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

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#### Abstract

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.


#### Abstract

'In the cabinets of the Naturalist, the shells of the Crepidulx and Calyptrææ 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

[^0]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
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 (ostraeids), 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 IndoPacific. 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 'Calyptracea' as a far more inclusive family including many limpetshaped taxa. For example Lamarck included Parmophorus, Emarginula, Siphonaria, Fissurella, Pileopsis, Calyptraea, Crepidula and Ancylus in his Calyptracea, 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 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Crepidula s.l. | Lamarck (1799) | C. fornicata | Oval | Posterior | Flat, attached on both sides | 0, 1, 2 |  | World-wide temperate and tropical |
| Bostrycapulus | Olsson \& Harbison (1953) | C. aculeata | Oval | Posteriorlateral | Flat, attached on both sides | 1 | Spines, medial ridge on shelf | World-wide temperate |
| Crepipatella | Lesson (1830) | C. dilatata | Rounded | Posteriorlateral | Slightly cupped, free on right side | 1 |  | Eastern Pacific, South Atlantic |
| Maoricrypta | Finlay 1927 | C. costata | Oval | Posterior | Flat, attached on both sides | 2 |  | New Zealand |
| Zeacrypta | Finlay 1927 | C. monoxyla | Oval | Posterior | Flat, attached on both sides | 2 |  | New Zealand |
| Janacus | Mörch 1852 | C. unguiformis | Flat, oval | Posterior | Flat, attached on both sides | 0 | White | World-wide temper ate and tropical |
| Crucibulum s.s. | Schumacher (1817) | C. rugosa-costatum | Conical | central | Cup-shaped | 0 |  | World-wide temper ate and tropical |
| Calyptraea s.s. | Lamarck (1799) | C. chinensis | Conical | Central | Spiral ramp | 1 |  | World-wide temperate and tropical |
| Trochita | Schumacher (1817) | T. trochiformis | Conical | Central | Spiral ramp | 1 | Thick, ribbed | World-wide |
| Sigapatella | Lesson (1830) | S.novozelandiae | Conical | Central | Spiral ramp | 1 |  | New Zealand |
| Zegalarus | Finlay 1926 |  | Conical | Central | Spiral ramp | 1 |  | New Zealand |
| Bicatillus s.s. | Swainson 1840 | B. extinctorum | Conical | Central | Tiny, flattened cup-shaped | 1 |  | Asia |
| Siphopatella s.s. | Lesson (1830) | S. washi | Flat | Lateral | Flat, folded | 1 |  | Old world |

[^1]

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 extinctorum, Singapore FMNH 299402. (F) Crepipatella 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 $=1 \mathrm{~cm}$.
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 |  |  |  |  |
| Crepidula (Bostrycapulus) Olsson \& Harbison (1953) |  |  |  |  |
| Crepidula aculeata Florida | Gmelin (1791) | Mote Marine Laboratory, Lido Key, Florida, USA $27^{\circ} 20^{\prime} \mathrm{N}, 82^{\circ} 42^{\prime} \mathrm{W}$ | ANSP A19745 FMNH 282365 BM20010455 | R. Collin and J. Wise |
| Crepidula cf. aculeata Panama |  | Venado, Pacific Coast, Panama $8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$ | FMNH 282273 ANSP A19740 BM 20010452 | R. Collin |
| Crepidula cf. aculeata Australia |  | Edwards Reef, Sydney, Australia $33^{\circ} 51^{\prime} \mathrm{S}, 151^{\circ} 13^{\prime} \mathrm{E}$ | FMNH 282302 <br> ANM C400000 | R.Collin, W. Ponder and P. Selvarkumaraswamy |
| Crepidula cf. aculeata Argentina |  | Playa Orengo, San Antonio <br> Oeste, Argentina <br> $40^{\circ} 53^{\prime} \mathrm{S}, 64^{\circ} 29^{\prime} \mathrm{W}$ | FMNH 282297 ANSP A 19744 BM20010456 | R. Collin |
| Crepidula cf. aculeata Brazil |  | Gois Beach, Santos Bay, São Paulo, Brazil $24^{\circ} 00^{\prime} \mathrm{S}, 46^{\circ} 21^{\prime} \mathrm{W}$ | FMNH 282350 | L. Simone |
| Crepidula cf. aculeata Mexico |  | Bahía de La Paz, Mexico $24^{\circ} 07^{\prime} \mathrm{N}, 110^{\circ} 24^{\prime} \mathrm{W}$ | FMNH 282193 FMNH 282194 | R. Collin |
| Crepidula cf. aculeata South Africa |  | Wooleys Pool, Muizenberg, South Africa $34^{\circ} 4^{\prime} \mathrm{S}, 18^{\circ} 20^{\prime} \mathrm{E}$ | FMNH 282277 BM20010453 | R. Collin, T. Ridgeway and K. Ruck |
| Crepidula gravispinosa | Kuroda \& Habe (1950) | Chijiwa, Nagasaki, Japan | FMNH 282336 | M. Katoh |
| Crepidula (Crepipatella) Lesson (1830) |  |  |  |  |
| Crepipatella capensis | Quoy \& Gaimard (1832-1833) | Muizenberg, Cape Province, South Africa $34^{\circ} 4^{\prime} \mathrm{S}, 18^{\circ} 20^{\prime} \mathrm{E}$ | FMNH 282278 | R. Collin, T. Ridgeway and K. Ruck |
| Crepipatella dilatata | Lamarck (1822) | Corral Bay, San Carlos, Chile $39^{\circ} 51^{\prime} \mathrm{S}, 73^{\circ} 27^{\prime} \mathrm{W}$ | BM 20010461 | R. Collin and <br> A. Reidemann |
| Crepipatella fecunda | Gallardo (1979) | Bahía de Coquimbo, IV Region, Chile $29^{\circ} 59^{\prime} \mathrm{S}, 71^{\circ} 19^{\prime} \mathrm{W}$ | FMNH 299425 | R. Collin and D. Véliz |
| Crepipatella lingulata | Gould (1846) | Shady Cove, Friday Harbor, Washington, USA. $48^{\circ} 20^{\prime} \mathrm{N}, 12301^{\prime} \mathrm{W}$ | FMNH 282293 <br> FMNH 285019 | R. Collin and B. Pernet |



| Crepidula (Maoricrypta Zeacrypta) Finlay (1927) |  |  |  |
| :---: | :---: | :---: | :---: |
| Crepidula immersa | Angas (1847) | Edithburg, York Penninsula, South Australia $35^{\circ} 03^{\prime} \mathrm{S} 137^{\circ} 26^{\prime} \mathrm{E}$ | FMNH 282298 |
| Crepidula monoxyla | Lesson (1830) | Leigh, North Island, New Zealand $36^{\circ} 10^{\prime} \mathrm{S}, 174^{\circ} 30^{\prime} \mathrm{E}$ | FMNH 282305 ANSP A19732 BM20010467 |
| Crepidula (Janacus) Mörch (1852) |  |  |  |
| Crepidula argentina | Simone et al. (2000) | Mar del Plata, Argentina $30^{\circ} 00^{\prime}$ S, $57^{\circ} 21^{\prime}$ W | ANSP A19738 FMNH 282346 BM20010457 |
| Crepidula atrasolea | Collin (2000) | Harbor Branch Oceanographic Institution, Florida, USA $28^{\circ} 30^{\prime} \mathrm{N}, 81^{\circ} 20^{\prime} \mathrm{W}$ | FMNH 282209 <br> FMNH 282213 |
| Crepidula coquimbensis | Brown \& Olivares (1996) | Bahía de Herradura, Coquminbo, IV Region, Chile $29^{\circ} 58^{\prime} \mathrm{S}, 71^{\circ} 21^{\prime} \mathrm{W}$ | FMNH 282311 |
| Crepidula depressa | Say (1822) | Sanibel Marina, Florida, USA $26^{\circ} 27^{\prime} \mathrm{N}, 82^{\circ} 02^{\prime} \mathrm{W}$ | FMNH 282201 ANSP 19187 FMNH 282211 |
| Crepidula fimbriata | Reeve (1859) | Friday Harbor, Washington, USA $48^{\circ} 20^{\prime} \mathrm{N}, 12301^{\prime} \mathrm{W}$ | FMNH 299426 |
| Crepidula lessoni Panama | Broderip (1834) | Chumical, Pacific Coast, Panama $8^{\circ} 30^{\prime} \mathrm{N}, 79^{\circ} 40^{\prime} \mathrm{W}$ | FMNH 282271 BM20010465 |
| Crepidula nummaria | Gould (1846) | Santa Cruz, California, USA $36^{\circ} 40^{\prime} \mathrm{N}, 122^{\circ} 02^{\prime} \mathrm{W}$ | FMNH 282245 |
| Crepidula cf. perforans |  | Santa Barbara, California, USA $34^{\circ} 20^{\prime} \mathrm{N}, 120^{\circ} 01^{\prime} \mathrm{W}$ | FMNH 282243 |
| Crepidula philippiana | Gallardo (1977) | Los Molinos, Chile. $39^{\circ} 51^{\prime}$ S, $73^{\circ} 27^{\prime}$ W | FMNH 282349 |
| Crepidula plana | Say (1822) | Woods Hole, Massachusetts, USA $41^{\circ} 30^{\prime} \mathrm{N}, 70^{\circ} 40^{\prime} \mathrm{W}$ | FMNH 282207, 282210, 282214, 282215 |
| Crepidula protea | d'Orbigny (1841) | Santos Bay, São Paulo, Brazil $23^{\circ} 20^{\prime}$ S, $46^{\circ} 25^{\prime}$ W | MZSP 32264 |
| Crepidula striolata | Menke (1851) | Rio Mar, Pacific Coast, Panama $08^{\circ} 18^{\prime} \mathrm{N}, 79^{\circ} 50^{\prime} \mathrm{W}$ | FMNH282331 |

Table 2. Continued

BM20010478


 FMNH 299431
FMNH 299368
FMNH282272
FMNH 282176
 $67 \& \& 66$ HNNH g98z88 HNWH ANSP A19741
 $07 \pm 667$ HNNH FMNH 282287
ANSP A19739
 FMNH 282337
FMNH 282316
L6L787-96LZ87 HNWH R. Collin and


Broderip (1834)
Conrad (1846)
Broderip (1834)
Williamson (1905)
Mörch (1877)
Sowerby (1824)


Dzilam de Bravo, Yucatan, Mexico $21^{\circ} 20^{\prime} \mathrm{N}, 88^{\circ} 55^{\prime} \mathrm{W}$
La Paz, Mexico
$24^{\circ} 17^{\prime} \mathrm{N}, 110^{\circ} 17^{\prime} \mathrm{W}$ $21^{\circ} 20^{\prime} \mathrm{N}, 88^{\circ} 55^{\prime} \mathrm{W}$
$\mathrm{La} \mathrm{Paz}$,Mexico
$24^{\circ} 17^{\prime} \mathrm{N}, 110^{\circ} 17^{\prime} \mathrm{W}$

Santa Maria, Peru $12^{\circ} 20^{\prime} \mathrm{S}, 76^{\circ} 45^{\prime} \mathrm{W}$ Venado, Panama
$8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$


Zorritos, Peru
$3^{\circ} 45^{\prime}$ S, $80^{\circ} 40^{\prime}$ W Panacea, Florida, USA
$30^{\circ} 00^{\prime} \mathrm{N}, 84^{\circ} 30^{\prime} \mathrm{W}$

Venado, Pacific Coast, Panama
$8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$
 $34^{\circ} 20^{\prime} \mathrm{N}, 120^{\circ} 01^{\prime} \mathrm{W}$

Morrocoy, Venezuela
Bocas del Toro, Panama
$9^{\circ} 20^{\prime} \mathrm{N}, 82^{\circ} 15^{\prime} \mathrm{W}$ Santa Barbara, $34^{\circ} 20^{\prime} \mathrm{N}, 120^{\circ} 01^{\prime} \mathrm{W}$

Venado, Pacific Coast, Panama
$8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$
Playa Orengo, San Antonio Oeste
Venado, Pacific Coast, Panama
$8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$
Playa Orengo, San Antonio Oeste
Argentina
$40^{\circ} 53^{\prime} \mathrm{S}, 64^{\circ} 29^{\prime} \mathrm{W}$
Calheta Funda, Sal Island, Cape
Verde $16^{\circ} 40^{\prime} \mathrm{N}, 22^{\circ} 03^{\prime} \mathrm{W}$

R. Collin and A. Indocochea
Gulf Specimen Co. R. Collin


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R. Collin and E. Rolán
R. Collin and T. Griffin

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Table 2. Continued

| Species | Author | Locality | Voucher numbers* | Collector(s) |
| :---: | :---: | :---: | :---: | :---: |
| Crucibulum radiata | Broderip (1834) | Venado, Pacific Coast, Panama $8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$ | FMNH 299399 | R. Collin |
| Crucibulum tenuis | Broderip (1834) | Venado, Pacific Coast, Panama $8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$ | FMNH 299436 | R. Collin |
| Calyptraea Lamarck (1799) Calyptraea aspersa | Adams (1852) | Islas de las Perlas, Panama $8^{\circ} 30^{\prime} \mathrm{N}, 79^{\prime} 02^{\prime} \mathrm{W}$ | FMNH 282342 | R. Collin |
| Calyptraea chinensis | Linneus (1758) | O'Grove Bay, Spain. | FMNH 299392 | E. Rolán |
| Calyptraea cf. conica |  | Venado, Pacific Coast, Panama $8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$ | FMNH 299437 | R. Collin |
| Calyptraea fastigata | Gould (1846) | Friday Harbor, Washington, USA $48^{\circ} 20^{\prime} \mathrm{N}, 12301^{\prime} \mathrm{W}$ | FMNH 282221 | R. Collin and B. Pernet |
| Calyptraea cf. lichen |  | Venado, Pacific Coast, Panama $8^{\circ} 55^{\prime} \mathrm{N}, 79^{\circ} 38^{\prime} \mathrm{W}$ | FMNH 282300 | R. Collin |
| Calyptraea mamillaris | Broderip (1834) | Punta Charmé, Pacific Coast, Panama $08^{\circ} 30^{\prime} \mathrm{N}, 79^{\circ} 40^{\prime} \mathrm{W}$ | FMNH 282363 | R. Collin |
| Trochita Schumacher (1817) <br> Trochita calyptraeformis South | Born (1778) | Bahía de Herradura, Region IV, Chile $29^{\circ} 58^{\prime} \mathrm{S}, 71^{\circ} 21^{\prime} \mathrm{W}$ | ANSP A19737 <br> BM20010476 | R. Collin |
| Trochita calyptraeformis North | Born (1778) | Santa Maria, Peru $12^{\circ} 20^{\prime} \mathrm{S}, 76^{\circ} 45^{\prime} \mathrm{W}$ | BM20010475 <br> FMNH 299424 | R. Collin and <br> A. Indocochea |
| Bicatillus Swainson (1840) <br> Bicatillus extinctorum | Lamarck (1822) | Changi Point Beach, East of Singapore $1^{\circ} 15^{\prime} \mathrm{N}, 103^{\circ} 39^{\prime} \mathrm{E}$ | FMNH 299402 | Tan Siong Kiat |

Omaha Bay, North Island, New
Zealand
$36^{\circ} 10^{\prime} \mathrm{S}, 174^{\circ} 30^{\prime} \mathrm{E}$

Koster, Sweden
$58^{\circ} 52^{\prime}$ N, $11^{\circ} 05^{\prime} \mathrm{E}$
FMNH 282220, 285018
UM-
T. Baumiller

W. Runball
G. Paulay
R. Collin and S. O'Shea
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 monoxyla, (E) Calyptraea chinensis, (F) Crucibulum cf. personatum. am = dorsal attachment muscle, $c g=$ capsule gland, $c p=$ connective tissue $p a d, c t=c t e n i d i u m, d g=$ digestive gland, $f=f o o t, g d=g o n a d$, $\mathrm{hg}=$ hypobranchical gland, $\mathrm{i}=$ intestine, $\mathrm{lm}=$ left shell muscle, os = osphradium, $\mathrm{pc}=$ pericardium, $\mathrm{rm}=$ right shell muscle, $\mathrm{sr}=$ seminal receptical, $\mathrm{ss}=$ style sac, $\mathrm{st}=$ 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, fgp $=$ female genital papilla, $\mathrm{gd}=$ gonad, $\mathrm{hg}=$ hypobranchial gland, $\mathrm{i}=$ intestine, $\mathrm{k}=$ kidney, $\mathrm{nr}=$ nerve ring, $\mathrm{pc}=$ pericardium, $\mathrm{sg}=$ salivary gland, $\mathrm{sr}=$ seminal receptical, $\mathrm{ss}=$ style sac, $\mathrm{st}=$ 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, $\mathrm{dg}=$ digestive gland, $\mathrm{i}=$ intestine, $\mathrm{m}=$ shell muscle, $\mathrm{nr}=$ nerve ring, $\mathrm{os}=$ osphradium, $\mathrm{pc}=$ pericardium, $\mathrm{sg}=$ salivary gland, $\mathrm{st}=$ 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, 16 S and nuclear 28 S 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) branchswapping, 1000 random additions, saving two trees at each step, and maxtrees set to 10000 . 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 ILDtest 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. $\mathrm{fp}=\mathrm{food}$ pouch, $\mathrm{g}=$ gill, $\mathrm{mm}=$ 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, $\mathrm{mm}=$ mantle margin, $\mathrm{cg}=$ capsule gland, $\mathrm{ag}=$ albumin gland and $\mathrm{sr}=$ seminal recepticals.

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

|  | No. <br> characters | No. <br> informative <br> characters | No. <br> taxa | MP tree <br> length | No. MP <br> trees | No. <br> islands | No. times <br> hit/ $/ 1000$ | CI** $^{*}$ | RI** $^{*}$ | RCI** |
| :--- | ---: | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Morphology | 120 | 114 | 77 | 909 | 3432 | 15 | $21 / 220$ | 0.227 | 0.644 | 0.146 |
| Shells | 40 | 39 | 77 | 258 | $>100000$ | - | - | 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 | 1782 | 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 28 S , 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 mostparsimonious 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 16 S 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 28 S 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

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

[^2]

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 $>70 \%$ boostrap in the 'best estimate tree'. $\dagger$ 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'. $\dagger$ 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 16 S DNA sequence data. Bootstrap support of $>70 \%$ are above the branches. *Branches supported with $>70 \%$ bootstrap in the 'best estimate tree'. $\dagger$ 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'. $\dagger$ 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 28 S DNA sequence data. Bootstrap support of $>70 \%$ are above the branches. *Branches supported with $>70 \%$ bootstrap in the 'best estimate tree'. $\dagger$ 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 28 S 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'. $\dagger$ 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 16 S , 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 Crepipatella (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 Calyptraeamorphs 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 CrucibulumCalyptraea 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 28 S 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

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



Figure 18. A single most parsimonious tree from the analysis of all the DNA data. Bootstrap support of $>70 \%$ are above the branches. *Branches supported with $>70 \%$ boostrap in the 'best estimate tree'. $\dagger$ Branches conflicting with $>70 \%$ bootstrap supported branches in the 'best estimate tree'. Species without genus names are Crepidula species.


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'. $\dagger$ 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'. $\dagger$ 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'. $\dagger$ 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'. $\dagger$ 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'. $\dagger$ 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'. $\dagger$ 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

|  | No. nodes with <br> $>70 \%$ bootstrap <br> support | No. correct nodes <br> with $>70 \%$ <br> bootstrap support | No. incorrect nodes <br> with $>70 \%$ <br> bootstrap support |
| :--- | :--- | :--- | :--- |
| Character Groups |  |  |  |

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, 28 S 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 wellresolved 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, Calyptraea, 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 Calyptraea 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 Calyptraea 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-Pacfic. 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-Pacfic. 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.

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## 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. Crubibulum spp.)
$1=$ present (e.g. C. norisarum, C. costata)
2 = horseshoe-shaped (e.g. Hipponix spp.).
S2. Left muscle/scar

$$
0=\text { absent (e.g. C. fornicata, Crucibulum spp.) }
$$

$1=$ 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).

[^3]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. monoxyla

> 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. Crepipatella 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
$0=\operatorname{solid}$ (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 ethanolpreserved 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. norrisiarum (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

$$
0=\text { open }
$$

$1=$ 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 threadlike 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 pseudopropodium. 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 Crepipatella 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 pseudopropodium (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 suspensionfeeding 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 Calyptraea 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

$$
0=\text { short (e.g. Fig. 4) }
$$

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. calyptreaids)
$1=$ 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. calyptreaids)
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
$\left.\begin{array}{llllll}\hline & \begin{array}{l}\text { Number } \\ \text { of states }\end{array} & \begin{array}{l}\text { Expected } \\ \text { quality }\end{array} & \begin{array}{l}\text { Length on } \\ \text { the best tree }\end{array} & \text { CI on the best tree }\end{array}\right]$ RI on the best tree

Appendix 2 Continued
$\left.\begin{array}{llllll}\hline & & \\ \text { Number } \\ \text { of states }\end{array} \quad \begin{array}{lllll}\text { Expected } \\ \text { quality }\end{array} \quad \begin{array}{c}\text { Length on } \\ \text { the best tree }\end{array}\right]$

Appendix 2 Continued
$\left.\begin{array}{llllll}\hline & \begin{array}{l}\text { Number } \\ \text { of states }\end{array} & \begin{array}{l}\text { Expected } \\ \text { quality }\end{array} & \begin{array}{l}\text { Length on } \\ \text { the best tree }\end{array} & \text { CI on the best tree }\end{array}\right]$ RI on the best tree

## APPENDIX 3

Data matrix

|  | s1 | s2 | s3 | s4 | s5 | s6 | s7 | s8 | s9 | s10 | s11 | s12 | s13 | s14 | s15 | s16 | s17 | s18 | s19 | s20 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| depressa | 0 | 0 | 1 | ? | 0/1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| cf. onyx | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0/1 | 1 | 1 |
| ustulatulina | 0 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| nummaria | 0 | 0 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| philippiana | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| cerithicola | 1 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| aff. onyx | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| protea | 0 | 0 | 1 | ? | 0/1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| cf. aplysioides | 0 | 0 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0/2 | 0 | 1 | 0 |
| arenata | 0 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| immersa | 0 | 1 | 1 | ? | 0/1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| cf. perforans | 0 | 0 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| convexa | 0 | 1 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| onyx | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| aff. williamsi Washington | 0 | 0 | 1 | ? | 0/1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| walshi | 0 | 0 | 1 | ? | 1 | 1 | 1 | 1 | 0 | 3 | 8 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| incurva | 1 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0/1 | 1 | 1 |
| naticarum | 1 | 1 | 1 | ? | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0/1 | 1 | 1 |
| atrasolea | 0 | 0 | 1 | ? | 0/1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| williamsi | 0 | 0 | 1 | ? | 0/1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| complanata | 0 | 0 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0/1 |
| argentina | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| marginalis | 0 | 0 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 0/1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| excavata | 0 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| striolata | 0 | 0 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| fornicata | 0 | 0 | 1 | ? | 1 | 0/1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| fimbriata | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| cf. convexa | 0 | 0 | 1 | ? | 0/1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| grandis | 0 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1/2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| aff. williamsi Alaska | 0 | 0 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| monoxyla | 1 | 1 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| plana | 0 | 0 | 1 | ? | 0 | 0/1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| navicula | 0 | 0 | 1 | ? | 0/1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| lessoni | 0 | 0 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| incurva Panama | 0 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0/1 |
| incurva Peru | 0 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| porcellana | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| Crep. n. sp. pt. | 0 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| coquimbensis | 0 | 0 | 1 | ? | 0/1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| adunca | 1 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| maculosa | 0 | 1 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0/1 | 0/1 | 1 | 1 |
| T. calyptraeformis North | 0 | 1 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 0 | 0/1 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 |
| T. calyptraeformis South | 0 | 1 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| cf. aculeata Australia | 0 | 1 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| cf. aculeata Brazil | 0 | 1 | 1 | ? | 0/1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| cf. aculeata Panama | 0 | 1 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0/1 | 0 | 0 |
| gravispinosa | 0 | 1 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| cf. aculeata Mexico | 0 | 1 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| cf. aculeata South Africa | 0 | 1 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 0/1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| cf. aculeata Argentina | 0 | 1 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| aculeata Florida | 0 | 1 | 1 | ? | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| fecunda | 0 | 1 | 1 | ? | 2 | 0 | 0 | 1 | 0 | 3 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 |
| dilatata | 0 | 1 | 1 | ? | 2 | 0 | 0 | 1 | 0 | 3 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 |
| capensis | 0 | 1 | 1 | ? | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| dorsata | 0 | 0 | 1 | ? | 2 | 1 | 0 | 1 | 0 | 3 | 0 | 0 | 1 | 1 | 0 | 0 | 0/2 | 1 | 0 | 1 |
| Cruc. tenuis | 0 | 0 | 1 | ? | 2 | 1 | 1 | 2 | 0 | 7 | 7 | 0 | 7 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| Cruc. scutellatum | 0 | 0 | 1 | ? | 2 | 1 | 1 | 2 | 0 | 7 | 7 | 0 | 7 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| Cruc. spinosum Peru | 0 | 0 | 1 | ? | 2 | 1 | 1 | 2 | 0 | 7 | 7 | 1 | 7 | 1 | 1 | 0 | 2 | 1 | 0 | 1 |
| Cruc. spinosum Panama | 0 | 0 | 1 | ? | 2 | 1 | 1 | 2 | 0 | 7 | 7 | 0 | 7 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| Cruc. radiata | 0 | 0 | 1 | ? | 2 | 1 | 1 | 2 | 0 | 7 | 7 | 0 | 7 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| Cal. aspersa | 0 | 0 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 1 |
| B. extinctorum | 0 | 1 | 1 | ? | 2 | 0 | 1 | 0 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| Z. tenuis | 0 | 1 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| Cal. cf. conica | 0 | 1 | 1 | ? | 0 | 0 | 0 | 3 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| Cal. chinensis | 0 | 1 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| Cal. fastigata | 0 | 1 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| Cal. mamallaris | 0 | 1 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| Cal. cf. lichen | 0 | 1 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| S. novaezelandiae | 0 | 1 | 1 | ? | 1 | 0 | 0 | 3 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| T. cancellata | 0 | 3 | 0 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 0 | 0 | 1 | 0 | 1 | 8 | 8 |
| Cap. ungaricus | 2 | 2 | 0 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 1 | 0 | 0 | 1 | 1 | 1 | 8 |
| Vanikoro sp. | 0 | 3 | 0 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 0 | 0 | 1 | 1 | 1 | 8 | 8 |
| Cheilea equestris | 0 | 0 | 1 | ? | 3 | 0 | 0 | 0 | 0 | 7 | 7 | 0 | 7 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| Hipponix Australia | 2 | 2 | 0 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 1 | 1 | 0 | 0 | 1 | 1 | 8 |
| Sabia conica Australia | 2 | 2 | 0 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 1 | 1 | 0 | 0 | 1 | 1 | 8 |
| Leptonetis perplexus | 2 | 2 | 0 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 1 | 0 | 0 | 2 | 1 | 0 | 8 |
| Hipponix South Africa | 2 | 2 | 0 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 1 | 1 | 0 | 0 | 1 | 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 | 1 | 2 | 0 | 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 | 0 | 1 | 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 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| depressa | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| cf. onyx | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| ustulatulina | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 4 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| nummaria | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| philippiana | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| cerithicola | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| aff. onyx | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| protea | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| cf. aplysioides | 1 | 1 | 0 | 0 | 0 | 0 | 2 | ? | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| arenata | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 |
| immersa | 1 | 1 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 0 |
| cf. perforans | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 2 | 2 | 0 |
| convexa | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 4 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| onyx | 1 | 1 | 0 | 0 | 0 | 0 | 0 | ? | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| aff. williamsi Washington | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| walshi | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 |
| incurva | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 |
| naticarum | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| atrasolea | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 4 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| williamsi | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| complanata | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| argentina | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| marginalis | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| excavata | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| striolata | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| fornicata | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| fimbriata | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| cf. convexa | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 4 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| grandis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 2 | 0 |
| aff. williamsi Alaska | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| monoxyla | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 |
| plana | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| navicula | 1 | 1 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| lessoni | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| incurva Panama | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 |
| incurva Peru | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| porcellana | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| Crep. n. sp. pt. | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| coquimbensis | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| adunca | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 |
| maculosa | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 |
| T. calyptraeformis North | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 |
| T. calyptraeformis South | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 |
| cf. aculeata Australia | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| cf. aculeata Brazil | 0/1 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| cf. aculeata Panama | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| gravispinosa | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| cf. aculeata Mexico | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| cf. aculeata South Africa | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| cf. aculeata Argentina | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| aculeata Florida | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| fecunda | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 |
| dilatata | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 |
| capensis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1/2 | 2 | 0 |
| dorsata | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 5 | 1 | 1 | 0 | 2 | 1 | 2 | 2 | 0 |
| Cruc. tenuis | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 2 | 0 |
| Cruc. scutellatum | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 2 | 0 |
| Cruc. spinosum Peru | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 2 | 2 | 1 | 2 | 2 | 0 |
| Cruc. spinosum Panama | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 0 |
| Cruc. radiata | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 0 |
| Cal. aspersa | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 3 | 1 | 2 | 2 | 0 |
| B. extinctorum | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 0 |
| Z. tenuis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 2 | 0 |
| Cal. cf. conica | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 0 |
| Cal. chinensis | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 0 |
| Cal. fastigata | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 0 |
| Cal. mamallaris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | ? | 2 | 2 | 0 |
| Cal. cf. lichen | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 0 |
| S. novaezelandiae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 0 |
| T. cancellata | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 3 | 0 |
| Cap. ungaricus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 3 | 3 | 0 |
| Vanikoro sp. | 1 | 0 | 1 | 2 | 0 | 0 | 0 | ? | ? | ? | 1 | 0 | 3 | 3 | 0 | 3 | 3 | 0 | 0 | 0 | 2 |
| Cheilea equestris | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 3 | 1 | 3 | 0 | 0 | 0 | 0 | 2 |
| Hipponix Australia | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 2 |
| Sabia conica Australia | 0 | 0 | 1 | 1 | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 3 | 3 | 1 | 3 | 0 | 0 | 0 | 0 | 2 |
| Leptonetis perplexus | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 3 | 1 | 3 | 0 | 0 | 0 | 0 | 2 |
| Hipponix 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 | 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 | 1 | 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 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 1 | 0 | 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 | 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 | 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 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | ? | 1 | 0 | 2 | 0 | 0 | 0 |
| 0 | 1 | 5 | 1 | 0 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 |
| 0 | 0 | 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 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| depressa | 1 | 1 | 1 | 0 | 0 | 0/1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| cf. onyx | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| ustulatulina | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| nummaria | 1 | 1 | 1 | 0 | 0 | 4 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| philippiana | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| cerithicola | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| aff. onyx | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| protea | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| cf. aplysioides | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| arenata | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| immersa | 1 | 1 | 1 | 0 | 0 | 0 | 0/2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 |
| cf. perforans | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| convexa | 1 | 1 | 1 | 0 | 0 | 1/4 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| onyx | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| aff. williamsi Washington | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| walshi | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| incurva | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| naticarum | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| atrasolea | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| williamsi | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| complanata | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| argentina | 1 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| marginalis | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| excavata | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| striolata | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 |
| fornicata | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0/1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| fimbriata | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| cf. convexa | 1 | 1 | 1 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| grandis | 1 | 1 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| aff. williamsi Alaska | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| monoxyla | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| plana | 1 | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| navicula | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| lessoni | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0/1 | 0 | 0 | 0 |
| incurva Panama | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 |
| incurva Peru | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 |
| porcellana | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| Crep. n. sp. pt. | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| coquimbensis | 1 | 1 | 0 | 0 | 0 | 0/1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| adunca | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| maculosa | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| T. calyptraeformis North | 1 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 |
| T. calyptraeformis South | 1 | 1 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 |
| cf. aculeata Australia | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 |
| cf. aculeata Brazil | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 0 | 0 |
| cf. aculeata Panama | 1 | 1 | 1 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 0 | 0 |
| gravispinosa | 1 | 1 | 1 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 |
| cf. aculeata Mexico | 1 | 1 | 1 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 0 | 0 |
| cf. aculeata South Africa | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| cf. aculeata Argentina | 1 | 1 | 0 | 0 | 0 | 2/4 | 1 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 0 |
| aculeata Florida | 1 | 1 | 1 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 0 | 0 |
| fecunda | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 |
| dilatata | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 |
| capensis | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 0 | 0 |
| dorsata | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| Cruc. tenuis | 1 | 1 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| Cruc. scutellatum | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| Cruc. spinosum Peru | 1 | 1 | 0 | 0 | 1 | 4 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 |
| Cruc. spinosum Panama | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| Cruc. radiata | 1 | 1 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| Cal. aspersa | 1 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 |
| B. extinctorum | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| Z. tenuis | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 |
| Cal. cf. conica | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| Cal. chinensis | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 0 | 2 | 0 | 0 | 0 |
| Cal. fastigata | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 |
| Cal. mamallaris | 1 | 1 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| Cal. cf. lichen | 1 | 1 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 |
| S. novaezelandiae | 1 | 1 | 0 | 0 | 1 | 0 | 0/2 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 0 | 0 |
| T. cancellata | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 0 |
| Cap. ungaricus | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 0 |
| Vanikoro sp. | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 2/4 | 3 | 1 | 0 | 1 | 1 | 1 |
| Cheilea equestris | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 1 | 0 | 1 | 2 | 2 | 2 | 0 | 1 | 1 | 1 |
| Hipponix Australia | 0 | 0 | 0 | 0 | 2 | 0 | 2/3 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 |
| Sabia conica Australia | 0 | 0 | 1 | 0 | 2 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 1 |
| Leptonetis perplexus | 0 | 0 | 1 | 0 | 2 | 0 | 3 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 3 | 3 | 0 | 0 |
| Hipponix 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 | 0 | 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 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 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 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 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 | 1 | 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 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 0 |
| 0 | 1 | 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 | 1 | 1 | 0 | 0 | 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 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 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 | 0 | 2 | 2 | 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 | 0 | 2 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 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 | 1 | 2 | 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 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 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 |


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[^1]:    *Definitive characters, if any, are highlighted in bold text.

[^2]:    *Excluding uninformative characters.

[^3]:    S3. Septum
    $0=$ absent (e.g. Hipponix, capulids, trichotropids)
    $1=$ present (e.g. calyptraeids, Cheilea)

