

FIRST RECORD OF A CHITON FROM THE PALAEOCENE OF DENMARK (POLYPLACOPHORA: LEPTOCHITONIDAE) AND ITS PHYLOGENETIC AFFINITIES

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SYNOPSIS A new species of fossil polyplacophoran from the Danian (Lower Palaeocene) of Denmark is described from over 450 individual disarticulated plates. The polyplacophorans originate from the ‘nose-chalk’ in the classical Danish locality of Fakse Quarry, an unconsolidated coral limestone in which aragonitic mollusc shells are preserved through transformation into calcite. In plate architecture and sculpture, the new Danish material is similar to Recent *Leptochiton* spp., but differs in its underdeveloped apophyses and high dorsal elevation (height/width *ca.* 0.54). Cladistic analysis of 55 original shell characters coded for more than 100 Recent and fossil species in the order Lepidopleurida shows very high resolution of interspecific relationships, but does not consistently recover traditional genera or subgenera. Inter-relationships within the suborder Lepidopleurina are of particular interest as it is often considered the most ‘basal’ neoloricate lineage. In a local context, the presence of chitons in the faunal assemblage of Fakse contributes evidence of shallow depositional depth for at least some elements of this Palaeocene seabed, a well-studied formation of azooxanthellic coral limestones. This new record for Denmark represents a well-dated and ecologically well-understood fossil chiton with potential value for understanding the radiation of the Neoloricata.

KEY WORDS Neoloricata, Mollusc, systematics, phylogeny, Danian, Fakse

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INTRODUCTION

Polyplacophora (chitons) are known from all ages from Upper Cambrian to Recent (Smith 1960), but most fossils have

been recorded from the Cenozoic. Until now, no fossil Polyplacophora have been recorded from Denmark. Malacofaunal assemblages from the Late Oligocene and Miocene of Denmark have been thoroughly studied (Rasmussen 1956,

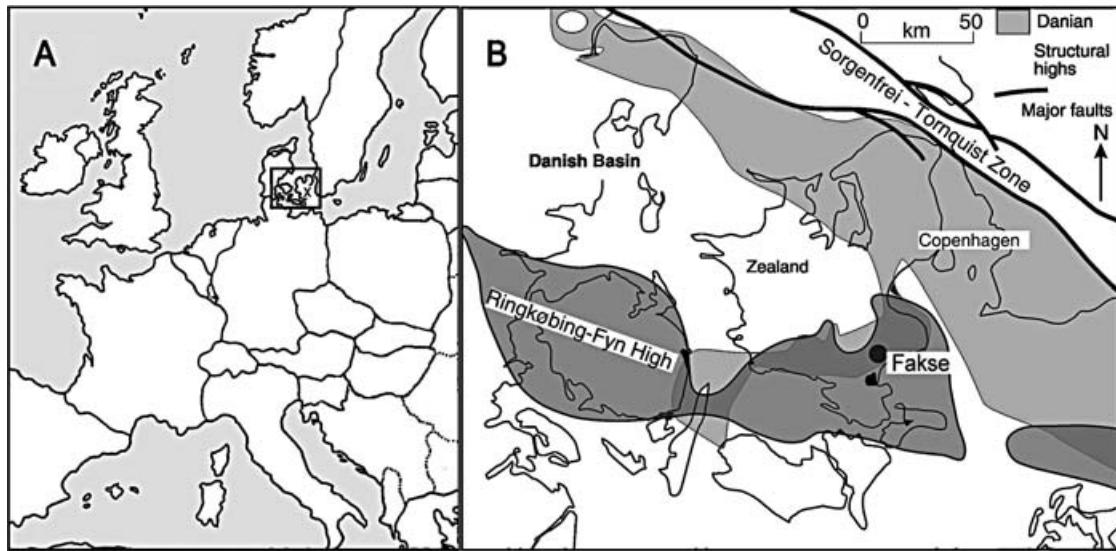


Figure 1 Palaeocene sediments in Zealand, Denmark. (A) outline map to show the location of the Fakse Quarry (X); (B) structural outline of the Danish Palaeocene basin to show outcrop of Danian sediments in the area of Fakse quarry.

1966, 1968; Sorgenfrei 1958; Schnetler & Beyer 1987, 1990), but come from sublittoral, soft-bottom habitats, where conditions may not be typically conducive to the preservation of Polyplacophora.

In this paper we describe the polyplacophoran remains found since 1972 in Fakse. We name a new species in the extant genus *Leptochiton* and present a novel hypothesis for its phylogenetic placement.

The Fakse quarry, located close to the city of Copenhagen (Fig. 1), is a classical Danish Cenozoic locality that has preserved a rich and highly diverse fauna of many marine invertebrate groups. The quarry, east of the small town of Fakse in Eastern Zealand, has been excavated continuously for several hundred years. The fauna has been listed extensively (Gravesen 2001, and references therein). Fakse has a rich molluscan fauna, although many taxa remain undescribed, and, as a rule, aragonitic shells are preserved as internal moulds and external imprints. However, one sequence of unconsolidated chalk has yielded rich material of molluscs with aragonitic shells preserved as calcite, including the present polyplacophoran material comprising more than 450 valve elements. This type of corallian limestone is informally named 'nose-chalk' (*næsekalk*) after a projecting part in the quarry called the nose (Ravn 1933: *le 'Nez'*). This place in the quarry was originally found *ca.* 1915 and was mentioned by Nielsen (1919), but has disappeared due to continued excavation. The 'nose-chalk' has been encountered twice since then (field trips in 1972 by S.B.A. and Sten Lennart Jakobsen and in the 1990s by Alice Rasmussen).

Fakse is situated in the Danish–Polish Trough, which is bounded to the north by the Fennoscandian Shield and to the south by the Ringkøbing–Fyn High (Fig. 1). Within the quarry, a section through a bryozoan–coral mound complex is exposed. A vast number of interbedded diagenetic microfacies may be recognised in the complex: bryozoan limestone, chalky limestone and coral limestone (for a review, see Surlyk & Håkansson 1999). Desor (1847) introduced the Danian Stage with the type localities Fakse Quarry and

Stevns Klint and considered the stage as the youngest part of the Cretaceous System. For many years the stratigraphic position of the Danian was discussed (Nielsen 1919; Ravn 1925; Rosenkrantz 1938), but the Danian is now generally considered to be the oldest part of the Palaeocene. Various subdivisions of the Danian have been suggested and the sequence at Fakse has been referred to the local *Tylocidaris bruennichi* echinoid Zone (Ødum 1926; Rosenkrantz 1938) of Middle Danian age and to nannoplankton zone NP3 (Perch-Nielsen 1979).

ABBREVIATIONS AND TERMINOLOGY

MGUH, Geological Museum, University of Copenhagen, Denmark; **BDA**, personal collections of B. Dell'Angelo; **BMNH PI**, The Natural History Museum, London (Palaeontology Department collections), UK; **NMING**, National Museum of Ireland Natural History Division, Dublin (Geological collections), Ireland; **MZB**, Zoological Museum of Bologna University, Bologna, Italy; **ZSM**, Bavarian State Collection of Zoology, Munich, Germany.

Measurements and terminology follow those used by Kaas & Van Belle (1985). The specimens from Fakse are neoloricate chitons, but like other members of the suborder Lepidopleurina, they lack insertion plates (lateral extensions of the articulamentum that anchor the shell in the girdle tissue). However, as in all neoloricates there is a distinctive separation between the outer dorsal tegmentum and interior ventral articulamentum. The anterior (head) and posterior-most (tail) plates are distinctive in their semicircular shape and distinguished from each other by the anterior extensions of articulamentum (apophyses) in the tail plate, as on all intermediate plates. The posterior valves also have a prominent raised dorsal apex (mucro), which is reflected in a ventral mucronal cavity. Terminology pertaining to plate anatomy and the position of measurements are summarised in Fig. 2.

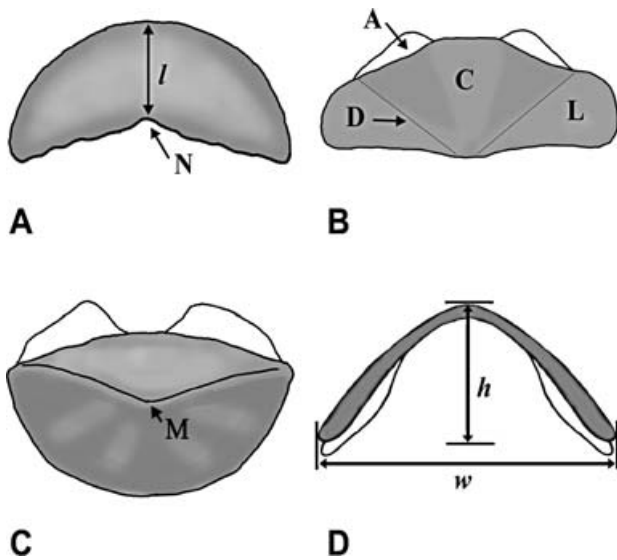


Figure 2 Line drawings of typical valve elements of *Leptochiton faksensis* sp. nov. The arrows indicate measurements (l , longitudinal distance; w , lateral distance; h , height; h/w , dorsal elevation) and typical morphological features (N, apical notch; A, apophyses; D, diagonal on lateral plates; C, central area; L, lateral area; M, mucro on posterior plate). (A) anterior (head) valve; (B) intermediate valve; (C) posterior (tail) valve; (D) intermediate valve, view of anterior face.

SYSTEMATIC PALAEOONTOLOGY

Class **POLYPLACOPHORA** Gray, 1821

Subclass **NEOLORICATA** Bergenhayn, 1955

Order **LEPIDOPLEURIDA** Thiele, 1910

Suborder **LEPIDOPLEURINA** Thiele, 1910

Family **LEPTOCHITONIDAE** Dall, 1889

Genus **LEPTOCHITON** Gray, 1847

Leptochiton faksensis sp. nov. (Fig. 3)

MATERIAL. 458 isolated plates from the private collections of A. Rasmussen (coll. ca. 1995), K.I. Schnetler (coll. 1972) by S.B.A. and S.L. Jakobsen), S.B. Andersen (coll. 1972), K. Gürs (coll. ca. 1990) and B. Dell'Angelo (BDA 4664). All material was collected from the quarry at Fakse and later rinsed and sorted by the collectors. In the present study, measurements were recorded (0.01 mm) for the dimensions of each plate, for all material that was visually judged to be at least 50% intact.

HOLOTYPE. MGUH 27820a-f (donated by A. Rasmussen); Paratypes (each paratype lot is represented by a set of three disarticulated plates, comprising a head, tail and single intermediate valve): ZSM Moll 20041262 (donated by K. Gürs); NMING F21753, F21754, F21755 (donated by K.I.S.); BMNH PITG 24812-24814 (donated by K.I.S.); MZB 43642 (6 valves, donated by B. Dell'Angelo).

LOCALITY AND STRATUM. Fakse Quarry. Coral Limestone, Middle Danian, Palaeocene.

DIAGNOSIS. Comparative morphological features that diagnose this taxon are as follows: distinctly highly elevated intermediate and anterior plates; tegmentum of all valves evenly covered with neatly separated, diagonally arranged granules in a 'close-packed' formation; intermediate plates relatively narrow (longitudinally) with lateral sides rounded; apophyses small and orientated posteriorly (not angled outward); valves thin, margins thickened only in posterior edge of posterior plate; insertion plates entirely absent. The following characters optimised by phylogenetic analysis (see below) also diagnose *L. faksensis*: ratio of combined diameter of apophyses/valve width ≤ 1.4 ; dorsal elevation (height/width) of intermediate plates > 0.4 ; head valve shape $<$ semicircular; post-mucronal slope straight; jugal sinus excavation convex; central areas of intermediate valves irregular quincunx; central area of intermediate valves—granule shape, roundish; lateral areas of intermediate valves neatly separated.

DERIVATION OF NAME. From the only known locality, the quarry in Fakse, Denmark, and the Latin *ensis* or 'out of'.

DESCRIPTION. This study incorporates measurements of all known polyplacophoran material ever recovered from the type locality. All specimens are individual, disarticulated plates ($n = 458$). The animal is small, with the average width of intermediate valves being 2.45 mm. These valves are distinctly highly elevated (average dorsal elevation = 0.51 in intact material), evenly rounded, subcarinate and not beaked, with side slopes evenly convex. Granule size typically ranges between 0.065 mm and 0.071 mm, but some individuals (irrespective of valve size) have granules in the range of 0.046–0.049 mm. An articulamentum is present, but apparently thin, without any distinctive muscle scars regularly preserved. A substantial majority of the examined material (68%) are tail valves.

Insertion plates are uniformly absent in all valves. The apophyses are small, short, broadly triangular (not rounded) and narrowly separated. The jugal sinus is broad and shallowly concave. The thin plates of these specimens are extremely fragile and often break with minimal manipulation. The relative preservation of different valve types have important taphonomic implications. These may be indicative of the range of variation between plates on an individual animal (as is seen in living species), but it is currently not possible to determine.

Head valves ($n = 84$; Figs 3A & B) are less than semicircular, but highly elevated, often almost conical and slightly thickened anteriorly. The intact material shows a slight, rounded apical notch and a generally rounded posterior margin. The dorsal surface is evenly granulated; small round granules are arranged closely in irregular quincunx. Dimensions range from 2.11–2.98 mm in lateral diameter and from 1.11–1.78 mm longitudinally (Fig. 4). Recovered material includes 52% of specimens intact and in pristine condition. In some head valve specimens, the granules are well-raised, dentating the posterior margin; the articulamentum is well-developed with a coarse surface texture.

Intermediate valves ($n = 147$; Figs 3C & D) slope (away from the apophyses) to a V-shaped, convex posterior margin. The anterior margin is straight to convex (curved) between apophyses, angled posteriorly down on lateral areas; side margins are slightly convex. Many plates are present as large fragments, fractured along the longitudinal axis of the

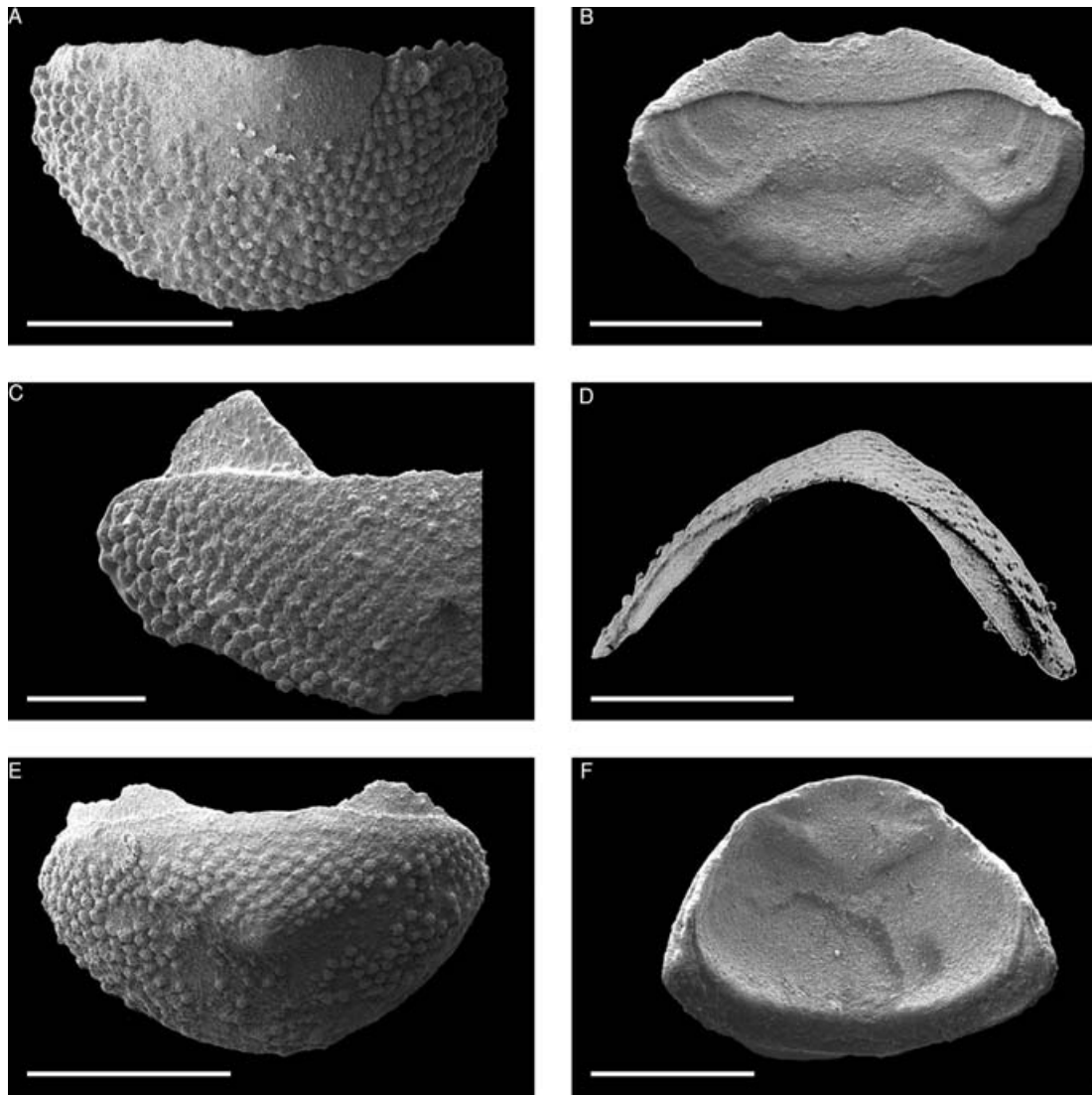


Figure 3 Holotype material of *Leptochiton faksensis* sp. nov. (A) anterior (head) valve, dorsal surface (MGUH 27820a); (B) anterior (head) valve, ventral surface (MGUH 27820b); (C) intermediate valve, right side, dorsal surface (MGUH 27820c); (D) intermediate valve, lateral views of anterior side (MGUH 27820d); (E) posterior (tail) valve, dorsal surface (MGUH 27820e); (F) posterior (tail) valve, ventral surface (MGUH 27820f). Scale bars = 1.0 mm.

valve. Of the specimens sufficiently intact to be measured, dimensions ranged from 1.85–3.09 mm in lateral diameter and by 0.83–1.68 mm longitudinally; dorsal elevation varies between 0.37–0.81 (Fig. 4). The majority of material is fragmentary, with only 24% being wholly intact. In intact material, approximately 60% of intermediate plates are semi-carinated and also with lateral areas very slightly inflated.

The dorsal surface of intermediate valves is sculpted like the anterior valve, with small, round granules arranged quincunxically. Granules are much closer together and smaller in the jugal area, graded outward to the pleural areas. This gradation continues onto lateral areas where granules are larger, well-raised and with interstices as wide as the granules. The pattern of sculpture blends contiguously onto lateral areas; however, granules are often absent (eroded) or sparsely arranged. Lateral areas are not elevated and not otherwise distinguished except by difference in sculpture.

Tail valves ($n = 227$; Figs 3E & F) are oval and narrower than the head valves. A prominent mucro is placed anterior

to the median. The postmucronal slope is concave immediately below the mucro, but straight in the posterior end. The dorsal surface is evenly granulated overall (as in the intermediate and head valves); the antimucronal area usually has slightly larger granules and slightly wider interstices than the postmucronal area (but they are never as widely separated or well raised as in lateral areas of intermediate plates). Of the specimens found, dimensions ranged from 1.65–2.70 mm in lateral diameter and by 0.98–2.18 mm longitudinally (Fig. 4). The largest proportion of posterior plates are complete, with 74% of posterior valves being in excellent condition.

Posterior valve tegmentum is finely granulated. Granules are small, round and arranged in quincunx. Apophyses in the tail valve are relatively widely separated. The articulation is thicker on posterior plates than others; a distinct chevron-shaped thickened ridge is always present anterior to the mucro on the ventral surface, reaching from the mucro to the exterior edge of apophyses (outlining the antimucronal tegmentum).

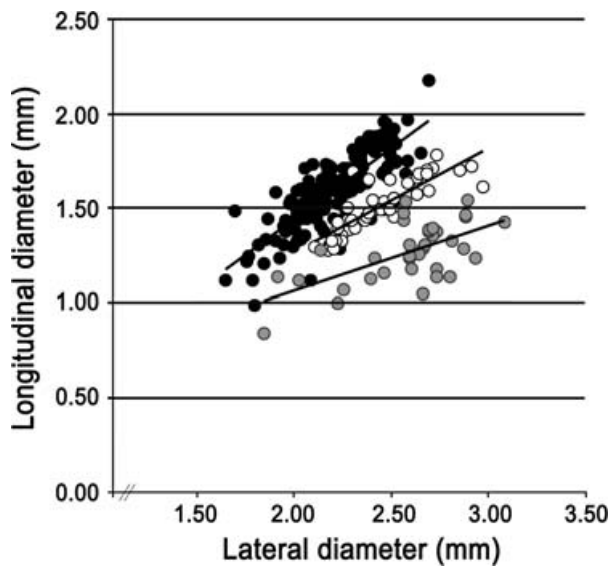


Figure 4 Longitudinal (anterior–posterior) versus lateral diameter of individual valves in completely intact material: tail plates (black; $n = 168$), head plates (white; $n = 44$) and intermediate plates (grey; $n = 36$). Linear regression lines indicate growth trends for the length/width ratio within valve types.

PHYLOGENETIC ANALYSIS AND DISCUSSION

Fifty-five original characteristics of the shell (Table 1) were coded into a matrix across an ingroup comprising 110 species of Lepidopleurina (see Appendix), as well as the present fossil material. Morphological features (characters) were considered variable between, but not within, individual species-level taxa; characters were coded on the basis of specimen material from the National Museum of Ireland (Natural History) and primarily from the revised species-level descriptions presented by Kaas & Van Belle (1985, 1990, 1995) and the revised taxonomy of Sirenko (1997). Multistate features were defined either on the basis of individual taxonomic variation or by the use of published taxonomic descriptions (i.e. variable features used by earlier workers to diagnose higher taxonomic categories).

Outgroups were selected from within the other extinct and extant families of Lepidopleurina, including 17 additional fossil taxa (i.e. Ferreiraelleidae, Protochitonidae, Hanleyidae and Nierstraszellidae). These were chosen to cover the breadth of diversity in Lepidopleurina (see Appendix) including species that are common and well described in literature. Based on a combination of codings from the ingroup taxa, an additional hypothetical ancestor taxon was coded and used as an eighteenth outgroup taxon.

The complete data set was analysed in two basic ways, either with all characters unordered (i.e. no direction of change inferred for multistate features; our preferred option), or using a simple ordering scheme for 5 characters for which a direction of change could be reasonably inferred (see Table 1). Data were subject to parsimony analysis using the heuristic search algorithm implemented in the standard software package PAUP* version 4.0b10 (Swofford 2002). However, because this data set comprises a relatively small

number of characters (55) compared to taxa (110), and is thus sensitive to incongruence, 1000 TBR branch swapping replicates were used to initially estimate the lengths of the shortest trees, before further searches were undertaken with random addition sequence replicates under a heuristic search strategy. Lastly, we employed the Parsimony Ratchet method described by Nixon (1999) implemented in PAUP* via the PAUPRat tool (Sikes & Lewis 2001) running 500 iterations and perturbing 25% of informative characters (Nixon 1999). This presents an efficient approach to search for the shortest trees in cases of data sets that are either too large or too incongruent for traditional heuristic methods. In all cases, all outgroups, including the hypothetical ancestor, were used.

Initial heuristic ordered and unordered searches with PAUP* generated large numbers of most-parsimonious-trees (MPTs), all greater than 1000 steps in length. While differing with regard to the relative placement of ingroup taxa, with respect to the root, examination of these trees and their consensus profiles allowed us to determine that character ordering had no effect on relationships. Parsimony Ratchet searches of the unordered data set recovered MPTs as short as 919 steps in length—strict consensus representation of these trees is shown in Fig. 5. Repeated iterations and random matrix sub-sampling using PAUPRat altering the numbers of iterations and the number of perturbed informative characters confirms that we were able to identify the shortest-tree islands from this matrix. Support for recovered clades was assessed by counting synapomorphic characters and by the use of bootstrap support statistics, generated from 1000 replicates in PAUP* (Fig. 5).

In all MPTs recovered by basic PAUP* heuristic searches the Danish fossil chiton, *L. faksensis*, is resolved deep within the topology, part of a clade that also comprises four other Recent taxa (Fig. 5). This clade includes three species from the genus *Leptochiton* (*fulginatus*, *hirasei* and *medinae*) and *Parachiton africanus* and is well-supported, present in all of the MPTs (as well as in trees up to five steps longer), on the basis of the following derived states (consistency index (C1) in brackets): character 3, apophyses inside separation/valve width: ≤ 0.8 (0.083); character 13, apices not usually worn (0.077); character 19, head valve without a V-shaped margin (0.133); character 31, jugal sinus concave (0.105).

Although this clade remains constant in all shortest trees, the placement of *L. faksensis* and ingroup relationships nevertheless remain unstable on the basis of available external morphological data. This represents a clear area for future study—our preferred tree (Fig. 5) does not, at this point, present a clear picture of leptochitonid relationships. A large clade of outgroup taxa, including all taxa from Hanleyidae and two taxa from other families appear within the crown group of ‘Leptochitonidae’. Two species of *Ferreiraelle* (*F. soyomaruae* and *F. bartletti*) group with the hypothetical ancestor as a well-resolved basal clade; however, other members of Ferreiraelleidae appear in different positions in the ingroup. Although there are clear synapomorphies that define these smaller families used as outgroups (Sirenko 1997, 2001), more character state information will be required to resolve relationships further (including determining monophyly) within Leptochitonidae and other families in this order. Additional characters will be required to fully resolve the taxon-level internal relationships of this clade; soft anatomical features and molecular data are, however,

Table 1 Characters formulated from shell morphology and used to code chiton taxa in the phylogenetic analysis.

1	Ratio of animal body length/width: ≤ 2 (0); > 2 (1).
2	Ratio of apophyses outside diameter/valve width: ≤ 1.4 (0); > 1.4 (1).
3	Ratio of apophyses inside separation/valve width: ≤ 0.8 (0); > 0.8 (1).
4	Ratio of combined diameter of apophyses/valve width: ≤ 1.4 (1); > 1.4 (0).
5	Thickened on terminal margins: no (0); yes (1).
6	Articulamentum thickened at side margins: no (0); yes (1).
7	Animal body shape: ovate (0); elongate oval (1); ovoid (2).
8	General character of arch (intermediate plates): straight sides (0); pointed arch (1); evenly rounded (2); concave (3)*.
9	Dorsal elevation (height/width) of intermediate plates: ≤ 0.4 (0); > 0.4 (1).
10	Carinate valves: not carinate (0); sub- or semicarinate (1); carinate (2).
11	Valve thickness: thin (0); thick (1).
12	Valves beaked: no (0); yes (1).
13	Apices usually worn: no (0); yes (1).
14	Lateral area elevated on intermediate plates: no (0); yes (1).
15	Intermediate plates with distinct diagonal separating lateral areas: no (0); yes (1).
16	Apophyses' jugal margin: straight (0); concave (1).
17	Head valve shape: semicircular (0); shape $<$ semicircle (1); shape $>$ semicircle (2).
18	Head valve with marginal notch: no (0); yes (1).
19	Head valve with V-shaped margin: no (0); yes (1); wavy (2)*.
20	Tail valve shape: semicircular (0); shape $<$ semicircle (1); shape $>$ semicircle (2).
21	Mucro prominent: no (0); yes (1).
22	Mucro position: median (0); posterior (1); anterior (2).
23	Post-mucronal slope: straight (0); concave (1); convex (2).
24	Articulamentum character: weak (0); moderate (1); strong (2).
25	Insertion plates present: no (0); yes (1).
26	Intermediate valves: apophyses shape (rounded top): no (0); yes (1).
27	Intermediate valves: apophyses consistent shape: no (0); yes (1).
28	Separation between apophyses: widely separated (1); ordinary (2); narrow (3).
29	Tail valve apophyses shape same as on intermediate valves: yes (0); no, difference(s) (1).
30	Jugal sinus width: widely separated (1); ordinary (2); narrow (3).
31	Jugal sinus excavation: straight (0); convex (1); concave (2).
32	Jugal sinus shape variable: no (0); yes, difference(s) (1).
33	Intermediate valve shape: trapezoidal (0); rectangular (1); ovate or circular (2).
34	Intermediate valves, anterior margin: straight (1); convex (2); projecting (3).
35	Intermediate valves, posterior margin: straight (1); convex (2); projecting (3); concave around apex (4)*.
36	Tegmentum, general sculpture: smooth (0); minutely granulose (1); finely granulose (2); granulose (3); pustulose (4); long threads (5)*.
37	Tegmentum, gradation of sculpture: regular (0); larger toward margin (1); faded posteriorly (2).
38	Tegmentum, dominant granule shape: no granules (0); oval (1); square (2); irregular (3); heart/pear shape (4); roundish (5).
39	Tegmentum, general granule profile: no granules (0); straight (1); convex (2); irregular (3); roundish (4).
40	Central areas of intermediate valves, distinct jugal sculpture: not distinct from pleural area (0); longitudinally granulate in jugal area; pleural areas coarser (1); jugal sculpture in quincunx, grading to radiating longitudinal series (2).
41	Central areas of intermediate valves, sculpture with longitudinal rows: no pattern (0); longitudinal rows (1); quincunx (2); irregular quincunx (3); wavy or zigzag (4).
42	Central areas of intermediate valves, sculpture with radial rows: no pattern (0); radial rows (1); quincunx (2); irregular quincunx (2); wavy or zigzag (4).
43	Central area of intermediate valves, granule size: irregular (0); pustulous (1); minute (2); small (3); graded out from jugal area (4).
44	Central area of intermediate valves, granule shape: no granules (0); oval (1); square (2); irregular (3); heart/pear shape (4); roundish (5).
45	Central area of intermediate valves, granule profile: no granules (0); straight (1); convex (2); irregular (3); roundish (4).
46	Central area of intermediate valves, granule elevation: not elevated (0); little (1); moderate (2); neatly separated (3).
47	Central area of intermediate valves, sculpture interstices: close/narrow (0); coalescing/beading (1); as wide as granules (2); widespread (3); shallow grooved (4); punctured (5); sandy (6).
48	Lateral areas of intermediate valves, granule size: irregular (0); pustulous (1); minute (2); small (3); graded out from jugal area (4).
49	Lateral areas of intermediate valves, granule shape: no granules (0); roundish (1); square (2); irregular (3); heart/pear shape (4).
50	Lateral areas of intermediate valves, granule profile: no granules (0); straight (1); convex (2); irregular (3); roundish (4).
51	Lateral areas of intermediate valves, granule elevation: not elevated (0); little (1); moderate (2); neatly separated (3); beaded (4)*.
52	Lateral areas of intermediate valves, sculpture interstices: close/narrow (0); coalescing/beading (1); as wide as granules (2); widespread (3); shallow grooved (4); punctured (5); sandy (6).
53	Lateral areas of intermediate plates with same sculpture as head plate: no (0); yes (1).
54	Postmucronal area with same sculpture as head plate: no (0); yes (1).
55	Antemucronal area with same sculpture as central area of intermediate plates: no (0); yes (1).

* Denotes characters for which an ordering scheme was inferred for analysis; all other multistate characters describe variation between included taxa but were not ordered (i.e. direction of character state change not inferred).

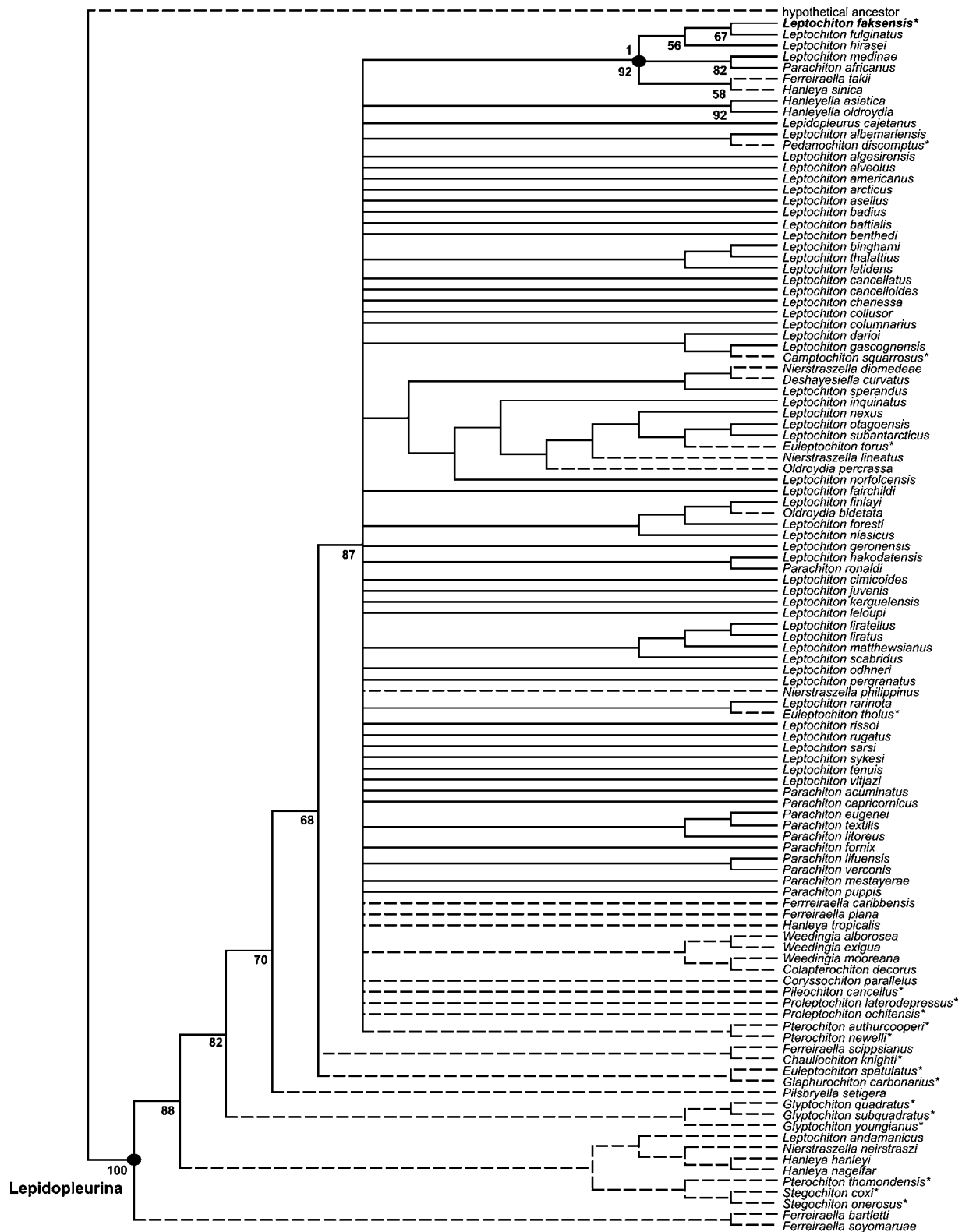


Figure 5 The phylogenetic position of *Leptochiton faksensis* sp. nov. within Lepidopleurina – strict consensus of eight most-parsimonious-trees (MPTs) generated by Parsimony Ratchet analysis of the data set in PAUP*. Numbers in bold underneath nodes are bootstrap support statistics (1000 replicates in PAUP*). Each of the eight shortest trees has a consistency index (CI) of 0.417 and a retention index (RI) of 0.519. Characters supporting the clade containing *Leptochiton faksensis* sp. nov. (filled circle denoted ‘1’) are discussed in the text. Apomorphies of this new fossil taxon, as hypothesised by this analysis (CI in brackets), are as follows: character 4, ratio of combined diameter of apophyses/valve width ≤ 1.4 (0.125); character 9, dorsal elevation (height/width) of intermediate plates > 0.4 (0.053); character 17, head valve shape $<$ semicircular (0.125); character 23, post-mucronal slope straight (0.083); character 31, jugal sinus excavation convex (0.105); character 41, central areas of intermediate valves irregular quincunx (0.182); character 44, central area of intermediate valves – granule shape roundish (0.238); character 51, lateral areas of intermediate valves neatly separated (0.211). Asterisks (*) denote fossil taxa.

not applicable to fossils. We can at least be sure that *L. faksensis* adds diversity to this clade by the time of the earliest Palaeocene.

From a taphonomic perspective, it is of note that the characteristic thickening of the posterior plate in *L. faksensis* has provided for better preservation of these elements. It is very probable that the dorsal elevation of the whole body of *L. faksensis* was a very high, subcarinate arch, but that the majority of these intermediate plates demonstrating even greater dorsal elevation than the present material were too fragile to survive disarticulation. Consequently, although this is an interesting taphonomic insight, it does not influence the cladistic analysis, which is based largely on generalised characters rather than those specific to posterior anatomy. Because the Fakse polyplacophorans were discovered incidentally to sorting a whole fauna, small fragments of plates could have been easily discarded. The preservation also has provided for considerably more juvenile specimens to be represented only by tail valves. The relatively constricted range in sizes of the thinner intermediate and head valves indicates that these are representative of the actual adult size of the animals.

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APPENDIX 1: CHARACTER-TAXON DATA SET UTILISED FOR THE PHYLOGENETIC ANALYSIS

Asterisks (*) denote fossil taxa.

	1	2	3	4	5	
	0	0	0	0	0	
Ancestor	0101000000	0010000000	0000001?0?	0011100000	0020000200	00111
<i>Leptochiton faksensis*</i>	?00110?211	0000101102	120200?002	1121421540	3225410314	33011
<i>Hanleyella asiatica</i>	0101000101	01?0?10111	0011000010	2013231540	00????????	??111
<i>Hanleyella oldroydia</i>	0101000112	00?0111012	020?001012	011?341511	10151321??	32111
<i>Lepidopleurus cajetanus</i>	10100012?0	?01111000?	122?0?????	?????00540	1525443200	06111
<i>Leptochiton albemarlensis</i>	??????200	?0?00?2?10	10????????	?????120540	223141?311	14111
<i>Leptochiton algesirensis</i>	011100220?	?010101110	020?00121?	??11130??0	113????3??	??111
<i>Leptochiton alveolus</i>	1110001211	?010000000	001?00101?	11????30110	033143?311	3?11?
<i>Leptochiton americanus</i>	0101001101	?0001?1110	0112001212	112??30541	113543?314	3?111
<i>Leptochiton andamanicus</i>	1?10101101	1011010000	0000001?0?	?000000000	0000000000	00111
<i>Leptochiton arcticus</i>	0111000?11	?000111111	0002011000	??11130??0	22?511??11	1?1?1
<i>Leptochiton asellus</i>	0111000?01	?100110001	111?0012?2	20????40110	111331?133	1?011
<i>Leptochiton badius</i>	1010001?01	00111?0112	02000??2?2	011?130540	1235413314	10111
<i>Leptochiton battialis</i>	100000121?	0001??????	001101101?	?0????31???	13????????	??001
<i>Leptochiton benthedi</i>	0???000?11	01?0?00100	11210??202	0?11130110	2235430014	30111
<i>Leptochiton binghami</i>	0?????10?2	?1010??00?	121???????	?????30541	1225411214	01111
<i>Leptochiton cancellatus</i>	111100120?	?011111011	121000121?	101?130540	11354?0314	?0111
<i>Leptochiton cancelloides</i>	0110001210	?0?0100010	1112001212	112?130540	1115432314	31111
<i>Leptochiton chariessa</i>	0000001112	?1?0101??2	111000120?	10?5430110	1131433311	3?011
<i>Leptochiton collusor</i>	1110??1111	?00111???0	111??01212	1014120511	1155141511	41111
<i>Leptochiton columnarius</i>	1110001?12	?00111000?	010100120?	??14120??0	1133340333	41111
<i>Leptochiton darjoi</i>	1010005210	?0101000??	121010020?	?0???30540	153542?314	2?111
<i>Nierstraszella diomedea</i>	0001001002	01?1100010	021200101?	11?1?3011?	4531441311	??111
<i>Leptochiton fairchildi</i>	111000?201	11?1110010	1112001202	0011?3???	111541??33	??111
<i>Leptochiton finlayi</i>	0101??1201	?000000011	0200?01202	101242?521	133022031?	?2011
<i>Leptochiton foresti</i>	0101101102	01?00100?0	0002011202	0012420540	1535422314	22111
<i>Leptochiton fuliginatus</i>	1000101101	100110000?	1112011012	21???21541	1213303?14	0?011
<i>Leptochiton gascognensis</i>	101000121?	?0?0010001	1111011210	200?130540	1135422314	23111
<i>Leptochiton geronensis</i>	1101001201	0010010001	0200001010	00???30540	123543?314	3?111
<i>Leptochiton hakodatensis</i>	0000000200	00?0000000	1010011212	00?4?30???	125544????	??011
<i>Leptochiton hirasei</i>	1000011200	0000110???	121000100?	?02?11011?	11214????14	0?011
<i>Leptochiton inquinatus</i>	1001001200	?011110110	0100011010	??11120??0	113??4?2??	4?111
<i>Leptochiton juvenis</i>	0111001?02	0000110110	0212011212	0111130540	1235440214	10111
<i>Leptochiton kerguelensis</i>	0000001210	?011100??0	001000121?	?0?1?00541	222540?214	0?111
<i>Leptochiton latidens</i>	0000000210	000111??1?	02110112?2	00?21?????	12?51????14	??111
<i>Leptochiton leloupi</i>	11110012?0	?011110000	00100?1200	??1??40540	1113333133	33111
<i>Leptochiton lirattellus</i>	001000??1?	0?01101121	120100120?	??11130540	11354323??	42111
<i>Leptochiton liratus</i>	1000001?11	0011110112	112100120?	??12130??1	153??423??	42111
<i>Leptochiton matthewsianus</i>	0000001201	0010110110	010100120?	??11130540	1135433314	32111
<i>Leptochiton medinae</i>	0000001200	?00010???	1100001212	2014120111	1131410311	10111
<i>Leptochiton nexus</i>	0???000101	?010101010	101?01121?	??11?10210	11221??221	??111
<i>Leptochiton niasicus</i>	0101000101	0100000000	0202011212	100?420110	2235412314	00111
<i>Leptochiton norfolcensis</i>	0101011101	?011110112	1112011101	001?131510	1135130311	30111
<i>Leptochiton odhneri</i>	1110000201	?110100010	1010001200	??12130541	12354??314	??111
<i>Leptochiton otagoensis</i>	0?????1??1	????1?????	?21???????	?????4???	112????2??	??111
<i>Leptochiton pergranatus</i>	0???001102	?00011000?	0211001002	00???10540	1235431314	32111
<i>Leptochiton rarinata</i>	1???001?1?	00100?0???	?1??0?????	??1??41110	??133??133	?????
<i>Leptochiton rissoi</i>	0001001012	0101100012	0011001010	?01?420??0	1240006000	06011
<i>Leptochiton rugatus</i>	????000200	?0011?1100	10?000121?	1012150??0	115004?500	4?111
<i>Leptochiton sarsi</i>	001000111?	?01011100?	0010001210	?0??130540	1235434314	34111
<i>Leptochiton scabridus</i>	0000001201	?010110010	?010001200	??11131540	11354??314	????0?
<i>Leptochiton sperandus</i>	??????1201	?0111?011?	121???????	??1?130511	1535122311	20111
<i>Leptochiton subantarcticus</i>	?101????210	?0?10?????	?????1?2?2	2????4033?	112??402??	40????
<i>Leptochiton sykesi</i>	1000001012	?101110010	11120012?2	00??450??0	125004?500	4?111
<i>Leptochiton tenuis</i>	001000121?	?1?1110002	0211001240	?01??10541	1125446214	46111
<i>Leptochiton vitjazi</i>	1110??111?	001001?0??	111??10?1?	???1130540	3035410314	10111
<i>Parachiton acuminatus</i>	101000120?	00?1100?11	0110001202	0012110440	11244?4244	?4111

Appendix 1 continued.

	1 0	2 0	3 0	4 0	5 0				
<i>Parachiton africanus</i>	1???	001200	0??01?0??2	0110001202	?011120110	11314?0311	10111		
<i>Parachiton capricornicus</i>	1???	001200	?0?00?0??2	11000?1200	?01?130540	123141?314	1?111		
<i>Parachiton eugenei</i>	111000120?	00?0110?10	010001121?	?121120??0	123211?2??	1?111			
<i>Parachiton fornix</i>	1010001200	0010110??1	0100001202	0011110??0	1534416244	101??			
<i>Parachiton lifuensis</i>	1111???2?0	?10110??0	1121??????	?????0??1	115??2?5??	2?111			
<i>Parachiton litoreus</i>	1110001200	00001????1	110001120?	?011?20540	11321??314	??111			
<i>Parachiton mestayerae</i>	0???	001101	00?01?2111	111?00120?	?01?120440	1231420344	10111		
<i>Parachiton puppis</i>	1???	001200	00111?0?01	111?00120?	?01??20540	112??52??	?1001		
<i>Parachiton soyomaruai</i>	0???	001200	?0101?0??0	1111011202	001?130540	125540??14	0?001		
<i>Parachiton textilis</i>	?110???	210 ?0???	1?????1	11?1??????	??2??20??0	125??1?5??	1????1		
<i>Parachiton verconis</i>	??????????	?????0???	112?????0?	?????50???	??5???????	?????			
<i>Ferreiraella bartletti</i>	0000?	0?00	1??0?00??0	021200120?	??11110000	0020000200	00111		
<i>Ferreiraella caribbensis</i>	0000001002	0100100012	001?001200	1011130540	33354??354	??111			
<i>Ferreiraella plana</i>	0111001301	1100010022	1112010212	102?120540	2235410314	10?11			
<i>Ferreiraella scippsianus</i>	1???	001???	?111100???	122?0012??	?00??00??0	0003300033	00111		
<i>Ferreiraella soyomaruai</i>	0000?	1200	1??0000??1	01020012??	?12??10000	0020000200	00111		
<i>Ferreiraella takii</i>	0000?	?020?	01?1100002	111?00???	2?02320540	103111?255	1?111		
<i>Hanleya hanleyi</i>	1001021100	0000000000	0000000000	0000000000	0000000000	00000			
<i>Hanleya nagelfar</i>	1011011010	0000100000	0000000000	0000000000	0000000000	000??			
<i>Hanleya tropicalis</i>	0000?0?	112	110010???	2	1201111010	??11330510	2235100354	33??0	
<i>Hanleya sinica</i>	00000?0?0?	?1?0100101	111?1012??	2?123205?0	1031???	35?	??111		
<i>Weedingia alborosea</i>	0000111101	110000000?	1011101000	1001431541	12454??354	??111			
<i>Weedingia exigua</i>	0?0?111101	110000000?	1011101000	1001431541	12454??354	??111			
<i>Weedingia mooreana</i>	1000111101	1100000001	1121111200	?111431541	12454??354	??111			
<i>Oldroydia bidetata</i>	0101001?01	110000???	1	0000100002	2123350541	1?251?1211	2?111		
<i>Oldroydia percassa</i>	1101001101	1110011010	0112011010	2023??0511	11033??011	?0111			
<i>Deshayesiella curvatus</i>	1001001200	1111102010	1202001002	00?1?3???	1	15114?0114	??011		
<i>Nierstraszella lineatus</i>	1101001201	1000101010	0112001010	001?112??0	4420041200	41111			
<i>Nierstraszella philippinus</i>	1101101?12	0100010010	0012001012	?112360520	22???	?????	??111		
<i>Nierstraszella neistraszi</i>	1?1000201	0010000000	00000120?	?000000000	0000000000	00111			
<i>Camptochiton squarrosus*</i>	0???	00?300	00?00011?1	1110001?0?	??1??30540	013542?314	2?111		
<i>Chauliochiton knighti*</i>	1??????001	00?110???	???	00???	1011401210	000210??21	?????		
<i>Colapterochiton decorus*</i>	1??????0?	?????0???	2	112?0012??	???????????	???????????	?????		
<i>Coryssochiton parallelus*</i>	1????0?001	10?0002000	111?011?0?	1011120540	1125430214	3?111			
<i>Euleptochiton spatulatus*</i>	0??????02	00???	0?0?	11?0011202	00011401?0	000???	0??	??111	
<i>Euleptochiton tholus*</i>	1????00?010	00?000???	1110001?0?	??1?420330	2213322133	22111			
<i>Euleptochiton torus*</i>	?????????1?	???	01?????	0	121?0?????	00???????	?????????	?????	
<i>Glaphurochiton carbonarius*</i>	0??????0?	00???	0?0?	???	0011202	00111401?0	000???	0??	??111
<i>Glyptochiton quadratus*</i>	?????0????	10?000???	???	00???	1	2?23332541	000000?000	00???	
<i>Glyptochiton subquadratus*</i>	?????0????	10?000???	???	200???	1	2?23332541	000000?000	00???	
<i>Glyptochiton youngianus*</i>	?????0????	10?000???	???	00???	1	2?23332541	000000?000	00???	
<i>Pedanochiton discomptus*</i>	1??????001	00?0002012	1210001?0?	0011120540	223541?31?	??111			
<i>Pileochiton cancellus*</i>	0??????00?	00?11?20?1	10000?1?0?	000??305?1	223??4????	3?111			
<i>Proleptochiton laterodepressus*</i>	????00?1?0	00?010???	???	00012?2	0011130540	2235432314	32111		
<i>Proleptochiton ochitensis*</i>	1???	00?1?0	00?000???	???	00012?2	0011130540	2255432214	32111	
<i>Pterochiton authurcooperi*</i>	1??????00?	00?01020?2	11?1001?0?	??02110??0	002???	??2??	??111		
<i>Pterochiton newelli*</i>	1??????01?	00?01020?2	11?1001?0?	??02110??0	002???	??2??	??111		
<i>Pterochiton thomondensis*</i>	????00?101	11?011111?	???	10012??	0?11100000	0000000000	001??		
<i>Stegochiton coxi*</i>	????????111	?0?010???	???	00?2?2	1012150001	220004?000	00???		
<i>Stegochiton onerosus*</i>	????????111	10?010???	???	00?2?2	1012140001	22133??133	?????		