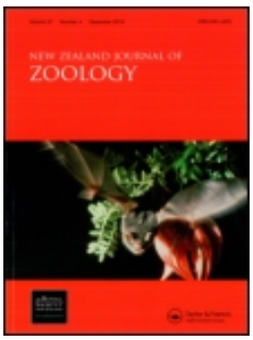

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Subgeneric classification of New Zealand and Australian species of *Paphies* Lesson (Bivalvia: Mesodesmatidae), and names for the two species of tuatua in New Zealand

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Abstract Comparison of hinge detail shows that *Paphies* (*Mesodesma*) Deshayes, 1832 (= *Ceronia* Gray, 1853) should be restricted to a subgenus for American species, which all have transversely ridged lateral teeth. *Paphies* (*Paphies*) Lesson, 1831 (= *Machaena* Gray *ex* Leach MS., 1843, = *Taria* Gray, 1853) is used for the New Zealand species of *Paphies*, which are all large and have smooth or weakly pustulose lateral teeth. *Paphies* (*Amesodesma*) Iredale, 1930 is regarded as a further subgenus to contain the Australian *P. elongata* (Reeve, 1854) (= *Mesodesma angustum* Reeve, 1854, = *M. nitidum* Reeve, 1854, = *Amesodesma perfugum* Iredale, 1930), the Philippine *P. angula* (Reeve, 1854), and the Indonesian *P. altenai* (De Rooij-Schuiling, 1972), which are all small and have oblique, protruding resilifers. The remaining small Australian species *P. cuneata* (Lamarck, 1818) (= *Amphidesma glabrellum* Lamarck, 1818) and *P. erycinaea* (Lamarck, 1818), which have almost vertical resilifers, are placed in the subgenus *Paphies* (*Atactodea*) Dall, 1895. The presumed holotype of *Mactra subtriangulata* Wood, 1828 shows that the valid name for the predominantly northern species of tuatua with a short, biangled posterior end of concave outline is *Paphies* (*Paphies*) *subtriangulata* (Wood, 1828). A lectotype designated for *Mesodesma spissum* Reeve, 1854 shows that this name is a synonym of *P. subtriangulata* (Wood). The holotype of *Mya donacina* Spengler, 1793, the syntypes of *Mesodesma quoyi* Deshayes, 1832, and the holotype of *Mesodesma latum* Deshayes, 1843 confirm that *Paphies* (*Paphies*) *donacina* (Spengler, 1793) is the valid name for the predominantly southern species of tuatua with a more elongate posterior end of convex outline. A neotype designated for *Taria stokesii* Gray, 1853 shows that this name is a further synonym of *P. donacina* (Spengler).

Keywords Bivalvia; Mesodesmatidae; *Paphies*; subgenera; classification; *Mesodesma*; *Amesodesma*; *Atactodea*; *Machaena*; *Regterenia*; *Taria*; *Paphies subtriangulata*; *Paphies donacina*; tuatua; hinge tooth morphology; neotype designation.

INTRODUCTION

Two large, similar species of *Paphies* have long been confused and both given the common name 'tuatua' in New Zealand. Richardson et al. (1982) have conclusively demonstrated that the opinions of early taxonomists from Deshayes (1832) to Lamy (1914) and Finlay (1927) were correct, and 2 species of tuatua live on the same beaches in central New Zealand. This paper sets out to determine the valid names to be used for these species—an unexpectedly complicated task, as few of the early names are now supported by clearly identified type specimens, making it difficult to identify the earliest names for the 2 species. We also revise the subgeneric classification of species of *Paphies* in America, the western Pacific, and South Africa.

TAXONOMY

Family MESODESMATIDAE

Genus *Paphies* Lesson, 1831

Subgenus *Paphies* sensu stricto

Paphies Lesson, 1831: 424. Type species, by monotypy, *Paphies* (*Crassatella*) *roissyana* Lesson, 1831 (= *Mya australis* Gmelin, 1791); Pliocene to Recent, New Zealand.

Machaena Gray *ex* Leach MS., 1843: 252 (in synonymy of *Mesodesma chemnitzii* Deshayes, 1832). Type species, here designated, *Machaena ovata* Gray *ex* Leach MS., 1843 (= *Mya australis* Gmelin, 1791). [Genus name available, as used with original authorship and date by Fischer (1887, p. 1112).]

Taria Gray, 1853: 44. Type species, by monotypy, *Taria stokesii* Gray, 1853 (= *Mya donacina* Spengler, 1793); Pliocene to Recent, New Zealand.

The comments on hinge features and subgenera of larger Mesodesmatidae by Beu (1971, p. 116–119) were incorrect. As was quite correctly pointed out

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by numerous earlier workers—e.g., Dall (1898, p. 911), Lamy (1912, p. 246; 1914, p. 6); Keen *in* Moore (1969, p. N608)—*all* living American species of *Mesodesma* Deshayes, 1832 have transversely ridged lateral teeth (including *M. arctatum* (Conrad, 1830); *M. deauratum* (Turton, 1822), type species of *Ceronia* Gray, 1853; *M. mactroides* Reeve, 1854; and *M. donacia* (Lamarck, 1818), type species of *Mesodesma*). The transversely ridged teeth of *M. donacia* are illustrated in Fig. 2. By contrast, all Indo-Pacific, Australian, and New Zealand species of *'Mesodesma'* we have examined have smooth or weakly pustulose lateral teeth (Fig. 1). As *Mesodesma* (sensu stricto) has an apparent ancestor with transversely ridged lateral teeth in the Eocene (Claiborne Group) of North America (*Mactropsis* Conrad, 1854; Dall 1898, p. 910) and typical fossil species in the Miocene (*Mesodesma marianum* Glenn (1904, p. 285, pl. 69 fig. 1–3) and *M. spathum* Gardner (1944, p. 115, pl. 18 fig. 8 and 12)), and the smooth-toothed group has fossil members in New Zealand as old as Lower Miocene (*Paphies anteaustralis* (Dell), Otaian Stage (Dell 1950, p. 32, fig. 3 and 4)), the American and New Zealand groups appear to be distinct phylogenetic entities, worthy of subgeneric separation. In this interpretation *Ceronia* Gray, 1853 is a subjective synonym of *Mesodesma* (sensu stricto), and another subgeneric name must be found for New Zealand taxa.

Iredale (1915, p. 489) and Beu (1971, p. 117) showed that *Paphies* Lesson dates from 1831, whereas *Mesodesma* Deshayes dates from 1832. There seems no reason not to use *Paphies* Lesson as the genus for most larger Mesodesmatidae, with *Mesodesma* Deshayes as a subgenus for American species. De Rooij-Schuiling (1972a, p. 56, footnote) intended to apply to the International Commission on Zoological Nomenclature to suppress *Paphies* Lesson and, following *ICZN* Article 80, she continued to use *Mesodesma*. However, the application has not been submitted, and *Paphies* has long had currency in New Zealand. Following Iredale (1915, p. 491), *Paphies* has been used consistently in New Zealand as a full genus or as a subgenus for *'Amphidesma' australe* (Gmelin, 1791), the estuarine 'pipi' (Finlay 1927, p. 469 (as a genus); Dell 1950, p. 32 (as a subgenus); Powell 1976, p. 129 (as a genus, but as a subgenus in 4 earlier editions, 1937 to 1962); Beu 1971, p. 117 (as a genus); Powell 1979, p. 415–416 (as a genus); and in many other ecological papers and popular books), and so does not qualify as a *nomen oblitum*. The name has been familiar to and in current use by New Zealand molluscan taxonomists and shell collectors for most of this century, and during the past 10 years has become accepted again as the generic name for New Zealand mesodesmatids (following Beu 1971). So no major nomenclatural changes result from the recognition of *Paphies* as the genus for most larger mesodesmatids and of *Paphies* (*Mesodesma*) as a subgenus for the American mesodesmatids.

Should a separate subgenus be recognised for the strongly inequilateral species of *Paphies*? The type species, *P. australis* (Gmelin), has its umbo only slightly on the posterior side of the centre of the dorsal margin, whereas in most other New Zealand species of *Paphies* it is near the posterior end. As noted above, most New Zealand taxonomists during this century have recognised a separate subgenus for the more inequilateral species. However, populations of unusually elongate *Paphies donacina* (Spengler)—e.g., RM 4979, Westshore Beach, Napier; RM 4960, Horseshoe Bay, Stewart Island; both in N.Z. Geological Survey—have the posterior end only a little shorter than in some of the less strongly equilateral specimens seen in all populations of *P. australis*. Microscopic comparison of hinges of all 4 living New Zealand mesodesmatids showed no significant differences. We can see no justification for recognising a separate subgenus for the inequilateral species of *Paphies*. This was also the opinion of De Rooij-Schuiling (1972a, p. 56, footnote), although she placed all these species in *Mesodesma*. All New Zealand Mesodesmatidae are here placed in subgenus *Paphies* (*Paphies*).

The status of Leach's manuscript name *Machaena* has long been in doubt, as it was first published by Gray (1843, p. 252) in the synonymy of *Mesodesma chemnitzii* Deshayes, 1832 (= *Mya australis* Gmelin, 1791). The name has been used as a valid genus-group name by Mörch (1843, p. 17) and, with its original authorship and date, by Fischer (1887, p. 1113), and so is available (*ICZN* Article 11(d)). Gray (1843, p. 252) originally listed the 2 names "*Machaena ovata*, and *M. subtriangulata*. Leach, MSS., Brit. Mus.". Even if, as this synonymy (probably incorrectly) implies, these 2 originally included nominal taxa of *Machaena* were intended to apply to the same biological taxon, one of them must be designated as type species of *Machaena*. In the strictest sense, no previous type designations are valid. Fischer (1887, p. 1113) and Lamy (1914, p. 6) selected names that were not one of Gray's 2 originally included taxa (and, in any case, Fischer's listings should be considered type designations only where he stated "Type: ..."). Dall (1898, p. 912) and most other authors merely listed *Machaena* in the synonymy of *Paphies*, without selecting a type species. Keen *in* Moore (1969, p. N610) incorrectly (in the strictest sense) stated that the type had been selected by monotypy. We here designate *Machaena ovata* Gray *ex* Leach MS., 1843 (= *Mya australis* Gmelin, 1791) as the type species of *Machaena* Gray *ex* Leach MS., 1843, thereby confirming *Machaena* as an objective synonym of *Paphies* Lesson, 1831.

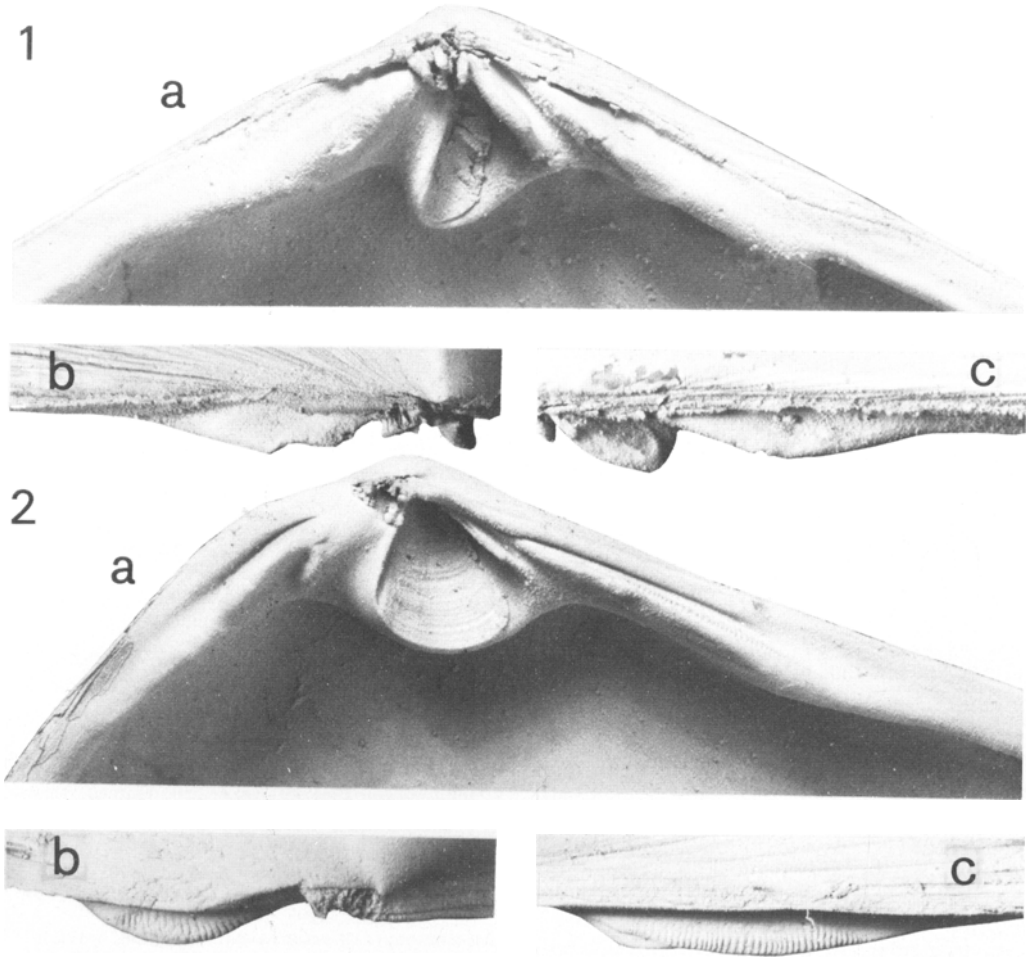


Fig. 1 *Paphies* (*Paphies*) *donacina* (Spengler). Hinge of left valve, whitened with ammonium chloride and enlarged to show lack of transverse ridges on lateral teeth (RM 1328, Gisborne, east coast North Island, New Zealand; N.Z. Geological Survey). **a,** whole hinge (×3.4); **b,** dorsal view of dorsal surface of posterior lateral tooth (×4.0); **c,** dorsal view of dorsal surface of anterior lateral tooth (×4.3).

Fig. 2 *Paphies* (*Mesodesma*) *donacia* (Lamarck), type species of *Mesodesma* Deshayes. Hinge of left valve, whitened with ammonium chloride and enlarged to show transverse ridges on opposing faces of lateral teeth (cardinal teeth incomplete) (WM 3578, Calbaco, Chile; N.Z. Geological Survey). **a,** whole hinge (×3.4); **b,** dorsal view of dorsal surface of posterior lateral tooth (×4.0); **c,** dorsal view of dorsal surface of anterior lateral tooth (×3.2).

If some significant taxonomic criterion should be discovered for the more inequilateral New Zealand species of *Paphies*, an available subgeneric name for them is *Taria* Gray, 1853. Gray (1853, p. 44) proposed the genus in two lines: "Shell oblong, subequilateral, attenuated behind, hinder slope keeled; lateral teeth very small. *T. stokesii*, n.s.". No separate description or figure of *Taria stokesii* was included, and opinions on its identity have been divided almost equally between *Paphies donacina*, *P. subtriangulata*, and *P. ventricosa* ever since.

Mr David Heppell (Royal Scottish Museum, and Commissioner, ICZN), in a letter to A.G.B. dated 15 June 1981, stated that in his opinion *Taria stokesii* is an available species name, satisfying the requirements of *ICZN* Article 16(a)(vi), as a single combined description of a new genus and a new species. The problem is to identify the species to which Gray (1853) intended this name to apply.

As is described more fully under the heading '*Paphies donacina* (Spengler)', it now seems very likely that the British Museum (Natural History) specimen of *P. donacina* collected in New Zealand by the famous hydrographer Captain John Lort

Stokes, R.N., who surveyed the New Zealand coastline in H.M.S. *Acheron* between 1847 and 1850, is the missing holotype of *Taria stokesii* Gray, 1853. However, this cannot be proved from existing data. Below, we formally designate this specimen, BM(NH) 1852.3.16.292, as the neotype of *Taria stokesii* Gray, 1853, which is therefore a junior synonym of *Paphies donacina* (Spengler, 1793). As we can see no reason to place the more strongly inequilateral species of *Paphies* in a different subgenus from the more nearly equilateral species, we regard *Taria* Gray, 1853 as a subjective synonym of *Paphies* (*Paphies*) Lesson, 1831.

Amesodesma Iredale (1930, p. 402 and 407) is also here considered a useful subgenus of *Paphies*. We regard *Mesodesma angustum* Reeve, 1854, *M. nitidum* Reeve, 1854, and *Amesodesma perfugum* Iredale, 1930 as synonyms of *Paphies* (*Amesodesma*) *elongata* (Reeve, 1854). As first revisers, we select the name *Mesodesma elongatum* Reeve, 1854 as the name to be used for the taxon named *Mesodesma elongatum*, *Mesodesma angustum*, and *Mesodesma nitidum* by Reeve (1854), by all who regard these names as synonyms. Tomlin (1931) pointed out that all these species date from Reeve (July 1854) rather than from Deshayes (May 1855), to whom they had previously been attributed. Careful comparison of hinges showed that *P. elongata* (Reeve), from south-eastern Australia, *P. altenai* (De Rooij-Schuiling) from Indonesia (De Rooij-Schuiling 1972a, p. 56, fig. 1a,b), and *P. angula* (Reeve, 1854) from the Philippine Islands have unusual hinge features, with a strongly inclined resilifer protruding below the hinge line and a massive, triangular, right posterior ventral lateral tooth. These 3 species seem worth placing in their own subgenus, *Paphies* (*Amesodesma*).

The remaining small Australian species of *Paphies*, *P. erycinaea* (Lamarck, 1818) and *P. cuneata* (Lamarck, 1818), have hinges more like those of the large New Zealand species of *Paphies* (*Paphies*) than those of *P.* (*Amesodesma*), with the resilifer slightly inclined (*P. cuneata*) or vertical (*P. erycinaea*), and a right posterior ventral lateral tooth that is larger than in *Paphies* (*Paphies*) but markedly smaller than in *Paphies* (*Amesodesma*). The general shell form and size, the hinge, and the shallow pallial sinus agree closely with those of *Atactodea striata* (Gmelin, 1791), type species of *Atactodea* Dall, 1895. In our opinion *P. erycinaea*, *P. cuneata*, and *Atactodea striata* should be allied in the subgenus *Paphies* (*Atactodea*).

De Rooij-Schuiling (1972b) proposed a subgenus *Mesodesma* (*Regterenia*) for the South African Recent species *Donacilla africana* Turton, 1932, which lacks a pallial sinus. This species has smooth lateral teeth in a hinge resembling that of *Paphies* (*Atactodea*) rather than that of *Donacilla cornea* (Poli), the type species of *Donacilla*, and we now classify it as *Paphies* (*Regterenia*) *africana*.

Paphies (*Paphies*) *subtriangulata* (Wood, 1828)

(Fig. 3–10)

?*Erycina subangulata* [sic?] Gray, 1825: 135 (*nomen nudum*).

Mactra subtriangulata Wood *ex* Gray MS., 1828: 4, no. 10, pl. 1 fig. 10.

Mesodesma subtriangulata; Gray *in* Griffith & Pidgeon, 1834: 598, pl. 22 fig. 4 (facing p. 420); Gray, 1843: 252; Gray, 1844: 408; Hanley, 1856: 202, suppl. pl. 1, *Mactra* fig. 10.

Mesodesma cuneata Hanley, 1842 (*in* 1842–56): 38; Hanley, 1843: 38; Hutton, 1873: 68. Not *Crassatella cuneata* Lamarck, 1818.

Mesodesma cuneatum; Catlow & Reeve, 1845: 16; Reeve, 1860: 140.

Mesodesma spissa Reeve, 1854: pl. 3 fig. 18; Paetel, 1873: 135; Hutton, 1873: 68; Hutton, 1878: 48; Hutton, 1880a: 146; Hutton, 1880b: 204.

Paphia (*Taria*) *spissa*; H. & A. Adams, 1858: 43; Tryon, 1868: 124.

Mesodesma reentsii Römer, 1862: 134.

Mesodesma (*Taria*) *spissum*; Martens, 1873: 43.

Mesodesma (*Anapa*) *cuneatum*; Martens, 1873: 43 (in part).

Mesodesma spissum; Martens, 1874: 2.

Mesodesma subtriangulatum; Hutton, 1880a: 146; Suter, 1910: 12; Lamy, 1912: 249; Suter, 1914: 8; Thomson, 1917: 417; Lamy, 1917: 176; Suter, 1921: 17, 25, and 26; Bucknill, 1924: 99, pl. 12 fig. 13.

Paphia cuneata; Grasset, 1884: 250.

Paphia spissa; Grasset, 1884: 250; Hutton, 1884: 519.

Ceronia spissa; Paetel, 1890: 66.

Ceronia reentsii; Paetel, 1890: 66.

Paphia (*Donacilla*) *spissa*; Hutton, 1893: 78.

Atactodea subtriangulata; Suter, 1902: 221; Hutton, 1904: 90; Moss, 1908: 36, pl. 8 fig. 24.

Mesodesma (*Donacilla*) *subtriangulatum*; Suter, 1913: 957, pl. 59 fig. 19 (in part); Ihering, 1927: 252.

Mesodesma (*Taria*) *subtriangulatum*; Lamy, 1914: 22, fig. 2 on p. 24.

Amphidesma (*Taria*) *gaymardi* Iredale, 1915: 491 (as *gaimardi*, p. 492). Not *Mesodesma gaymardi* Deshayes, 1832.

Amphidesma (*Taria*) *subtriangulata*; Iredale, 1915: 491, footnote; Powell, 1937: 60, pl. 11 fig. 7.

Amphidesma subtriangulata; Oliver, 1923a: 186; Oliver, 1923b: 539, pl. 49 fig. 1; Finlay, 1927: 467–469.

?*Taria subtriangulata*; Finlay, 1928: 280 (Chatham Islands).

?*Amphidesma* (*Taria*) *subtriangulata*; Powell, 1933: 183 (Chatham Islands).

Amphidesma subtriangulatum; Powell, 1947a: 21, fig. 76 (also in many later impressions); Rapson, 1952: 170, fig. 5A–C; Fleming, 1953: 260; Rapson, 1954: 493; Cassie, 1955: 348, pl. 2 fig. 1 and 2; Dell, 1955: 43, fig. 99 [1960 impression seen]; Dawson, 1959: 39–54, pl. 4; Grace, 1966: 67 and 69; Waugh & Greenway, 1967: 408; Morton & Miller, 1968: 443, 445, 449, 460–462, and 535, fig. 170(2); McKnight, 1968: 710; Greenway, 1969: 336; Penniket & Moon, 1970: 102, pl. 48 fig. 1; Norris, 1972: 581 and 585; Miller & Batt, 1973: 86 and 87, fig. 111.

Amphidesma (*Taria*) *subtriangulatum*; Powell, 1947b: 61, pl. 11 fig. 7; Powell, 1957: p. 83, pl. 11 fig. 7; Powell, 1962: 124, pl. 11 fig. 7; Fleming, 1966: 32; Goldberg & Carter, 1979: 409.

Amphidesma cf. *subtriangulatum*; Laws, 1950: 17; Te Punga, 1952a: 157 and 159.
Amphidesma subtriangulatum cookianum Dawson, 1959: 53 (*nomen nudum*).
Amphidesma subtriangulatum subtriangulatum; Dawson, 1959: 53.
Donacilla subtriangulatum subtriangulatum; Knox, 1963: 19.
Donacilla subtriangulatum cookianum; Knox, 1963: 19 (*nomen nudum*).
Donacilla subtriangulatum; Harvey, 1965: 150.
Paphies (*Mesodesma*) *subtriangulata subtriangulata*; Beu, 1971: 119, fig. 7; Redfearn, 1974: 13, 19, and 45; Powell, 1976: 129, pl. 18 fig. 7; Powell, 1979: 416, pl. 75 fig. 12.
Paphies subtriangulatum; Grace, 1974: 185 and 188; Grange, 1977: 118.

All discussion under this heading refers to the predominantly northern species of tuatua, usually known during this century as '*Amphidesma*' *subtriangulatum*, which differs from the predominantly southern species *Paphies donacina* (Spengler) in having a shorter posterior end which is concave (cf. convex) in outline over its upper half to two-thirds and has 2 weak ridges (cf. 1) extending from the umbo to the posterior ventral corner.

This species has perhaps the most complex nomenclatural history of any New Zealand endemic mollusc. The earliest name that may have been intended to apply to it is *Erycina subangulata* Gray, 1825, but this is not available. The presumed holotype of the first available name, *Mactra subtriangulata* Wood, 1828, has now been recognised in the British Museum (Natural History), so this is the valid name for the species under discussion. The history and status of the various synonyms are considered below, in chronological order.

Erycina subangulata Gray. The first name that seems to have been intended to apply to this species is *Ery*[*cina*] *subangulata* [sic?] Gray (1825, p. 135). The name appears, from Gray's (1843, p. 252) later list of New Zealand shells, to have been based on *Machaena subtriangulata* Leach, MS. (Gray 1843, p. 252, in synonymy of *Mesodesma chemnitzii* Deshayes, = *Paphies australis* (Gmelin)). The only indication of what Gray (1825) meant by this name is the queried name cited in its synonymy, *Crassatella cuneata* Lamarck (listed with incomplete bibliographic reference). Lamarck's (1818, p. 483) name actually applies to a quite different southern Australian species (see below). A queried name with incomplete bibliographic reference cannot be considered a strict 'indication' in the meaning of *ICZN* Article 16, so Iredale (1915, p. 491) was correct in considering *Erycina subangulata* Gray, 1825, a *nomen nudum*. Gray (1843, p. 252) later listed "*Erycina subtriangulata*. Gray. Ann. Phil." as the original reference for *Paphies subtriangulata*, implying that the name published in 1825 was either a simple error or an uncorrected typographical error, and that he was intending in 1825 that his mentor's manuscript name should be applied to one or the other species of tuatua. Several subsequent authors, including Lamy (1912, p. 249; 1914, p. 22), accepted Gray's (1843) authority, so the name has been attributed to Gray (1825) by most subsequent writers. In our opinion the name *Erycina subangulata* Gray, 1825 is not available.

Mactra subtriangulata Wood, 1828. As was pointed out by Iredale (1915, p. 491, footnote), following the listing of Wood's figure by Lamy (1912, p. 249), the name *Mactra subtriangulata* was first made available by Wood (1828, p. 4, pl. 1 fig. 10). Woodward (1915, p. 2353) published a note, hand-written by J. E. Gray in a British Museum (Natural History) copy of Wood (1828), stating that Wood's obvious use of Gray's MS. names was taken from "my MSS". Much more was supplied by Gray, but he did not supply quite all the new names, as "several of them were altered by Mr Wood". It seems inescapable that most at least of the references and new names in Wood (1828) were supplied by J. E. Gray and assembled, somewhat modified, by Wood. So in instances such as the present one, where the new name in Wood (1828) is clearly from Gray's MS., it should be attributed to Wood *ex* Gray MS. Perhaps a case could even be made for regarding Gray as the author of new names in this book. Dall (1921, p. 211) seems to have favoured this interpretation when he listed "(Gray)" after his reference to the book.

Wood (1828, pl. 1 fig. 10) published a small figure that clearly represents a New Zealand tuatua, but it is not possible to tell which species was intended. We have both searched the collections of the British Museum (Natural History) Mollusca Section at various times for type material of Wood's name, and although L.R-S. noted that one specimen of *Paphies subtriangulata* resembles Wood's (1828) figure, our results were equivocal.

Mrs Solene Morris (pers. comm.) has recently carried out a very detailed comparison of labels, figures, and glue patches on old specimens and the tablets they were formerly attached to, in order to try and recognise the 'missing' type material of this name as well as of *Taria stokesii* Gray, with happier results. A specimen now numbered BM(NH) 19821 bears a label, in what could be J. E. Gray's handwriting, stating on one side that it is "*assatella cuneata* Lamk." and on the other that it is "*Mesodesma cuneata* Desh.". The obviously truncated name must surely be the older, cut down inadvertently during relabelling on the reverse side after Deshayes (1832) published his genus *Mesodesma*. The earlier inscription, which presumably originally read '*Crassatella cuneata* Lamk.', is

the name used by Gray (1825, p. 135) in his incomplete reference to his name *Erycina subangulata*. Moreover, the small label is closely similar in (original) size and in style to labels accompanying type specimens of some of J. E. Gray's other names published in his 1825 list. There is little doubt, therefore, that this single right valve is the 'holotype' of Gray's (1825, p. 135) unavailable name *Erycina subangulata*. Evidence that it is also the holotype of *Mactra subtriangulata* Wood, 1828 is a little more circumstantial.

Firstly, the specimen appears to be that figured by Griffith & Pidgeon (1834, pl. 22 (facing p. 420) fig. 4), identified in the list at the rear, compiled by J. E. Gray, as *Mesodesma subtriangulata*. Size and outline are identical between specimen and figure; the unusually prominent angulation of the outline of the posterior end, where the median ridge of the posterior face meets the posterior margin, is especially notable. The colour appears to have been greatly overstressed in Griffith & Pidgeon's figure, yet its distribution—paler on the posterior slope and around the umbo—precisely matches that on BM(NH)19821. Certainly, then, this specimen was in the British Museum (Natural History) collection before Dieffenbach added more specimens during 1842, and the implication is that Gray chose the specimens to be illustrated in Griffith & Pidgeon (1834) as well as supplying their identifications. As far as we are aware this also means that this is the *only* specimen that has been mentioned in publications as having been in the collection of the British Museum (Natural History) before 1842.

Secondly, Wood (1828, pl. 4) published Gray's MS. name *Mactra subtriangulata* (the implication is that Gray supplied the name *Erycina subtriangulata*, *Mesodesma* Deshayes not having been proposed then, but Wood changed the generic assignment to *Mactra*), with the anglicised term 'truncated'. In Wood's other columns for location, synonymy, reference, and habitat he included only dashes. As the type specimens of some other Wood (1828) names from this book, also published with only dashes in the location column, are known to be present in the British Museum (Natural History) (Mrs S. Morris, pers. comm.), it appears that these dashes signify 'ditto' marks rather than blank entries. The previous name with a full entry, *Mactra cyprinus*, has the location "Br. Mus." (= British Museum; see Wood's list of abbreviations before p. 1), so the type specimen of *Mactra subtriangulata* Wood should be present in the collection of the British Museum (Natural History). In our opinion, it is very likely that BM(NH) 19821, almost certainly the 'holotype' of Gray's unavailable name *Erycina subangulata*, was the only specimen present in the British Museum (Natural History) by 1828, and that both the name and the specimen to be illustrated were supplied by Gray to Wood.

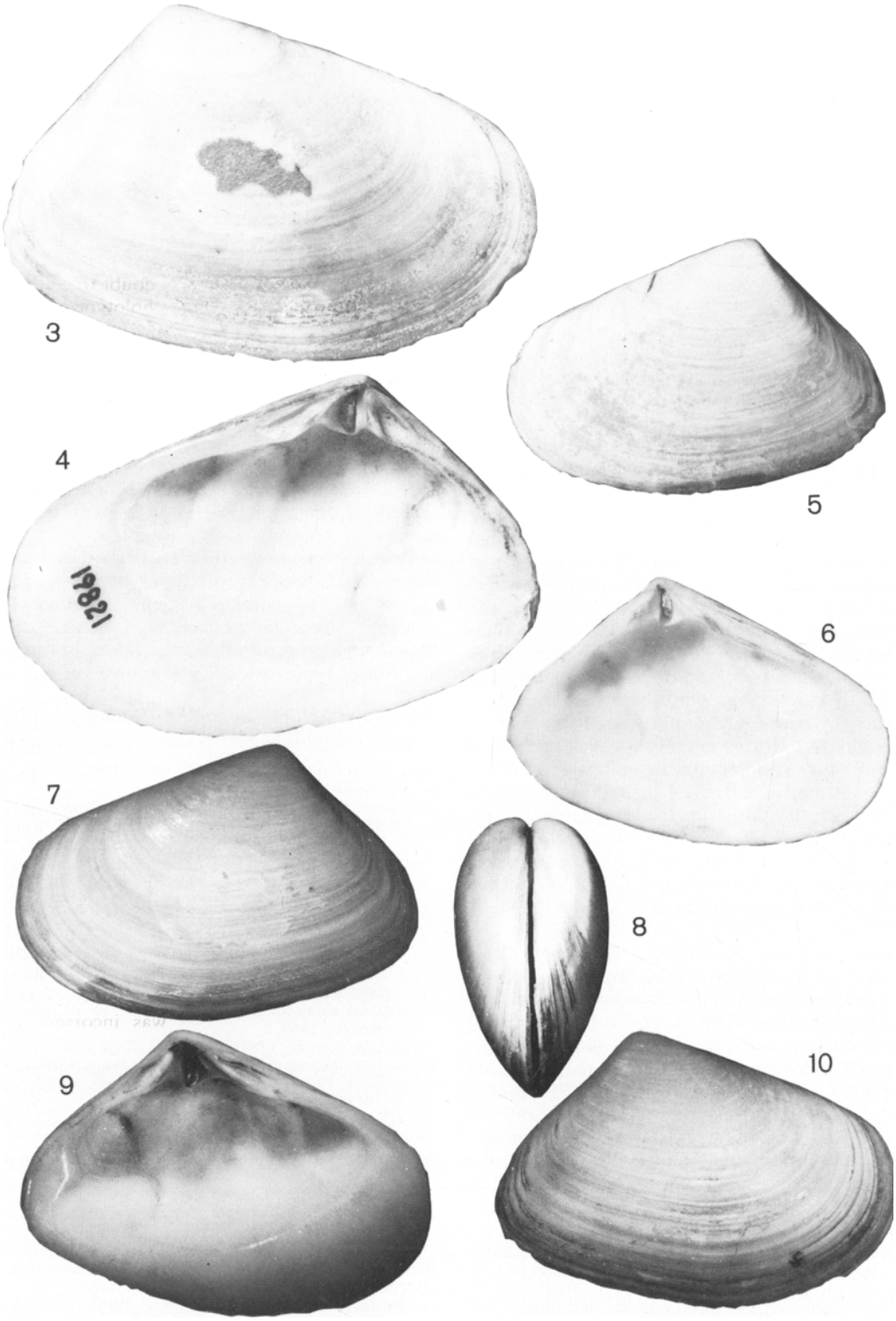
Thirdly, Wood's size code "*b*" on the figure (Wood 1828, pl. 1 fig. 10) indicates that the figured specimen is about 2 inches long, and BM(NH) 19821 is in fact 53.8 mm (2.12 inches) long.

We think there is very little doubt that BM(NH) 19821 (Fig. 3 and 4) is the holotype of *Mactra subtriangulata* Wood *ex* Gray MS., 1828, and are happy to regard this as a suitable basis for the species name. The specimen matches in all details the present concept of *Paphies subtriangulata*, and there is no doubt that Gray and Wood intended the name to apply to the species under discussion. The single right valve BM(NH) 19821 is at present associated with a slightly smaller left valve, but there is no evidence that this left valve was ever among the original type material, and the two are certainly not a pair, as the left valve belongs in *Paphies donacina* (Spengler).

That this species is the one Gray (1843, p. 252) intended the name *Mesodesma subtriangulata* to apply to is clearly shown by the 2 specimens brought to London by Dieffenbach, the ones listed by Gray (1843, p. 252). These articulated specimens, BM(NH) 1842.5.17.167–168, are clearly the species under discussion; the larger is illustrated here (Fig. 5 and 6).

Mesodesma gaymardi Deshayes, 1832. Iredale (1915, p. 491) initially used the name *Amphidesma gaymardi* Deshayes (1832, p. 444) for the species here called *Paphies subtriangulata* (Wood). He had not noticed Wood's (1828) usage of the name *Mactra subtriangulata*, but in a footnote (Iredale 1915, p. 491) he pointed out Lamy's (1912, p. 249) recording of Wood's name, and so re-introduced the name *Amphidesma subtriangulatum* (Wood) for the species. However, Iredale was incorrect to use *Mesodesma gaymardi* for this species in the first place. Lamy (1914, p. 34) included the name *Mesodesma gaymardi* (with query) in the synonymy of *Mesodesma glabrellum* (Lamarck, 1818) (= *Paphies* (*Atactodea*) *cuneata* (Lamarck, 1818). As first revisers, we here select *Crassatella cuneata*

Fig. 3–10 *(opposite page) Paphies* (*Paphies*) *subtriangulata* (Wood). **3, 4,** almost certain holotype of *Mactra subtriangulata* Wood, 1828, BM(NH) 19821, lacking locality (×1.5); a right valve, exterior and interior. **5, 6,** specimen identified as *Mesodesma subtriangulatum* by Gray (1853, p. 252), BM(NH) 1842.5.17.167, "West coast, North Island, New Zealand", collected by Dieffenbach (natural size); left valve (of 2), exterior and interior. **7–10,** figured syntype (here designated lectotype) of *Mesodesma spissum* Reeve, 1854, BM(NH) 198121, "New Zealand", H. Cuming Collection (natural size):(7, 9) left valve, exterior and interior; (8) posterior end of articulated shell, showing 2 weak ridges on posterior area; (10) right valve, exterior.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Lamarck (1818, p. 483) as the name to be used for the species named both *Crassatella cuneata* and *Amphidesma glabrellum* (p. 493) by Lamarck (1818), by all who consider these names to be synonyms. The holotype of *Mesodesma gaymardi* Deshayes, in the Muséum National d'Histoire Naturelle, Paris, has been examined by L.R-S., and proves to be a relatively small specimen of *Paphies* (*Atactodea*) *cuneata* (Lamarck) similar to the form named *Amphidesma glabrellum* by Lamarck (1818). Deshayes' incorrect locality "Nouvelle Zélande" presumably led Iredale (1915) to his wrong identification.

Mesodesma spissum Reeve, 1854. Even Reeve's (1854, pl. 3 fig. 18) name *Mesodesma spissum* is under a slight cloud—although the figured shell is clearly the present New Zealand species of tuatua, no specimen in the British Museum (Natural History) bears a label by Reeve or any later curator identifying it as Reeve's figured specimen. The shell we conclude to be the figured syntype of *Mesodesma spissum* (Fig. 7–10) bears the label "Mus. Cuming, acc. no. 1829, New Zealand", but is also labelled "*M. cuneata* Desh." in Deshayes' handwriting, as are all specimens of *P. subtriangulata* of early origin in the British Museum (Natural History). The specimen agrees closely in size (63.4 × 42.8 mm; Reeve's fig. 18 is 64.5 × 41.9 mm), shape, weak posterior biangulation, and disposition of the low, very faintly coloured growth ridges with the figure published by Reeve (1854, pl. 3 fig. 18), and as it agrees with this figure very much more closely than does any other specimen in the collection, there is little doubt that it is Reeve's figured syntype. This specimen, British Museum (Natural History) reg. no. 198121, is here designated the lectotype of *Mesodesma spissum* Reeve, 1854. It is the largest of 4 syntypes (2 paired specimens and 2 unmatched valves) of *Mesodesma spissum.*

Paphies cuneata (Lamarck). Deshayes' label "*M. cuneata* Desh." on British Museum (Natural History) specimens of *Paphies subtriangulata* is at first sight surprising. The name was first published as *Crassatella cuneata* by Lamarck (1818, p. 483). Lamarck's holotype (Muséum National d'Histoire Naturelle, Paris) was figured by Lamy (1912, p. 249; 1914, pl. 1 fig. 1 and 2), and was examined in Paris by L.R-S. and loaned to A.G.B. by Dr P. Bouchet. It still bears the original hand-written label by the collector, Péron, with the locality "île aux Kangaroos" (Kangaroo Island, South Australia). Although it is relatively large and heavy-shelled (28.8 × 19.6 mm, thickness of 2 valves 13.0 mm), there is no reason to doubt that it is an authentic southern Australian specimen of the species usually known as either *Paphies cuneata* (Lamarck) or *P. glabrella* (Lamarck). This was also the opinion of Lamy (1912, p. 250; 1914, p. 32). Application of the name *Paphies cuneata* to British Museum (Natural History) specimens of the present tuatua species presumably commenced from Gray's (1825, p. 134) citing the earlier name *Crassatella cuneata* in the synonymy of *Erycina subangulata*, and would have been reinforced by its use by Hanley (1842, p. 38) as the valid name for the present species. The original labels must date from an early period in Deshayes' work on *Mesodesma*, before most of Deshayes' species names and Reeve's (1854) monograph were published.

Dimensions of type specimens. *Mactra subtriangulata* Wood, 1828: holotype – length 53.8 mm, height 35.4 mm, inflation (1 valve) 8.8 mm. *Mesodesma spissum* Reeve, 1854: lectotype – length 63.4 mm, height 42.8 mm.

Location of type specimens. *Mactra subtriangulata* Wood, 1828: holotype in British Museum (Natural History), London, reg. no. BM(NH) 19821, without locality. *Mesodesma spissum* Reeve, 1854: lectotype in British Museum (Natural History), London, ref. no. BM(NH) 198121, with 3 paralectotypes (2 odd valves and 1 articulated shell), labelled "New Zealand", from the collection of Hugh Cuming. *Mesodesma reentsii* Römer, 1862: status and location of type material not known to us.

Paphies (*Paphies*) *donacina* (Spengler, 1793)

(Fig. 1 and 11–21)

Mya donacina Spengler, 1793: 40; Mörch, 1870: 106; Lamy, 1914: 23 (footnote).
Mesodesma quoyi Deshayes, 1832: 443; Deshayes, 1839: 314, "Explication des planches" p. 7, pl. 10 fig. 13 and 14; Catlow & Reeve, 1845: 16; Reeve, 1860: 140; Lamy, 1912: 247.
Mesodesma lata Deshayes, 1843: pl. 80; Hutton, 1873: 68; Hutton, 1878: 48; Hutton, 1880a: 146.
Taria stokesii Gray, 1853: 44.
Mesodesma lata "Deshayes MS" Reeve, 1854: pl. 1 fig. 4.
Paphia (*Taria*) *lata*; H. & A. Adams, 1858: 413; Chenu, 1862: 78, fig. 338; Tryon, 1868: 124; Paetel, 1873: 135; Paetel, 1890: 65.
Mesodesma elongata Hutton, 1873: 68. Not *M. elongatum* Reeve, 1854.
Taria lata; Tryon, 1884: 162, pl. 110 fig. 28.
Pahia lata; Schaufuss, 1869: 104; Grasset, 1884: 250.
Mesodesma (*Taria*) *latum*; Fischer, 1887: 1113; Lamy, 1912: 247.
Mesodesma (*Donacilla*) *subtriangulatum*; Suter, 1913: 957 (in part).
Mesodesma (*Taria*) *quoyi*; Lamy, 1914: 21, fig. 1 on p. 24; Thiele, 1935: 898.
Amphidesma (*Taria*) *quoyi*; Iredale, 1915: 492.
Amphidesma subtriangulata pliocenica Oliver, 1923a: 187, unnumbered fig.; ?Finlay, 1924: 510.
Amphidesma forsteriana Finlay, 1927: 468.
?*Taria forsteriana*; Finlay, 1928: 280 (Chatham Islands).
Amphidesma (*Taria*) *latum*; Marwick, 1928: 468.
Amphidesma (*Taria*) *forsteriana*; Powell, 1937: 60; Fleming, 1950: 24.

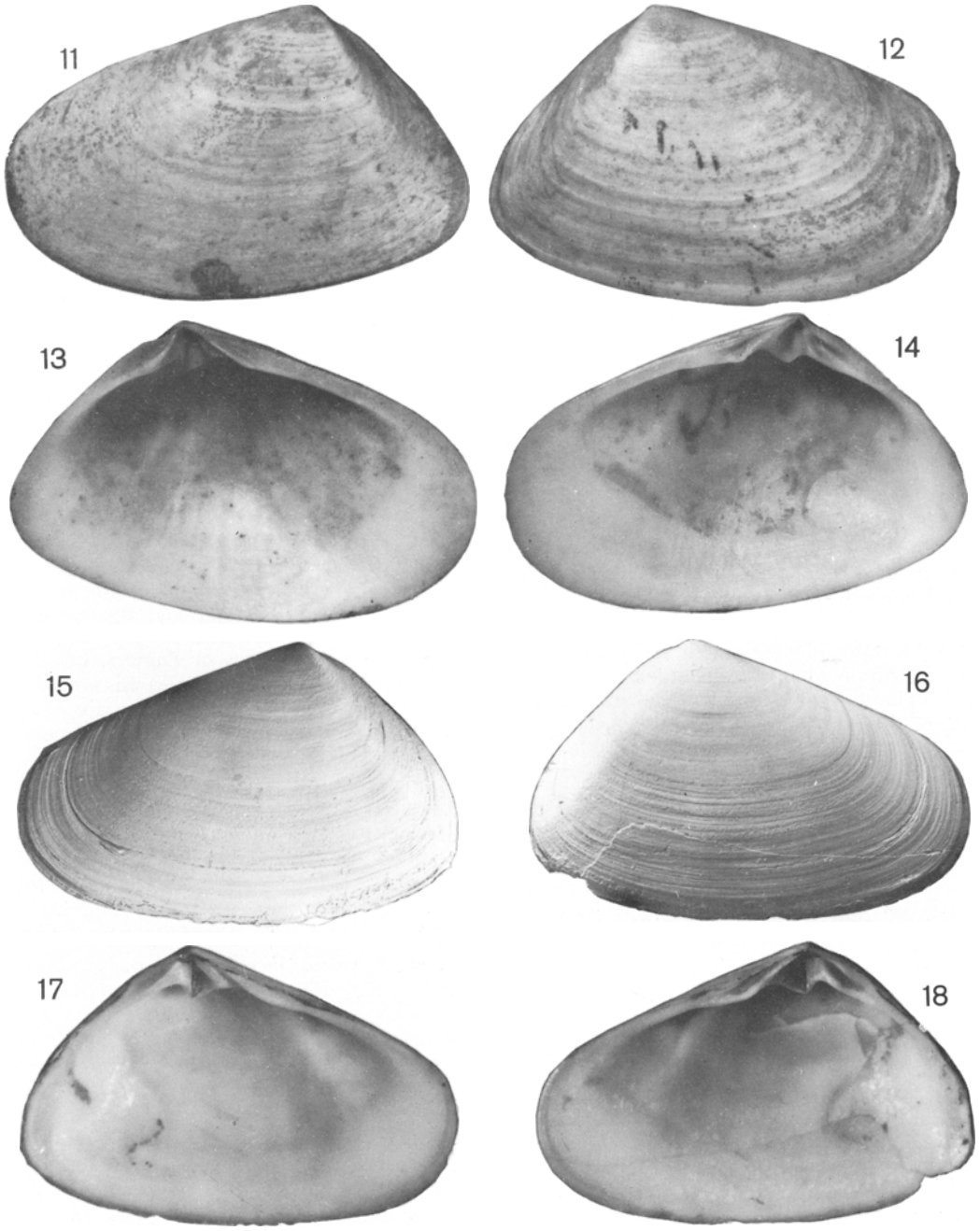

Fig. 11–18 *Paphies* (*Paphies*) *donacina* (Spengler). **11–14,** holotype of *Mya donacina* Spengler, 1793, Zoological Museum, University of Copenhagen, "South Seas" (×1.5): (11, 13) left valve, exterior and interior; (12, 14) right valve, exterior and interior. **15–18,** largest syntype of *Mesodesma quoyi* Deshayes, Deshayes Collection, Muséum National d'Histoire Naturelle, Paris, "Nouvelle Zélande" (×1.5): (15, 17) left valve, exterior and interior; (16, 18) right valve, exterior and interior.

Amphidesma (*Taria*) *forsterianum*; Powell, 1947: 61; Powell, 1957: 83; Powell, 1962: 124; Fleming, 1966: 32.
Amphidesma pliocenicum; Te Punga, 1952a: 157; Te Punga, 1952b: 21, 22, and 24; Fleming, 1953: 234, 235, 242, and 260.
Amphidesma (*Taria*) aff. *pliocenicum*; Fleming, 1953: 112, 139, 150, 158, 163, and 173.
Amphidesma aff. *pliocenicum*; Fleming, 1953: 146.
Amphidesma cf. *pliocenicum*; Fleming, 1953: 214.
Amphidesma (*Taria*) *pliocenicum*; Fleming, 1953: 217, 238, 244, and 272, pl. 31 fig. 2; Scott *in* Kingma, 1971: table 10A.
Amphidesma (*Taria*) cf. *pliocenicum*; Fleming & Suggate, 1964: 355.
Amphidesma forsterianum; Cassie, 1955: 348; Dawson, 1959: 45–54, pl. 4; Penniket & Moon, 1970: 102, pl. 48 fig. 2; Norris, 1972: 581 and 586 (as *fosterianum*, p. 581).
Amphidesma subtriangulatum pliocenicum; Dawson, 1959: 53.
Donacilla subtriangulatum pliocenicum; Knox, 1963: 19.
Donacilla forsterianum; Harvey, 1965: 140.
Paphies (*Mesodesma*) *subtriangulata quoyi*; Beu, 1971: 119, fig. 7; Powell, 1976: 129; Powell, 1979: 416, pl. 75 fig. 14.
Paphies pliocenica; Grant-Taylor & Beu, 1974: 495–498.

All discussion under this heading refers to the more predominantly southern species of tuatua, usually known in New Zealand as '*Amphidesma*' *forsterianum* Finlay, differing from *Paphies subtriangulata* in its relatively long posterior end and lacking the central, weak, biangling rib of the posterior end of *P. subtriangulata* (distinguished more fully below). The history and status of the various synonyms are considered below, in chronological order.

Mya donacina Spengler. Lamy (1914, p. 23, footnote 2) pointed out this earliest name for a species of tuatua. He noted that Mörch (1870, p. 106) equated *Mya donacina* Spengler (1793, p. 40) with "*Mesodesma subtriangulata* Gray". Almost all of Spengler's type specimens remain in the Zoologisk Museum in Copenhagen, and presumably these were the basis of Mörch's (1870) review of Spengler's shells. At the time of writing the holotype of *Mya donacina* Spengler, 1793 (Fig. 11–14) is on loan to L.R-S., and we have both examined the specimen. Dr J. Knudsen (Zoologisk Museum, Copenhagen) kindly provided the following translation of Spengler's (1793, p. 40) description.

"No. 15. *Mya donacina*. Testa crassuscula laevi, margine antice obtussino, postico compresso, dentibus accessoriis binis marginalibus.

"If one did not completely rely on the accepted infallible characters of the hinge, one would undoubtedly refer it to a *Donax*, since it has all the outer characters of this genus. *Donax cuneata* Linn, which comes in abundant numbers from Tranquebar, is so similar to this South-Sea *Mya*, as if they came from the same mould. In outline this unusual *Mya* is triangular. From the umbo, which is placed far from the centre and near the anterior end, the back commences in a straight line, ending posteriorly in a rounding which unites with the lower opposite margin of the back. The anterior part of the shell forms a straight line towards the umbo, in the truncate or cut off part, which is the feature making the genus *Donax* so easily recognisable from the others. Inside, the excavated tooth is placed from the tip of the umbo, very impressed inside; it is however small and not enclosed by any margin anteriorly. In one shell lies, obliquely on each side, a long tooth, of which the anterior is the stronger, and these are encased by adjusted depressions in the other shell so that the two shells are firmly joined by means of this lock. The big muscle scars, which can be seen close to the upper margin towards both ends, show the attachment of the animal to the valves. The shell is smooth and narrowly compressed outside, it is thickest at the umbo, and runs wedge-shaped to the posterior end. Inside it looks like dull mother-of-pearl, rainbow-coloured, outside it is reddish yellow, and below, at the extreme border, it is encased by a greenish band on the one shell. Its length is $1\frac{3}{4}$ ins, its breadth 1 in. 1 lin. [1 line = $\frac{1}{12}$ inch]. It comes from the South Sea."

Assuming that Spengler had the anterior and posterior reversed, we would take this to be a description of a species of *Paphies*, but it is not possible to be sure which species was intended. The only other mention of this name we are aware of is by Deshayes (1839, p. 315), who included "*Mya donacina*? Spengler [ref.]" in the synonymy of the small Mediterranean species *Donacilla cornea* (Poli).

Spengler's holotype (Fig. 11–14) is clearly identified by Spengler's original label, "*Mya donacina*... No. 15", and a later label (by Mörch?) declaring it the "Orig. [of] Sp[engler] N.S.S.3,1.p.40.no15". There can be no doubt that this small, broad, little-inflated, paired specimen is the species long known in New Zealand as '*Amphidesma*' *forsterianum* Finlay; its relatively elongate, smooth posterior end, of convex outline, lacking a central weak biangling rib, is obvious. Therefore, the earliest name for this species is clearly established as *Mya donacina* Spengler, 1793. Spengler's name may not have been used by subsequent authors because of doubts about its availability, but we can see no reason why it should not be used.

The one unfortunate aspect of the name *Paphies* (*Paphies*) *donacina* (Spengler) is its close, potentially confusing, similarity to the name *Paphies* (*Mesodesma*) *donacia* (Lamarck, 1818), the well known South American type species of *Mesodesma*. Under *ICZN* Article 56(a) these names are not homonyms.

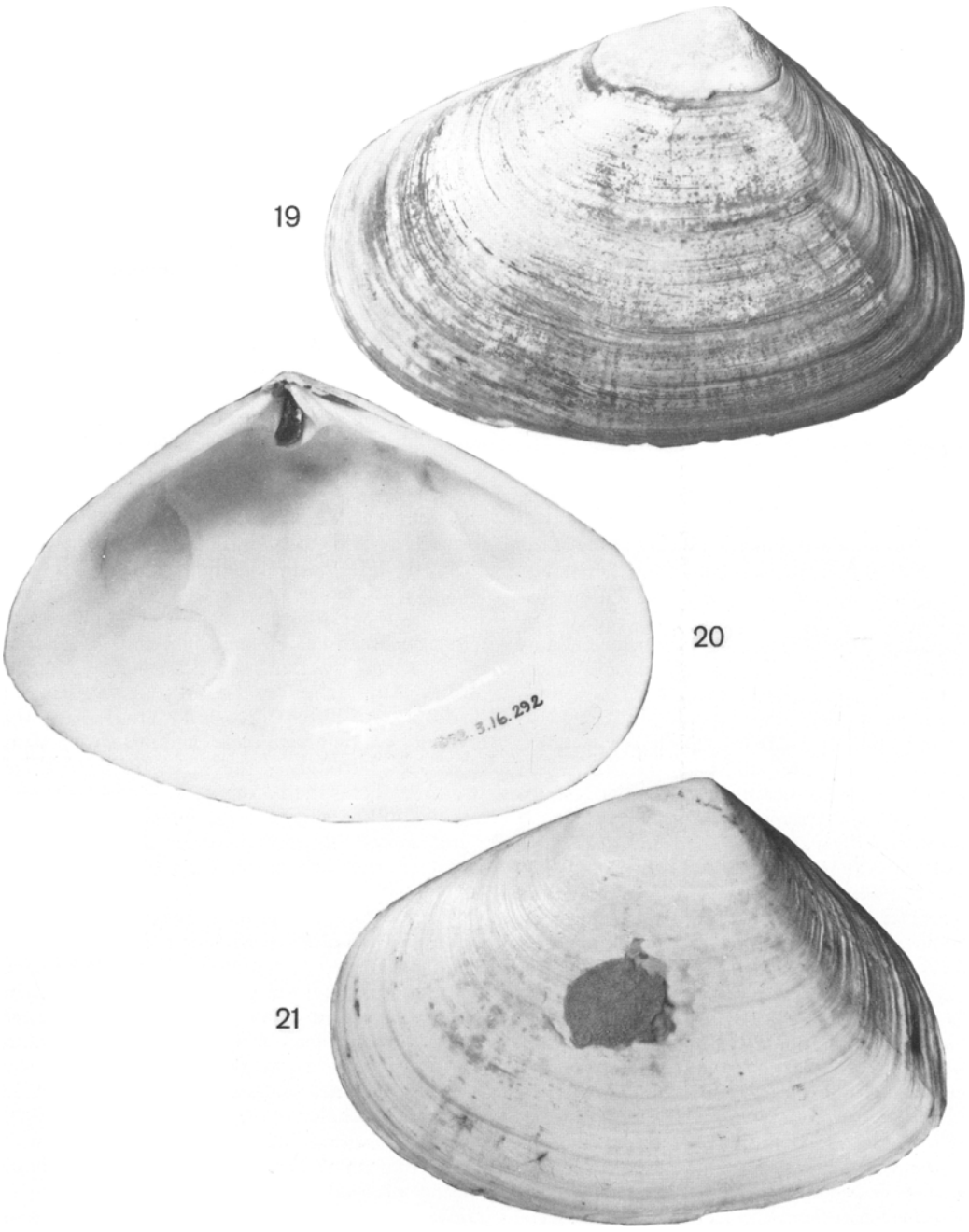

Fig. 19–21 *Paphies* (*Paphies*) *donacina* (Spengler). **19, 20,** neotype (here designated) of *Taria stokesii* Gray, 1853, BM(NH) 1852.3.16.292, "New Zealand", collected by Capt. J. L. Stokes, R.N. (natural size); left valve (of 2), exterior and interior. **21,** the other specimen formerly attached to same tablet as neotype of *Taria stokesii*, BM(NH) 1852.3.16.110, "New Zealand", collected by Lieut. Col. Bolton, R.E. (natural size); left valve (of 2), exterior.

A brief biography of Spengler was published recently by Hansen (1981), and useful background information on the history of Spengler's and other early collections in the Zoologisk Museum, Copenhagen, is given by Cernohorsky (1974, p. 143–147).

Mesodesma quoyi Deshayes, 1832. The 4 syntypes of *Mesodesma quoyi* Deshayes, 1832 (Fig. 15–18, examined in Paris by L.R-S. and kindly loaned to Dr J. R. Richardson and A.G.B. by Dr P. Bouchet, Paris, are immature specimens of the species usually identified in New Zealand as *'Amphidesma' forsterianum* Finlay. Deshayes (1839, p. 314, "Explication des planches" p. 7, pl. 10 fig. 13 and 14) illustrated the species shortly after he named it, in 2 slightly stylised water-colours that appear to have been based on the largest syntype, also figured here (Fig. 15–18). Lamy (1914, p. 24, fig. 1) also gave an outline drawing of *M. quoyi* that appears to have been based on the largest syntype.

Mesodesma latum Deshayes, 1843. The holotype of *Mesodesma latum* Deshayes, 1843 (held in 1979 by l'Université de Paris Sud at Orsay, but now in the Muséum National d'Histoire Naturelle, Paris) was examined by A.G.B. at Orsay during 1979, and has also been examined by L.R-S. As was suggested by Lamy (1912, p. 245–247) and later confirmed (Lamy 1914, p. 21, footnote), this was based on a larger specimen of the species Deshayes (1832) named *M. quoyi*. Reeve (1854, caption to pl. 1 fig. 4) apparently thought that Deshayes' name *Mesodesma latum* was unpublished, and that he was establishing a new species using Deshayes' manuscript name. The 3 syntypes of *M. latum* Reeve (*ex* "Deshayes MS.") were examined in the British Museum (Natural History) by A.G.B. during 1979 and again in 1980, and had been examined earlier by L.R-S. We confirm that all these specimens are conspecific with the holotype of *Mya donacina* (Spengler).

Taria stokesii Gray, 1853. Iredale (1915, p. 490) stated without explanation that he and E. A. Smith were able to identify a "somewhat abnormal" specimen of the toheroa, *Paphies ventricosa* (Gray), as the holotype of *Taria stokesii*. It seems possible that the specimen so identified was the holotype of *Mesodesma ventricosum* Gray (1843, p. 252) (Fig. 22–24). We deduce this not only from Iredale's statement but also from the fact that the holotype was figured under the name *Taria ventricosa* by Smith (1874, p. 5, pl. 3 fig. 6), although Smith neglected to state that the figured shell is the holotype of *Mesodesma ventricosum* Gray. However, there are no labels at present associated either with the holotype of *Mesodesma ventricosum* Gray or with any other specimens of this species in the collection of the British Museum (Natural History) that identify them with either of the names *Taria* or *stokesii*. The holotype of *Mesodesma ventricosum* is registered as BM(NH) 1842.5.17.169, was collected by Dieffenbach, and bears the locality label "North shore, Cook's Straits, New Zealand", i.e., the Paraparaumu–Waikanae area of Wellington's west coast.

During separate visits to the British Museum (Natural History) Mollusca Section over several years we both tried to locate a holotype or syntypes for *Taria stokesii* Gray, with only equivocal results. Early in 1982, however, Mrs Solene Morris rediscovered what appears to have been Gray's type specimen. A large specimen of what is here called *Paphies donacina* (Spengler), bearing the number BM(NH) 1852.3.16.292 (Fig. 19 and 20), is one of 2 removed from a cardboard tablet. This specimen, recognised by its glue patches as the upper one when mounted, is identified on the tablet as "292 (Stokes – upper specimen)" and in the accessions register as a specimen collected in New Zealand by Captain John Lort Stokes, R.N. The other specimen formerly glued to the same tablet is BM(NH) 1852.3.16.110, a similar large specimen of *Paphies donacina* (Spengler) collected in New Zealand by Lieut. Colonel Bolton, R.E. (Fig. 21). There are no other specimens of *P. donacina*, *P. subtriangulata*, or *P. ventricosa* that were collected by Captain Stokes. Although Gray did not state that he named *Taria stokesii* after Capt. J. L. Stokes, any other etymology is highly unlikely, and this circumstantial evidence strongly suggests that BM(NH) 1852.3.16.292 is the holotype—or at least a syntype, if some other syntypes have since been lost—of *Taria stokesii* Gray. However, there are no old labels in the British Museum (Natural History) collection that identify this or any other specimen in any way with either of the names *Taria* or *stokesii*, and no early figures with which the specimen can be compared. There is therefore no way to be certain that this specimen was among Gray's type material. To stabilise the name *Taria stokesii*, we here designate the specimen BM(NH) 1852.3.16.292 as the neotype of *Taria stokesii* Gray, 1853, which thereby becomes a junior synonym of *Paphies donacina* Spengler, 1793.

The first authors after Gray to use *Taria* were H. & A. Adams (1857, p. 413), who included only the 2 species of 'tuatua' in *Paphia* (*Taria*)—*P.* (*Taria*) *quoyi* (Deshayes), = *P. donacina* (Spengler), and *P.* (*Taria*) *spissa* (Reeve), = *P. subtriangulata* (Wood). Presumably, then, the many subsequent authors who regarded one or the other species of tuatua as type-species of *Taria* were following H. & A. Adams; e.g., Fischer (1887, p. 1113), Dall (1898, p. 912), Lamy (1914, p. 21), and Keen *in* Moore

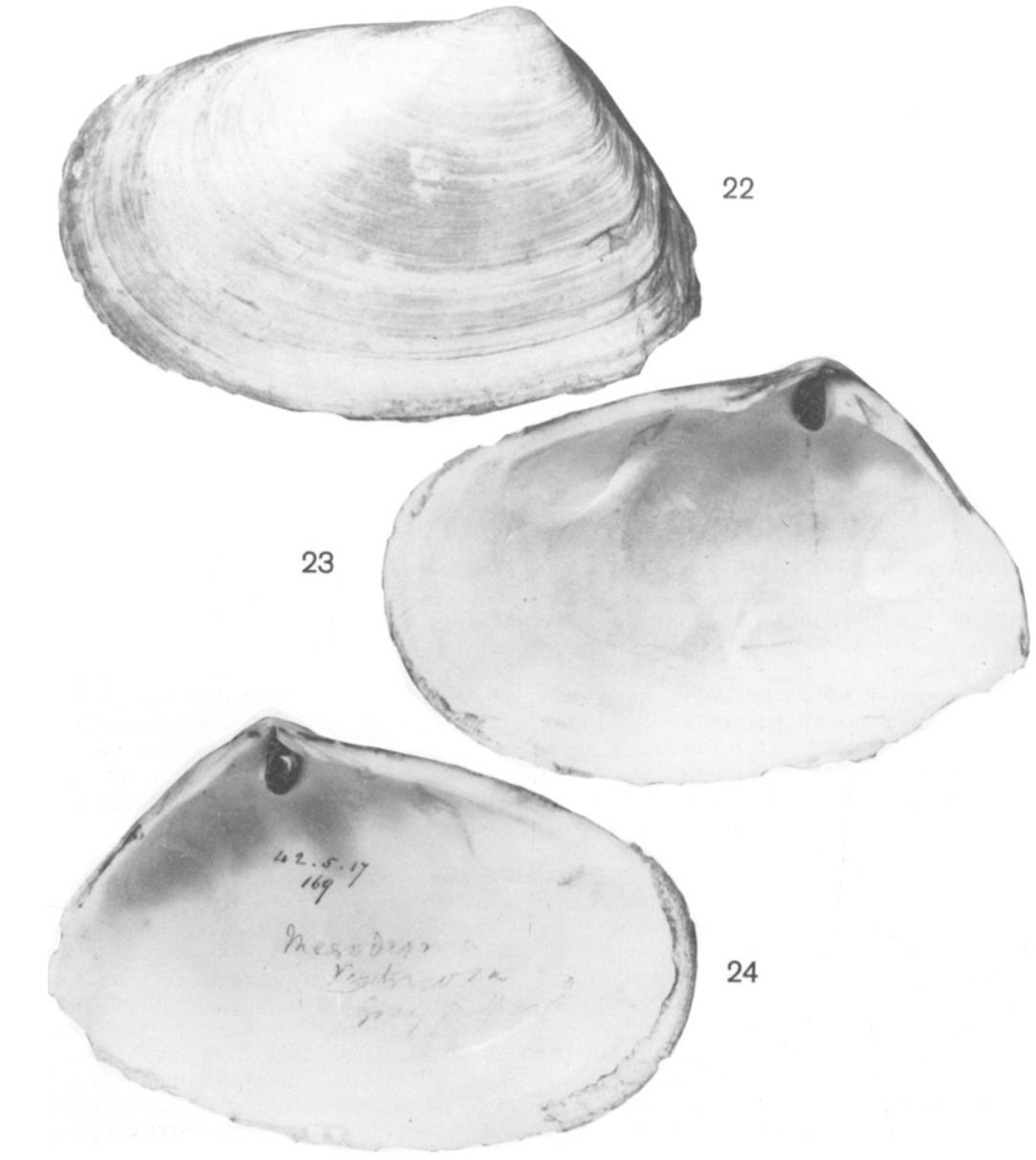

Fig. 22–24 *Paphies* (*Paphies*) *ventricosa* (Gray). Holotype of *Mesodesma ventricosum* Gray, 1843, BM(NH) 1842.5.17.169, "North shore, Cook's Strait, New Zealand", collected by Dieffenbach (natural size). **22, 24,** left valve, exterior and interior (pencil writing inside appears to be in hand of T. Iredale). **23,** right valve, interior.

(1969, p. N610). However, Suter (1913, p. 958) presumably made an inference from Smith's (1874) usage of *Taria* when he regarded "*Mesodesma ventricosum*, Gray" as the type-species of *Taria*.

Neotype description. Shell large for the species, thick and solid. Anterior end long, with straight dorsal and weakly convex ventral margins; anterior margin regularly convex in outline. Posterior end long for the species, straight in outline over the dorsal half of its height and strongly convex in outline over the ventral half of its height, smooth apart from weak comarginal growth ridges, passing imperceptibly into anterolateral area of valves.

Hinge typical of *Paphies* (*Paphies*), relatively thin and lightly built for the large size of the specimen, with a deep, narrow resilifer in the centre and a short ligament behind the resilifer on the valve margin; lateral teeth large and prominent, short, smooth, with correspondingly large sockets; cardinal teeth consisting of very thin, high lamellae (broken in the neotype, as in almost all adult specimens of *Paphies subtriangulata* and *P. donacina*). Adductor muscle scars deeply impressed, the anterior one with weakly defined 'quick' and 'catch' areas of which the upper is the larger, separated by a very faint, diagonal straight line crossing the scar from the point of incidence of the pallial line. Pallial sinus deeply impressed, extending only a few mm in front of anterior margin of posterior adductor scar, weakly subquadrate in outline; dorsal anterior angle slightly more rounded than ventral anterior angle. Remainder of pallial line regularly curved. Exterior almost smooth, sculptured with weak periostracal wrinkles and faint, irregular, comarginal growth ridges, and with a prominent growth-check ridge (presumably caused by injury to the mantle edge or the shell edge) at a distance of 17.5 mm (right valve; 18.0 mm on left valve) from the umbo.

Exterior greyish cream where free of periostracum, but most of surface (all but umbonal area and upper part of posterior area) bearing a thin, straw-yellow to bright yellow periostracum, stained bright brownish orange near the anterior end, on the interiormost edge of the posterior area, and parallel to some comarginal growth ridges, notably in 3 narrow, equally spaced, comarginal bands (the uppermost immediately below the obvious growth check) that appear to correspond to annual growth rings; interior cream, slightly darker in the adductor scars.

Dimensions and location stated below (Type Data).

Comparison with closely related taxa. The neotype of *Taria stokesii* Gray, 1853 is a specimen of *Paphies* (*Paphies*) *donacina* (Spengler, 1793). Shells of *P. donacina* can be distinguished from those of the very similar *Paphies* (*Paphies*) *subtriangulata* (Wood, 1828) by their longer, smoother posterior area at a lower angle to the rest of the shell and blending imperceptibly into it (shorter, with more obvious angulation between posterior and lateral areas, and weakly biangled by 2 radial ridges, in *P. subtriangulata*); by the straight to weakly or, in most specimens, quite strongly convex outline of the posterior end (shallowly concave over the upper half of the posterior slope, and strongly convex over the lower half of the posterior slope, in *P. subtriangulata*); by their thinner hinge; by the resilium projecting further below the hinge line; by their more shallowly impressed adductor scars; and by their more rounded pallial sinus (the ventral anterior angle of the pallial sinus is more nearly square than the dorsal, obtuse one in most specimens of *P. donacina*, whereas the 2 angles are about equally marked in most specimens of *P. subtriangulata*). Further differences in anatomy and protein composition and a statistical treatment of shell shape differences are given by Richardson et al. (1982). The 2 species live sympatrically in some North Island beaches alongside the commercially valuable toheroa, *Paphies* (*Paphies*) *ventricosa* (Gray), which differs from them both in reaching a much larger size, in having a much deeper pallial sinus, in having a much more strongly biangled posterior end, and in having a taller anterior end with more nearly parallel dorsal and ventral margins.

Dimensions of type specimens. *Mya donacina* Spengler, 1793: holotype (Fig. 11–14) – length 42.7 mm, height 27.2 mm, thickness (2 valves) 14.1 mm. *Mesodesma quoyi* Deshayes, 1832: largest syntype (Fig. 15–18) – length 41.3 mm, height 26.3 mm. *Mesodesma latum* Deshayes, 1843: holotype – length 61.4 mm, height 42.8 mm. *Mesodesma latum* Reeve, 1854: 3 syntypes – length 85.8 mm, height 57.3 mm, thickness (2 valves) 27.4 mm; length 97.0 mm, height 65.8 mm, thickness (2 valves) 29.0 mm; length 104.2 mm, height 75.0 mm, thickness (2 valves) 28.7 mm. *Taria stokesii* Gray, 1853: neotype (Fig. 19 and 20) – length 90.3 mm, height 62.1 mm, thickness (2 valves) 28.3 mm.

Location of type specimens. *Mya donacina* Spengler, 1793: holotype (2 separate, matching valves) in University Zoologisk Museum, Copenhagen; currently on loan to L.R-S. *Mesodesma quoyi* Deshayes, 1832: syntypes (4 paired shells, formerly glued to white card) in Muséum National d'Histoire Naturelle, Paris, labelled "Nelle. Zélande". *Mesodesma latum* Deshayes, 1843: holotype (2 matching but separated valves formerly glued to red card) in Muséum National d'Histoire Naturelle, Paris. *Mesodesma latum* Reeve, 1854: syntypes (3 paired shells) in British Museum (Natural History), London, registered number BM(NH) 1968506, labelled "New Zealand", from the collection of Hugh Cuming. *Taria stokesii* Gray, 1853: neotype (designated herein) in British Museum (Natural History), London, registered number BM(NH) 1852.3.16.292, labelled "New Zealand", collected by Capt. J. L. Stokes, R.N. *Amphidesma forsterianum* Finlay, 1927: holotype in Auckland Institute and Museum (Powell 1941, p. 242).

As was noted by Keyes (1971, p. 70), the holotype of *Amphidesma subtriangulatum pliocenicum* Oliver is not in New Zealand's National (formerly

Dominion) Museum, where it was stated to be by Oliver (1923a, p. 187), and apparently it is lost. However, a specimen in the National Museum is labelled "co-type", and is also labelled on the interior in Oliver's handwriting "Castlecliff, blue mud, WRBO, 26 Jan. 1909", as is the interior of the holotype in the figure given by Oliver (1923a, p. 187). This remaining specimen (M12047) is therefore a paratype or, as it is a valve opposite from the holotype and matches Oliver's figure closely, possibly one valve of the holotype. Certainly there is no doubt as to which species Oliver's name applies to. Judged from its large size and good preservation, the "co-type" probably was collected from the shellbed at the base of the Shakespeare Cliff Sandstone in the cliff section west of Castlecliff, Wanganui, where large shells of *Paphies donacina* are common.

DISTRIBUTION

The following summary of the distribution of the 2 species of tuatua is compiled from examination of the collection of the National Museum, and from information supplied by Mr E. K. Saul (Science Information Division, DSIR), who has recently studied tuatua ecology and distribution.

Paphies subtriangulata occurs all round the North Island, and is particularly common in the far north and along the east coast to East Cape, where *P. donacina* is absent. Along much of the western North Island, at least as far north as Dargaville beaches, and again along the southern and south-eastern coasts as far north as East Cape, it is sympatric with *P. donacina*. There appear to be very few records of *P. subtriangulata* from the South Island; specimens in the National Museum from Farewell Spit, Collingwood, Nelson, and the Marlborough Sounds are small *P. donacina*. However, on 6 April 1982 B. A. Marshall (National Museum) and G., C., C., and J. Hindmarsh collected many specimens of both *P. subtriangulata* and *P. donacina* on Parapara Beach, Collingwood. The two species are evidently sympatric along the shores of Cook Strait.

Paphies donacina occurs around the North Island except for the northernmost west coast (probably absent from Ninety Mile Beach only) and the east coast north of East Cape. Except on the north coast it is the only species of tuatua around the South Island, and on Stewart Island it occurs along the north coast and at Mason Bay. Four large, elongate, but brown-stained and bored specimens in the National Museum (M21687) from 60 m in Colville Channel, north of Coromandel Peninsula (r.v. *Ikatere*, 14 September 1965, coll. W. F. Ponder), are presumably young fossils, demonstrating that *P. donacina* migrated northwards to occupy the north-eastern North Island during a late Pleistocene glacial phase.

Populations living at the Chatham Islands and many Pleistocene fossil populations at Wanganui and in Hawke's Bay require more investigation before they can be understood taxonomically.

PROPOSED CLASSIFICATION OF *PAPHIES*

Genus *Paphies* Lesson, 1831

Subgenus *Paphies* sensu stricto (= *Machaena* Gray *ex* Leach MS., 1843; = *Taria* Gray, 1853)

Paphies (*Paphies*) *anteaustralis* (Dell, 1950); Lower Miocene, N.Z.
australis (Gmelin, 1791); Pliocene to Recent, N.Z.
crassiformis (Marshall & Murdoch, 1920); early Pleistocene, N.Z.
donacina (Spengler, 1793); Pleistocene and Recent, N.Z.
porrecta (Marwick, 1928); early Pleistocene (and living?), Chatham Islands
subtriangulata (Wood, 1828); Lower Miocene(?), early Pliocene to Recent, N.Z.
ventricosa (Gray, 1843); Pleistocene and Recent, N.Z.

Subgenus *Mesodesma* Deshayes, 1832 (= *Ceronia* Gray, 1853)

American species only

Subgenus *Amesodesma* Iredale, 1930

Paphies (*Amesodesma*) *altenai* (De Rooij-Schuiling, 1972), Indonesia
angula (Reeve, 1854), Philippine Islands
elongata (Reeve, 1854), south-eastern Australia

Subgenus *Atactodea* Dall, 1895

Paphies (*Atactodea*) *cuneata* (Lamarck, 1818), south-eastern Australia
erycinaea (Lamarck, 1818), south-eastern Australia
striata (Gmelin, 1791), Indo-West Pacific

Subgenus *Regterenia* De Rooij-Schuiling, 1972

Paphies (*Regterenia*) *africana* (Turton, 1932), South Africa

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