	1	0	1	0	0
<i>Vanikoro</i> sp.	0	0	0	0	2	0	2	0	0	0	1	2/4	3	1	0	1	1	1
<i>Cheilea equestris</i>	0	0	0	0	3	0	3	0	1	0	1	2	2	2	0	1	1	1
<i>Hippinx</i> Australia	0	0	0	0	2	0	2/3	0	1	0	1	2	1	0	0	1	1	1
<i>Sabia conica</i> Australia	0	0	1	0	2	0	3	0	0	0	1	2	1	1	0	1	0	1
<i>Leptonetis perplexus</i>	0	0	1	0	2	0	3	0	0	2	2	2	0	0	3	3	0	0
<i>Hippinx</i> South Africa	0	0	1	0	2	0/4	2	0	0	0	1	2	1	0	0	1	1	1

a61	a62	a63	a64	a65	a66	a67	a68	a69	a70	a70a	a71	a72	a73	a74	a75	a76	a77	a78	a79
0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	2	1	2	0	1	0	0	0	0
0	0	1	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	0	0
0	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1	1	1	0	0
0	0	1	0	0	0	0	?	?	?	?	?	?	?	?	1	0	0	0	0
0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0
0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
0	0	1	0	0	0	0	1	1	0	0	0	1	2	0	1	0	0	0	0
0	0	1	0	0	0	0	1	0	1	0	0	1	2	0	1	0	0	0	0
0	0	1	0	0	0	0	1	?	?	?	?	1	2	0	1	1	0	0	1
0	0	1	0	2	0	0	1	1	1	0	0	1	1	1	1	0	0	0	0
0	0	1	0	0	0	0	0	1	1	0	0	2	1	1	1	0	0	0	0
0	0	1	0	0	0	0	1	0	1	0	0	1	1	1	1	0	1	0	1
0	0	1	0	0	0	0	1	0	0	1	0	1	2	1	1	0	0	0	1
0	0	1	0	2	0	0	0	0	1	0	0	1	2	0	1	0	0	0	0
0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0
0	0	1	0/1	0	0	0	0	1	0	0	2	1	0/1	0	1	1	0	0	1
0	0	1	0	0	0	0	0	1	1	0	2	1	2	1	1	0	0	0	0
0	0	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0
0	0	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0
0	0	1	0	0	0	0	1	1	1	1	0	2	1	0	1	0	0	0	0
0	0	1	0	2	0	0	1	0	0	1	0	2	2	1	1	0	0	0	0
0	0	1	0	0/2	0	0	1	1	1	0	0	1	2	1	1	1	0	0	0
0	0	1	0	0	0	0	0	1	1	0	0	1	2	0	1	1	0	0	1
0	0	1	0	0	0	0	1	0	1	1	0	?	?	0	1	0	0	0	0
0	0	1	0	0	0	0	1	0	0	1	0	2	2	1	1	0	0	0	0
0	0	1	0	0	0	0	1	1	1	0	0	1	2	1	1	0	0	0	0
0	0	1	0	0	0	0	1	0	0	1	0	1	0/2	1	1	0	0	0	0
0	0	1	0	0/1	0	0	1	0	1	1	0	1	2	0	1	1	0	0	0
0	0	1	0	1	0	0	1	1	0	0	1/2	1	2	0	1	0	0	0	0
0	0	0	0	2	0	0	1	1	1	0	2	2	1	0	1	0	0	0	0
0	0	1	0	0	0	0	1	0	0	1	0	1	2	1	1	0	1	0	0
0	0	1	0	0	0	0	1	1	0	0	2	1	2	1	1	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	0	1	?	0	1	0	0	0	0
0	0	1	0	0	0	0	0	1	1	0	0	?	?	0	1	0	0	0	0
0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1
0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0
0	0	1	0	0	0	0	1	0	1	1	2	1	1	0	1	0	0	0	0
0	0	1	0	0	0	0	1	0	0	1	2	0/1	1	2	1	0	0	0	0
0	0	1	0	0	0	0	0	1	1	0	0	1	0/2	1	1	0	0	0	0
0	0	1	0	0	0	0	1	1	1	0	0	1	2	1	1	1	0	0	0
0	0	1	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	0	1
0	0	1	0	0	0	0	1	0	1	1	0	0	0	3	1	0	1	0	0
0	0	1	0	1	0	0	1	0	1	1	2	0	0	0	1	1	0	0	0
0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	0
0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0
0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0
0	0	1	0	0	0	0	1	1	1	0	0	1	2	0	1	1	0	0	0
0	0	1	0	0	0	0	1	1	1	0	0	1	2	0	1	1	?	0	0
0	0	1	0	0	0	0	1	0	0	1	0/3	1	0	0	1	1	0	0	0
0	0	1	0	0	0	0	1	0	0	1	0/3	1	0	0	1	1	0	0	0
0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0	0
0	0	1	0	2	0	0	0	1	1	0	0	2	1	0	1	0	0	0	0
0	0	1	0	1	0	0	1	0	1	1	0	1	2	0	1	1	0	0	0
0	0	1	0	2	0	0	0	0	1	0	2	2	0	0	1	1	0	0	0
0	0	1	0	0	0	0	1	1	1	1	1	2	0	1	1	0	0	0	0
0	0	1	0	0	0	0	1	0	1	0	0	2	2	0	1	1	0	0	0
0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	1	1	2	0	1	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	2	2	0	1	0	0	0	0	0
0	0	1	0	0	0	0	1	1	1	1	0	1	0	0	1	1	0	0	0
0	0	1	0	0	0	0	1	0	1	1	2	0	0	0	1	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	2	2	0	1	0	0	0	0	0
0	0	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0
0	0	1	0	0	0	0	1	0	1	1	2	0	0	0	1	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	1	2	0	0	1	0	0	0	0
0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	0	0	0	1/2	1	0	0/1	0	0
0	1	1	2	2	0	1	1	0	0	1	0	2	1	0	0	0	0	0	0
0	1	1	0	2	1	1	1	0	0	1	0	2	2	0	0	0	0	0	0
0	1	1	0	0	1	1	1	0	0	1	0	2	1	0	0	0	0	1	0
0	1	0	1	0	1	1	1	0	0	0	0	0/1	0	0	0	0	0	1	0
1	1	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0
1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
1	1	0	1	2	1	0	1	0	0	1	2	2	0	3	0	0	0	1	0
1	1	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0