

The World's Largest Lucinid is an Undescribed Species from Taiwan (Mollusca: Bivalvia)

Philippe Bouchet* and Rudo von Cosel

Department of Systematics and Evolution, National Museum of Natural History, 55, rue Buffon, F-75005 Paris, France

(Accepted September 1, 2004)

Philippe Bouchet and Rudo von Cosel (2004) The world's largest lucinid is an undescribed species from Taiwan (Mollusca: Bivalvia). *Zoological Studies* **43**(4): 704-711. *Meganodontia acetabulum* is described as a new genus and species of the Lucinidae, based on valves trawled at 256~472 m depths on the Tashi fishing ground off the northeastern coast of Taiwan. The new genus is close to *Anodontia* but differs mainly in the small umbones, the perfectly circular outline, the hinge and ligament, and the large muscle impressions. It is the largest known Recent species of Lucinidae. Other species of bivalves, belonging to families symbiotically associated with chemautotrophic bacteria, have been taken at the same or nearby stations, suggesting that the Tashi fishing ground is a site where chemosymbiosis plays an important role in biomass production and ecosystem function. http://www.sinica.edu.tw/zool/zoolstud/43.4/704.pdf

Key words: Chemosymbiosis, Giant Lucinidae, Taiwan, Taxonomy.

he Tashi fishing ground on the northeastern coast of Taiwan near Kueishan Island (Turtle Mountain I.) is a busy fishing area, where numerous commercial trawlers based in the fishing port of Tashi catch shrimp and fish at depths down to about 600 m. In May 2001, the trawler Jin Tung Long No. 26 was used by a party of Taiwanese and French zoologists for the purpose of inventorying the still little-known, benthic, deep-sea fauna of Taiwan. Fifty-four hauls (stations CC63~CP116) were made between 66 and 800 m, mainly with a specially adapted beam-trawl. Four of them yielded material of a lucinid bivalve of an exceptionally large size, slightly in excess of 150 mm. Although this was, by far, the largest bivalve taken during that survey, and one of the largest bivalves of Taiwan, it unexpectedly represents a new genus and species, described herein as Meganodontia acetabulum gen. and sp. nov.

The Tashi fishing ground is trawled daily by several dozen fishing boats, and recently, quite a few new species of benthic gastropods and bivalves have been described based on materials collected as a by-product of their commercial operations (Lee and Wu 1998a b, Okutani and Lan 1999, Lan 2000 2001, Lan and Lee 2001 2002, Lee 2001, Lee and Lan 2002a b). It is thus unexpected that such a large species as *Meganodontia acetabulum* had remained undetected. However, many lucinid species burrow deeply in the sediment and are not successfully collected by commercial gear used for fish and decapod crustaceans. The Tashi fishing boats use otter trawls that do not normally dig into the bottom, whereas the new lucinid was taken by our beam trawl specially modified for collecting infaunal invertebrates.

Characteristics of the site

Most of the Tashi fishing ground consists of a gently sloping bottom of fine sediments, with occasional deep coral outcrops that are normally avoided by the trawlers. Hot springs are known to exist in shallow waters of Kueishan Island (see Ng et al. 2000, on the description of the endemic vent crab *Xenograpsus testudinatus* Ng, Huang and Ho, 2000), and fishermen know of discrete sites in deeper water (to 200 m) where gas bubbles to the

^{*}To whom correspondence and reprint requests should be addressed. E-mail: pbouchet@mnhn.fr; cosel@mnhn.fr

surface. We trawled 1 such site and collected blocks of a sulfur compound covered with a species of Idas (Bivalvia: Mytilidae) as well as numerous specimens of X. testudinatus. We also wanted to record the scattered occurrence, on the Tashi fishing ground, of large tubes of consolidated mud, the geochemistry of which indicates diffuse gas seepage (J. Frýda, pers. comm.). Sulfide-oxidizing bacteria have been identified in all members of the Lucinidae that have been investigated (Taylor and Glover 2000), and we assume that M. acetabulum also lives in association with such bacteria. Several other bivalves collected during our survey belong to families equally known to host chemosymbiotic bacteria: Acharax sp. (Solemyidae), Calyptogena s.l. sp. (Vesicomyidae), Lucinoma sp. nov. (Lucinidae), Alucinoma soyoae Habe, 1958 (Lucinidae), Conchocele sp., and Thyasira sp. (both Thyasiridae). Taken together, these suggest that the Tashi fishing ground is a site where chemosymbiosis plays an important role in biomass production and ecosystem function. At 3 stations (CP 68, CP 109, and CP 110), Meganodontia was found together with Lucinoma sp. nov., the latter represented by empty but fresh shells with the periostracum and ligament.

The world's largest modern lucinid

Incomplete specimens of Meganodontia were taken when the trawl dug into the bottom and brought loose and consolidated mud to the surface, and the bivalves may have been buried no deeper than 15~20 cm into the bottom. Two entire single valves and several fragments were collected, some of them were still embedded in solidified mud, but they were not in the life position. The valves have no periostracum, but a thick and hardened ligament is still present; two of the shell fragments are pieces of conjoined valves. The shells are weathered and slightly stained, as is typical of shells which have been buried in anoxic sediment. Despite the condition of these specimens, we believe that this giant lucinid belongs to the modern fauna and is not a fossil; all the other molluscs present with it in the catch in fact belong to the Recent fauna, for example Hindsia magnifica (Lischke, 1871), H. solida Kuroda and Habe, 1961, Siphonalia spadicea (Reeve, 1846), Fulgoraria rupestris (Gmelin, 1791), Leiosyrinx matsukumai Bouchet and Sysoev, 2001, Acila divaricata (Hinds, 1843), Nucula dorsocrenata (Habe, 1977), Carinineilo carinifera (Habe, 1951), Bathymalletia inequilateralis (Habe, 1951), Testyleda yokoyamai (Habe, 1958), Yoldia similis Kuroda and Habe, 1958, Alucinoma soyoae Habe, 1958, Meiocardia samarangiae Bernard et al., 1993, Waisiuconcha surugensis Habe, 1976, and Cardiomya alcocki (E.A. Smith, 1884).

Meganodontia acetabulum ranks as the world's largest Recent species of Lucinidae, surpassing even Codakia distinguenda (Tryon, 1872), a shallow-water species from the Panamic-Pacific faunal province, which at 140 mm was hitherto considered the largest living representative of the family (Hertlein and Strong 1946: 117, Olsson 1961). Although there may be numerous examples to the contrary, the present discovery supports the view that "shells of deep-water taxa are often larger than those of shallow-water sister taxa" (Barnes and Hickman 2001). However, the Tashi lucinid is not the largest that ever existed; the largest lucinid species known was Lucina megameris Dall, 1901, from the late Eocene of Jamaica and Florida. A specimen from Jamaica illustrated and discussed by Cox (1941: 136-138, pl. 8, fig. 1) measures 318 x 280 mm (J. Taylor, pers. comm.). Dall (1901) placed it in the subgenus Pseudomiltha P. Fischer, 1887 and Bretsky (1976: 290) stated that it "may be an Eomiltha".

The discovery of a giant new lucinid off Taiwan is paralleled by 2 equally unexpected recent discoveries that together demonstrate the patchiness of lucinid occurrences. *Mesolinga soliditesta* Okutani and Hashimoto, 1997, reaching a size of 64 mm, was discovered at 363 m in a well-investigated part of Japan (Okutani and Hashimoto 1997), and *Lucinoma kazani* Salas and Woodside, 2002, associated with cold seeps on mud volcanoes at 1700 m in the eastern Mediterranean (Salas and Woodside 2002), was the largest new molluscan species discovered in the Mediterranean for many decades.

SYSTEMATIC DESCRIPTION

Family Lucinidae Fleming, 1828 Meganodontia gen. nov.

Type species: Meganodontia acetabulum sp. nov.

Description: Shells very large, almost circular, tumid to very tumid, thick-shelled and heavy. Surface with dense, strong, irregular growth lines, but no sculpture. Hinge edentulous. Hinge plate rather sturdy, arched, with a thick, dorsally sunken ligament. Ligament plate horizontal and not slanting towards the cavity of the valve. Umbones very shallow, not protruding, markedly bent forwards, situated well in front of the vertical midline. Greatest shell height (on the vertical midline rectangular to the line connecting the upper extremities of the adductor scars) not marked by the umbones but by the postumbonal dorsal shell margin, thus adding to the circular outline of the valves. Anterior adductor muscle scar long and broad, ventrally diverging from the pallial line for about 3/4 of its total length. Lower part of the muscle impression broader than the upper part close to the pallial line, giving the scar a somewhat spatulate form. Angle between diverging part and pallial line very wide, about 35° to 40°. Inner margin of valves smooth.

Meganodontia acetabulum sp. nov. (Figs. 1-3)

Type material: Holotype (reg. no NMNS-4524-001) in National Museum of Natural Sciences (NMNS), Taichung, Taiwan. 24°49.6'N, 122° 00.8'E, 370 m depth, Taiwan 2001 cruise stn. CP 68, a left valve, length 133.9 mm, height 122.8 mm (tumidity of valve, 40 mm). Paratype in Muséum national d'Histoire naturelle (MNHN), Paris. 24°48.3'N, 122°84.0'E, 246~256 m depth, Taiwan 2001 cruise stn. CP 109, a right valve, length 150.3 mm, height 135.2 mm (tumidity of valve, 48 mm). Collected 6 and 20 May, 2001, respectively

Type locality: Tashi fishing ground, off Tashi, NE coast of Taiwan.

Other material examined: 24°04.2'N, 122°04.3'E, 472~586 m depth, Taiwan 2001 cruise stn. CP 96, 1 fragment of a right valve with hinge plate (NMNS, reg. no. NMNS-4524-002); 24°48.3'N, 122°84.0'E, 246~256 m depth, Taiwan 2001 cruise stn. CP 109, 6 fragments embedded in solidified mud, among them 2 consisting of pieces of conjoined valves (1 NMNS (reg. no. NMNS-4524-003), 1 MNHN); 24°48.3'N, 122°04.0'E, 316~350 m depth, stn. Taiwan 2001 cruise stn. CP 110, 1 fragment of a left valve with hinge plate (MNHN). Collected 18 and 20 May, 2001.

Description: Shell extremely large for a lucinid, up to 150 mm long, somewhat variable, very thick and heavy, almost circular, length/height ratio 1.1, inequilateral, equivalve, very inflated. Umbones very shallow, very slightly or not protruding beyond the dorsal margin and situated well in front of the vertical midline, by almost 20 mm in the holotype. Greatest dorsoventral extension not

determined by the umbones but by the postumbonal dorsal margin. Anterior margin broadly rounded, either evenly or slightly more in its middle. Lunule very short. Dorsal margin behind umbones convex, no marked postero-dorsal corner. Posterior margin broad and evenly rounded, passing into the rounded ventral margin without postero-ventral corner.

Exterior with numerous densely set, strong, irregular growth lines and growth waves; no sculpture except for very fine and very irregular, more or less commarginal wrinkles, best visible under a lens. Postero-dorsal slope not set off from the rest of the valve; anterodorsal slope with abroad, very shallow depression.

Hinge plate narrow for shell size but strong, toothless. Lunule short, variable, narrow in left valve, broader in right valve, rather deeply sunken, delimited by a more or less sharp keel. Escutcheon not defined as this, but as a very narrow and deep sunken ligamental area, of which the delimiting keel is transformed to a thick lamella which projects over the ligamental area, leaving only a narrow slit dorsal to the ligament, when intact and when both valves conjoined. Anterior adductor scar long and broad, for 3/4 its length separate from the pallial line, becoming broader ventrally. Adductor scars with weak, irregular radial striae. Anterior margin of valves smooth, ventral and posterior margin occasionally with very small, irregular crenulations on the interior.

Derivatio nominis: The name Meganodontia reflects the large size (Greek mega) and the close resemblance to Anodontia. The specific epithet acetabulum (Latin), meaning salad bowl, refers to the exceptional size and the outline of the valves; used as a noun in apposition.

DISCUSSION

Generic comparison

Meganodontia is most similar to species of the genus Anodontia Link, 1807 (type species A. alba Link, 1807, Western Atlantic) and, like them, it is characterized by the absence of hinge teeth and a very inflated shell. We have examined the West African species Anodontia subfragilis Dautzenberg, 1910, A. subrostrata Cosel, 1989, 2 other undescribed species in the MNHN, and the Caribbean A. (Pegophysema) schrammi (Crosse, 1876) (type species of Pegophysema Stewart, 1930). From these, and from the species illustrat-

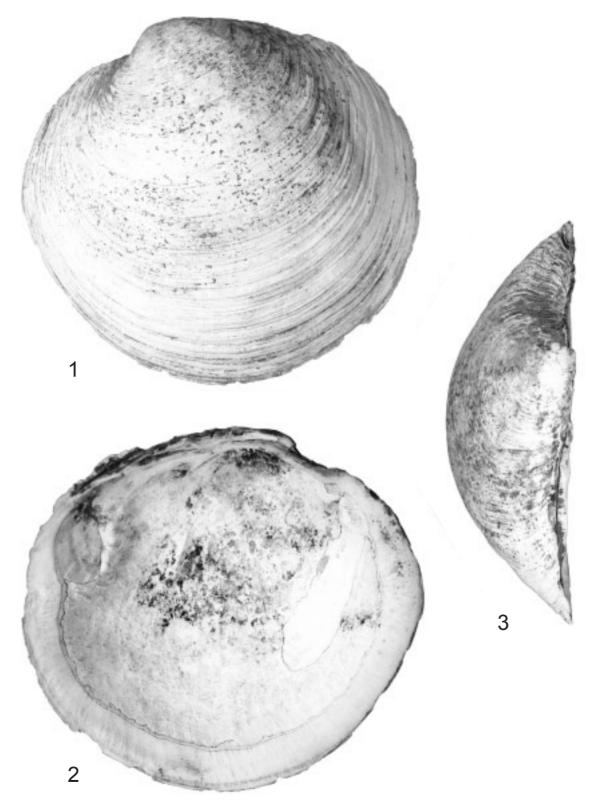


Fig. 1. Meganodontia acetabulum sp. nov. Holotype NMNS, external view.
Fig. 2. Internal view of holotype.
Fig. 3. Dorsal view of holotype. Length 133.9 mm, height 122.8 mm.

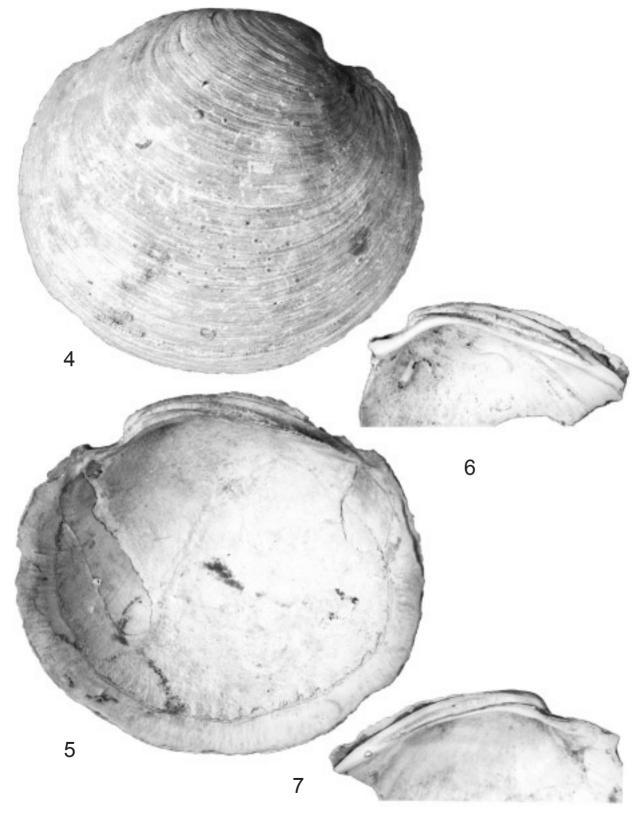


Fig. 4. Meganodontia acetabulum sp. nov. Paratype MNHN, external view.

Fig. 5. Internal view of paratype. Length 150.3 mm, height 135.2 mm.

Fig. 6. Fragment of a right valve, hinge view, length 96.0 mm, Taiwan 2001, stn. CP 96, NMNS. **Fig. 7.** Fragment of a left valve, hinge view, length 93.0 mm, Taiwan 2001, stn. CP 110, MNHN.

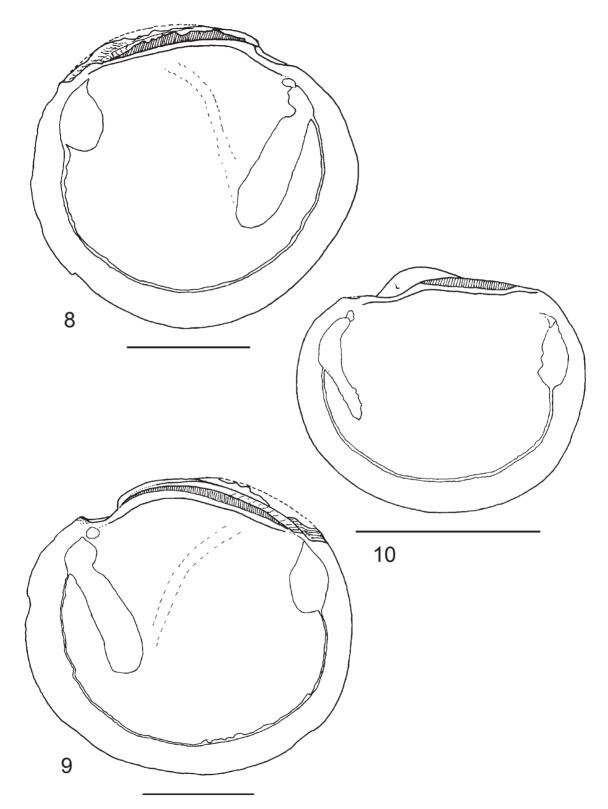


Fig. 8. Meganodontia acetabulum sp. nov. Semi-schematic drawing of the interior of the holotype.

Fig. 9. Meganodontia acetabulum sp. nov. Semi-schematic drawing of the interior of the paratype.

Fig. 10. Anodontia schrammi (Crosse, 1876). Semi-schematic drawing of the interior of the holotype (MNHN) to show the difference from Anodontia. Scale bar: 50 mm.

ed by Bretsky (1976: pl. 35, figs. 4-11), Meganodontia is distinguished principally by the very large anterior adductor scar, the thicker shell, and very small and low, almost non-protruding umbones. These fit exactly into the nearly circular outline of the shell, in which the lunular area forms only a rather short indentation. The cross-section of a valve of *Meganodontia* passing through the beaks forms an arc that is not interrupted by more or less prominent umbones: the conjoined valves have the form of a thick lens. The circular outline continues from the umbones posteriorly along the dorsal margin, and it is still more apparent because the dorsal margin is raised like a flange or thick lamella over the ligamental area, which is partly covered by it. The greatest dorsoventral extension of the Meganodontia shell lies behind the umbones within the 1st 1/2 of the ligamental margin, whereas in examined species of Anodontia, the greatest height of the valve is always marked by the more or less prominent umbones, situated on, or more or less in front of, the vertical midline. The dorsal margin of Anodontia is often less arched and thus interrupts the circular outline. An example is the already mentioned Anodontia (Pegophysema) schrammi (Fig. 10); it has small but prominent umbones and a narrower and straighter hinge and ligament plate. In contrast to shells of species of Anodontia, those of Meganodontia are rather thick and heavy. An important feature of the new genus is the conspicuously long, broad, and spatulate anterior adductor scar. In Anodontia, the anterior muscle scars are usually smaller and narrower and diverge from the pallial line at a lesser angle (e.g., in A. alba, see Bretsky 1976, pl. 35, fig. 5). These characters justify the separation from Anodontia as a distinct genus.

Among fossils, the genus Cryptolucina Saul, Squires and Goedert, 1996 (type species C. megadyseides Saul, Squires and Goedert, 1996, Eocene of Washington State, USA) at first seems to be close to Meganodontia The hinge is edentulous, the lunule is broader in the right valve, and the shell surface has strong, irregular growth lines. However, in contrast to Meganodontia, the shells of Cryptolucina are much less tumid and significantly elongated, a feature not so often seen in the Lucinidae and not shared by the Anodontia group. Furthermore, C. megadyseides is distinguished from M. acetabulum by well-marked radial striae on the interior, the broader and more prominent umbones, and the much broader and heavier hinge plate. Cryptolucina megadysoides attains a

shell length of 180 mm, and the height is about 72% of the length (Saul et al. 1996: 791).

Species classifiable in Meganodontia

We know of no Recent species that can be classified in Meganodontia. Among fossils, an Italian Pliocene fossil attributed by Sacco (1901) to "Lucina globulosa Deshayes" may possibly be classifiable in Meganodontia (The real Lucina alobulosa Deshayes, 1832, from the Miocene of France, has a rather straight dorsal margin, a more protruding umbo, a narrower hinge plate and a thinner shell (Cossmann and Peyrot 1912: 639-641, pl. 26, figs. 56-58), and belongs to Anodontia s.l.). The arched hinge line, ligament plate, shell outline, large size, and the spatulate form and angle of divergence of the anterior adductor scar of "Lucina globulosa" var. pseudofuchsi Sacco, 1901 (68, pl. 16, fig. 2, in the legend referred to as var. perlunuata Sacco, 1901) suggests that it may be referable to Meganodontia. "Lucina globulosa" var. hoernea Sacco, 1901 (pl. 15, figs. 31-33, pl. 16, fig. 1) and the other variants of "L. globulosa" figured by Sacco (1901) have more globose and prominent umbones; their interior is not shown, and we do not consider them referable to Meganodontia

A couple of other large fossil lucinids have a superficial resemblance to Meganodontia, but their generic allocation remains inconclusive. Anodontia sphericula Basedow, 1902 from the Early Pleistocene of South Australia (Ludbrook 1984: 240, fig. 59d) and the Late Pliocene of Southwestern Australia (J. Taylor, pers. comm.) is a large (largest specimen 105 mm long, 95 mm high) species with typical, more prominent, and less forwardly bent umbones, and with the greatest shell height marked by the umbones, a narrower, less-arched hinge plate, and a shorter diverging part of the anterior adductor. These characters point to inclusion in Anodontia rather than in Meganodontia. "Loripes" goliath Yokoyama, 1929, as illustrated in Gu et al. (1976: 63, pl. 61, figs. 15-16) and Hu and Zeng (1991: 30, figs. 3, 4, 7, 8) is another large and very globose species. Although it is illustrated only as internal molds in both publications, it is clear that the umbones are more globose and form the highest part of the shell, whereas in Meganodontia acetabulum the extremely low umbones are also reflected in the interior and would be so on internal molds. As external and internal views of the valves of "Loripes" goliath are not available, its relation to Meganodontia cannot be further evaluated, and we are unable to formally assign those specimens to this genus.

Acknowledgments: The 1st author thanks Prof. Tin-Yam Chan, National Taiwan Ocean University, Keelung, for inviting him to participate in the survey of the Tashi fishing ground, and Dr B. Richer de Forges and Capt. J.F. Barazer, for their camaraderie and help on board the F/V *Jin Tung Long No. 26.* J. Taylor (BMNH), E. Glover (BMNH), A. Warén, and Prof. Tin-Yam Chan critically read earlier drafts of the manuscript and provided valuable comments. The cruise Taiwan 2001 was supported by the National Muséum of Marine Science and Technology, Keelung, the National Science Council, Taiwan, R.O.C., the Muséum national d'Histoire naturelle, Paris, and the Institut de Recherche pour le Développement (IRD), Paris.

REFERENCES

- Barnes P, C Hickman. 2001. Biogeography and ecology of shallow-water chemoautotrophic bivalves. In L Salvini-Plawen, J Voltzkow, H Sattmann, G Steiner, eds. Abstracts, World Congress of Malacology 2001, Vienna, Austria: Unitas Malacologica, p. 22.
- Bretsky SS. 1976. Evolution and classification of the Lucinidae (Mollusca: Bivalvia). Paleontograph. Am. 8: 215-337, pls. 25-36.
- Chavan A. 1959. Superfamily Lucinacea Fleming, 1828. In RC Moore, ed. Treatise on invertebrate paleontology, N, 2, Mollusca 6, Bivalvia: N491-518. Boulder, CO: Geological Society of America.
- Cossmann M, A Peyrot. 1909-1912. Conchologie néogénique de l'Aquitaine. Vol. 1. Pélécypodes (Clavagellidae à Lucinidae). 718 pp., 28 pls. (1909: 1-220, pls. 1-7; 1911: 221-428, pls. 8-18; 1912: 429-718, pls. 19-28). Bordeaux: Saugnac.
- Cox LR. 1941. Lamellibranchs from the White Limestone of Jamaica. Proc. Malacol. Soc. Lond. 24: 135-142, pls. 8-10.
- Dall WH. 1901a. A gigantic fossil Lucina. Nautilus 15: 40-42.
- Dall WH. 1901b. Synopsis of the Lucinacea and of the American species. Proc. US Natl. Mus. 23: 779-833, pls. 39-42.
- Gu ZW, BY Huang, CZ Chen, SX Wen et al. 1976. Fossil Lamellibranchia of China. Beijing: Science Press, 522 pp., 150 pls. (in Chinese)
- Hertlein LG, AM Strong. 1946. Eastern Pacific expeditions of the New York Zoological Society, XXXV. Mollusks from the west coast of Mexico and Central America. Part 4. Zool. Sci. Contr. New York Zoologica. Soc. **31:** 93-120, pl. 1.
- Hu CH, DM Zeng. 1991. Kaohsiung Hsien Jiaxianvillage neo-

Tertiary period molluscan Fossils. *In* Hu CH, Fossil mollusk fauna of Taiwan, 1(1), 65 pp., 13 pls. Taichung, Taiwan: National Museum of Natural Science. (in Chinese)

- Lan TC. 2000. The Taiwan Anomalodesmacea and Septibranchia. Pei-yo **26:** 50-63. (in Chinese)
- Lan TC. 2001. Designation of lectotypes and paralectotypes for the Taiwan Anomalodesmacea and Septibranchia. Bull. Malacol. Taiwan **25:** 79-82.
- Lan TC, YC Lee. 2001. Five new bathyal bivalves of Protobranchia from Taiwan. Malacol. Soc. Taiwan Mem. 1: 2-6.
- Lan TC, YC Lee. 2002. A new deep water *Amalda* in the family Olividae from Taiwan. Malacol. Soc. Taiwan Mem. 2: 18-20.
- Lee YC. 2001. Two new bathyal turrids (Gastropoda: Turridae) from West Pacific. Malacol. Soc. Taiwan Mem. 1: 7-9.
- Lee YC, TC Lan. 2002a. Two new bathyal cancellariids (Gastropoda: Cancellariidae) from Taiwan. Malacol. Soc. Taiwan Mem. **2:** 21-24.
- Lee YC, TC Lan. 2002b. A new *Colus* in the family Buccinidae from NE Taiwan. Malacol. Soc. Taiwan Mem. **3:** 30- 33.
- Lee YC, WL Wu. 1998a. A new trochid (Gastropoda: Trochidae) from the Kue-Shan I., NE of Taiwan. Bull. Malacol. Taiwan ROC **22:** 57-60.
- Lee YC, WL Wu. 1998b. A new subgenus and three new species of epitoniid (Gastropoda: Epitoniidae) from Taiwan. Bull. Malacol. Taiwan ROC **22**: 61-66.
- Ludbrook NH. 1984. Quaternary molluscs of South Australia. Handbooks S. Australia Dept. of Mines and Energy, 9, 327 pp. Adelaide: DJ Woodman, Govt. Printer.
- Ng NK, JF Huang, PH Ho. 2000. Description of a new species of hydrothermal crab, *Xenograpsus testudinatus* (Crustacea: Decapoda: Brachyura: Grapsidae) from Taiwan. Nat. Taiwan Mus. Special Publ. Ser. **10:** 191-199.
- Okutani T, J Hashimoto. 1997. A new species of lucinid bivalve (Heterodonta: Lucinidae) from Kanesu-no-Se Bank near the mouth of Suruga Bay, with a review of the Recent species of the chemosynthetic genus *Lucinoma* from Japan. Venus (Jpn. J. Malacol.) **56**: 271-280.
- Okutani T, TC Lan. 1999. Three new bathyal bivalves from Taiwan. Venus (Jpn. J. Malacol.) **58**: 19-23.
- Olsson AA. 1961. Mollusks of the tropical eastern Pacific, particularly from the southern half of the Panamic-Pacific faunal Province (Panama to Peru). Panamic-Pacific Pelecypoda. 574 pp, 86 pls. Ithaca, NY: Paleontological Research Institution.
- Sacco F. 1901. I Molluschi dei terreni terziarii del Piemonte e della Liguria. Part 29. 216 pp., 29 pls. Torino, Italy: C Clausen.
- Salas C, J Woodside. 2002. *Lucinoma kazani* n. sp. (Mollusca: Bivalvia): evidence of a living benthic community associated with a cold seep in the eastern Mediterranean. Deepsea Res. PT. I **49**: 991-1005.
- Saul LR, RL Squires, JE Goedert. 1996. A new genus of cryptic lucinid bivalve from Eocene cold seeps and turbiditeinfluenced mudstone, Western Washington. J. Paleontol. 70: 788-794.