# THE SANGIRAN FOSSIL SHELL ASSEMBLAGES CATALOGUE

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***Abstrak. Katalog Himpunan Fosil Kerang Sangiran.*** *Makalah ini merupakan pemutakhiran himpunan fosil cangkang Sangiran di Jawa Tengah. Tujuannya untuk mendokumentasikan dan menyajikan gastropoda dan kerang dari seri Kalibeng atas dan Pucangan Bawah Kubah Sangiran dari periode Plio-Pleistosen. Tercatat 61 taksa moluska hingga tingkat genus. Informasi yang dikumpulkan dari kumpulan moluska ditentukan oleh sejarah geologi dan lingkungan Sangiran. Mereka diasosiasikan dengan fasies yang berbeda: a) napal masif dan lempung biru, b) lapisan batugamping lempung, c) lempung kelabu berlumpur, d) breksi vulkanik dan lahar dan e) lempung hitam, dan terdiri dari sedimen yang merepresentasikan lingkungan laut hingga rawa yang mengarah ke perkembangan kontinental. Pola kuantitatif yang dicatat dalam kumpulan moluska menjelaskan palaeo-lingkungan dan hubungan antara kumpulan palaeodataset yang mapan dari analisis dan tingkat variabilitas dalam data paleontologi. Selain itu, cangkang yang teridentifikasi dapat digunakan sebagai referensi untuk perwakilan taksonomi Sangiran dan moluska di lapisan Kalibeng dan Pucangan Cekungan Solo di Jawa Tengah.*

***Kata Kunci:*** *Keragaman, Sangiran, Mollusca, Bivalvia dan gastropoda laut dan air tawar, Jawa Tengah*

**Abstract.** This paper is an update of fossil shell assemblages of Sangiran in Central Java. It is aimed to document and present the gastropods and bivalves from the Upper Kalibeng and Lower Pucangan series of the Sangiran dome from the Plio-Pleistocene period. There are 61 mollusc taxa recorded up to the genus level. Information gathered from mollusc assemblages are determined by the geological and environmental history of the Sangiran. They are associated with different facies: a) massive marls and blue clays, b) layered clayey limestone, c) silty gray clay, d) volcanic breccia and lahars and e) black clays, and composed of sediments representing marine to swampy environments leading to continental development. The quantitative patterns recorded in mollusc assemblages elucidate the palaeoenvironment and the relationship between the established palaeodatasets of analysis and the levels of variability in palaeontological data. Moreover, the identified shells may be utilized as a reference for Sangiran and molluscan taxonomic representative in Kalibeng and Pucangan layers of Solo Basin in Central Java.

**Keywords :** Diversity, Sangiran, Mollusca, Marine and freshwater bivalves and gastropods, Central Java.

## 1. Introduction

Sangiran Dome, the World Heritage Hominid bearing site in Java and part of the Sunda arc/bridge, is considered as one of the Earth's biodiversity hotspots. Sangiran is situated in a complex region of Sundaland interplayed by plate movements, palaeogeography, ocean circulation, and climate during the Quaternary period (Sodhi

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*et al.*, 2004; Bird *et al.*, 2005; Simons *et al.*, 2007; Hall *et al.*, 2009; Metcalfe, 2011). Significant fossils and palaeosols sequence amassed in the dome of Solo Basin were studied pertinent to the evolution of history and dispersals during the Early and Middle Pleistocene. The dome also uncovers the movement of early hominins as early as 1.8 Ma, including the first islanders, *Homo erectus*, about the lowering of the sea level during the Pleistocene period, which produced many land bridges and sea barriers in Sundaland (von Koenigswald, 1940; van Bemmelen, 1949; Zaim *et al.*, 2011).

Sangiran of the Solo Basin has a sequence of layers that are complete and continuous from the Upper Late Pliocene up to the Pleistocene. The dome was created more than two million years ago due to volcanic and tectonic activities, and numerous climatic cycles in the Solo basin (von Koenigswald, 1940; van Bemmelen, 1949; Sémah, 1986). Afterward, the dome was truncated by erosion, exposing a concentric pattern of strata, with older strata surrounded by younger (Hyodo, 2011), filling the basin with sediment deposits from volcanism, tectonic movement, and climatic cycle runoffs. They presented various environments, from coastal marine, marine regressions to various continental settings characterized by four strata namely, Kalibeng, Pucangan, Kabuh, and Notopuro layers in the dome area during the Quaternary period (von Koenigswald, 1940) (Figure 1).

Kalibeng is the oldest layer of the dome, blue clay deposited in a marine environment, dating to the late Pliocene from about 2.2 Ma (Ninkovich and Burckle, 1978). It was followed by the lahar and black clay with volcanic and swamp facies of the Pucangan Formation, dated to the Lower Pleistocene, from 1.8-0.73 Ma (Swisher *et al*., 1994; Sémah *et al*., 2000). The next layers are the Kabuh volcano-pluvial sandy sediments of 0.73-0.2 Ma (Larick *et al.,* 2001), succeeded by the Notopuro sands and volcano-fluvial gravels of 0.2-0.12 Ma (Suzuki and Wikarno, 1982; Watanabe and Kadar, 1985; Sémah, 1986; Sémah *et al*., 2000; Larick *et al.,* 2001; Bettis *et al.*, 2004), and by recent deposits from the floods of the Cemoro, Brangkal and Pohjajar rivers.

In the oldest deposits of Kalibeng and Pucangan, the presence of molluscs revealed aquatic ecological changes. Gastropods and bivalves in particular turned out to be of the greatest value for the differentiation of palaeobiogeographical units due to sensitive reactions to all environmental parameters and occupying a wide range of ecological niches. Patterns in biostratigraphical implications were recognized in paleontology, which has been used as a biogeographic model in Sangiran fauna and flora remains (von Koenigswald, 1934, 1935; de Vos, 1982; Sondaar, 1984; Sémah AM, 1982; Aziz, 2001).

However, molluscan diversity remains poorly unknown in Sangiran. The role of mollusc deposited in Sangiran has been overlooked by scholars working in the area. Research is mostly focused on human and animal fossils, artifacts or geochronology, and lithostratigraphy. With this premise, an annotated checklist of the Sangiran fossil shells is presented, based on specimens deposited in the four facies from the Upper Kalibeng to Lower Pucangan beds namely the Blue Clay, *Corbicula* Bed, Lower Lahar (Breccia) and the Black Clay. Shells collected were composed of marine and freshwater gastropods and bivalves that provided an up-to-date inventory of molluscan taxa and characterized the molluscan stage from Sangiran stratigraphic units of Kalibeng and Pucangan.

## 2. Method

### Molluscan Taxonomy of Sangiran Bivalves and Gastropods

Fossil and bulk samples (sediment and mollusc shells) were collected in Kalibeng and Pucangan layers from several localities in Sangiran dome namely, Krikilan, Ngampon,

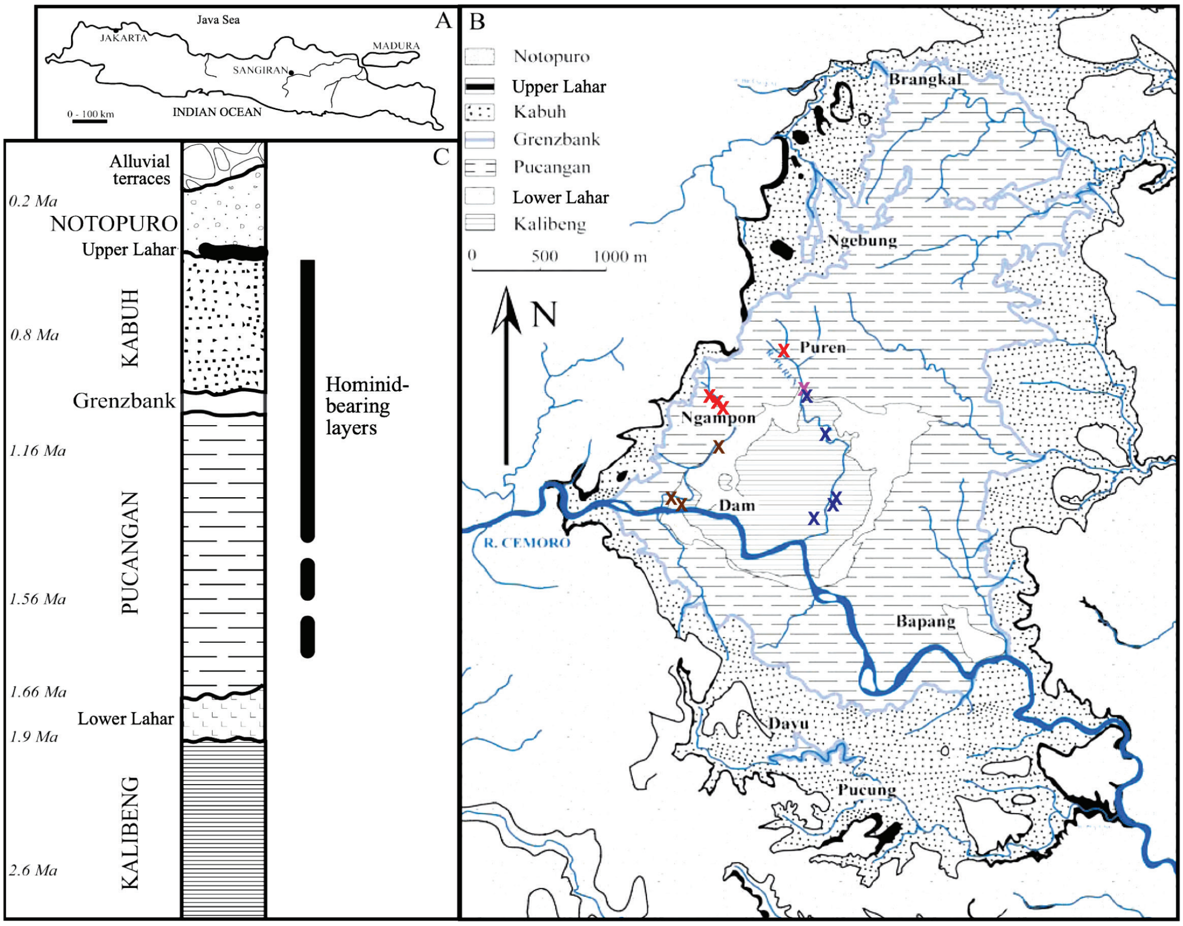


**Figure 1.** A) Location of Sangiran in Java Island. B) Sangiran lithostratigraphy. C) Shell sampled sites in Sangiran, marked in X, belonging to Upper Kalibeng and Lower Pucangan series. Geological map of Sangiran and its stratigraphy based on Von Koenigswald plan (1940) modified by Watanabe and Kadar (1985) and Sémah *et al.* (1992). (Source: Brasseur *et al*., 2015.)

Pablengan Kulon, and Pondok (See Figure 1). These assemblages are considered as the latest and updated fossil mollusc reference in relation to different stratigraphical units of Sangiran. During our fieldwork, carried out in November 2015 and June 2016, several species included in the list of van Bethem Jutting (1937) and Oostingh (1923, 1935) were found along with several previously unrecorded ones. Fossils were taken from exposures of natural cuttings and well-preserved outcrops along the Puren River. Location and elevation of all sites were recorded with the aid of a GPS. For quantitative data, three of 1,000 cm3 or 1 L of complete samples (sediment and biogenic content) were taken in each site.

Molluscs retained from wet sieving in 1.5 and 5 mm mesh was dried. All molluscs recovered were identified and counted to the lowest possible taxonomic rank. They were composed of bivalves and gastropods from marine to freshwater environments. Information on the environmental attributes and habitat preferences of each mollusc present in the sample was gathered from literature on modern molluscs from Indonesia (Dharma, 1988 and 1992), the Philippines (Lozouet & Plaziat, 2008; Poppe, 2008; Springsteen *et al*., 1986), Thailand (Robba *et al*., 2002 and 2005), Japan (Okutani, 2000) and Compendium of Shells (Abbott & Dance, 2000) and the living marine resources of the Western Central Pacific of UNESCO (Carpenter & Niem, 1998). MolluscaBase, World Register of Marine Species (WoRMS), and Ocean Biogeographic Information System (OBIS) Indo-Pacific Molluscan Database were consulted in verifying the accepted name of the taxon. They are the taxonomically oriented databases that provide account authority of all molluscan species. Conducted freshwater mollusc studies in Java, Indonesia, were also consulted: Jutting (1937, 1959), Köhler & Glaubrecht (2001), Marwoto & Isnaningsih (2012) and Robba (2013). All shell samples were also compared with the shell reference collection at the Biology Laboratory of Marine Invertebrates and Malacology, Muséum National d'Histoire Naturelle, Paris, and Archaeozoology Laboratory of the University of the Philippines.

## 3. Research Result and Discussion

The Sangiran fossil molluscs are represented by 46 species of marine molluscs, 24 are bivalves and 22 are gastropods; and 15 species of freshwater molluscs, four bivalves, and 11 gastropods. Table 1 is a list of Sangiran molluscan taxa reference. Most parts of the species were identified at the generic level. The sampled material does not permit a more accurate determination. Shell diagnostic characteristics were mainly based on the books of Western Central Pacific of UNESCO (Carpenter and Niem, 1998) and Recent and Fossil Indonesia Shells (Dharma *et al.*, 2005) for marine molluscs and monographs on Pachychilidae (Köhler & Glaubrecht, 2001; Marworto & Isnaningsih, 2012), Thiaridae (Glaubrecht, 1999; Appleton *et al.*, 2009); Viviparidae (Marwoto & Nurinsiyah, 2009) and Non-Marine Mollusca from Fossil Horizons in Java with Special Reference to the Trinil Fauna (van Benthem Jutting, 1937) for freshwater molluscs.

The classification adopted in this account largely draws on that followed in the Treatise on Invertebrate Palaeontology, Part I, Mollusca 1 (Moore R.C., Ed., 1960), with modifications according to more recently proposed changes (see Herbert, 1987; Hickman & McLean, 1990).

### 3.1 Bivalves and Gastropods Assemblage in Upper Kalibeng Formation

The Kalibeng layer is the oldest formation of the Sangiran dome. It started to develop from the late Miocene period to the Pliocene period in Central Java. Kalibeng is exposed only in the central part of the dome. It was composed of volcanic materials namely, the bluish-gray clay and silty clay on top of the *Globerigina* marls between the Late Miocene and Upper Pliocene (Marks, 1957). This was followed by silty sand strata and corresponds to *Turritella* beds (van Es, 1931). Above this, the *Balanus* limestone deposited in shallow seas and possibly originated in a tidal zone. Overlying the limestone is clay and silt sediments. The molluscs are deposited in the upper part of the formation in blue clay, silty sand, and silty clay deposits. From the samples, 19 bivalves and 21 gastropods were identified. All belong to the full marine environment, mostly in the soft-bottom sublittoral zone. Bivalve shells belong to two families Arcidae/ Noetiidae and Veneridae, 17 to genus level (*Alveinus sp., Amusium sp., Anadara sp., Arca sp., Arcopsis sp., Bathythormus sp., Cardiolucina sp., Corbula sp., Glycymeris sp., Mimachlamys sp., Myochama sp., Myrtea sp., Placuna sp., Plicatula sp., Timoclea sp., Varicorbula sp. and Venus sp.*). Gastropods identified are a species from family ?Muricidae, and 19 belongs to genus ?*Callliostoma sp., Cerithium sp., Chrysallida sp., Cryptospira sp., Cymatium sp., Diodora sp., Drillia sp., Epitonium sp., Fusinus sp., Gemmula sp., Melanella sp., Mitrella sp., Nassarius sp., Olivella sp. Polinices sp., Ringicula sp., Solariella sp., Turritella sp.* and *Vaceuchelus sp.* and one species of T*urritella terebra.*

Mollusc assemblages from the samples in the upper part of Kalibeng indicates by a complex interplay of a near-shore, shallow marine environment with marine marls at the bottom (Table 2). They are comprised of shallow-living taxa, concentrated together with allochthonous elements such as deep-living taxa

**Table 1.** List of molluscs taxa recovered from Kalibeng and Pucangan layers in Sangiran

A. Class Gastropoda

| Taxonomy | Taxon and its description |
|---|---|
| Order LEPETELLIDA<br>Family FISSURELLIDAE | *Diodora JE Gray,* 1821<br><br>Outline ovate narrowing anteriorly from point of maximum diameter in the posterior half of the shell. Apical orifice subcircular, located slightly anterior to center. Exterior sculptured by fine radial ribs that become broader toward the periphery. Radial ribs beaded by a system of closely spaced, fine concentric ridges. A few irregularly spaced concentric folds superimposed upon the finely beaded radial sculpture. |
| Order SEGUENZIIDA<br>Family CHILODONTAIDAE | *Vaceuchelus Iredale,* 1929<br><br>Small, globular, turreted, stout, nacreous within, imperforate or narrowly umbilicate; columella without basal tooth; whorls convex, marked with strong spiral ribs crossed by well-developed axial lamellae that give ribs a beaded appearance and form deep pits in spaces between ribs. |
| Order TROCHIDA<br>Family CALLIOSTOMATIDAE | ?*Calliostoma Swainson,* 1840<br><br>Shell moderately low, pyramidal. Whorls trapezoidal, regularly increasing in size. Initial sculpture of three equal and equidistant spirals, the anterior and posterior of which gradually become more prominent relatively and absolutely; intercalary introduced on early whorls. Base flattened, sculptured with simple lirae, those nearer the axis the broader and the more irregular in size and spacing. Aperture somewhat broke, rudely rhomboidal; outer margin imperfect but angulated at the periphery. Inner margin concave reflected. |
| Family SOLARIELLIDAE | *Solariella* SV Wood, 1842<br><br>Shape trochoid, whorls rounded or angular, suture impressed. Spire sculptured by a strong cord on middle whorl forming, carinate shoulder. Aperture corneus, thin with a central nucleus. |
| Unranked clade CAENOGASTROPODA/ SORBEOCONCHA<br>Family ?PACHYHILIDAE<br>P Fischer & Crosse, 1892 | Shell forms almost globular to narrowly elongated and are either ornamented by axial and/or spiral ribs and/or spines or smooth except for growth lines and basal lirae are present. It has an oval multispiral operculum with whorls that increase rapidly in diameter. |
| | *Sulcospira testudinaria* (Köhler & Dames, 2009)<br><br>Shell variable, turreted or elongated conic, solid, medium to large (22-40 mm), spire angle about 30°. Apex eroded. The sculpture consists only 2-3 spiral lirae near the suture, and 3-6 prominent spirals lirae at the base of the body whorl. Suture narrow and shallow. Suture narrow and shallow. Aperture oval, outer lip straight. Columella not thickened. Operculum oval with a sub-central nucleus. |
| | *Sulcospira Troschel,* 1857<br><br>Shell rather conical, with spiral lirae but lacking axial lirae. Operculum with 4 to 6 whorls. Protoconch smooth and inflated, with up to two whorls possessing a fine granular texture or faint growth lines. |
| Family THIARIDAE | *Tarebia* H Adams & A Adams, 1854<br>*Tarebia granifera* (Lamarck, 1822)<br>*Tarebia aff. granifera* (Lamarck, 1822) |

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| | The shell is turreted with the body whorl. The sculpture of rectangular knobs follows a spiral pattern. Sutures are distinct and the whorls are flat-sided. |
| | *Thiara* Röding, 1798<br>*Thiara winteri* (von dem Busch, 1842)<br><br>Shell large, solid, with a tall spire and a large body whorl; whorls are somewhat steeped; sculptured with weak axial folds which form a crown of short spines on the sharply angled whorl shoulder, some flat spiral ridges towards the body whorl base; aperture vertically ovate, pointed above and rounded below, the outer lip thin, lirate within and the columella heavily ridged. |
| Unassigned CAENOGASTROPODA<br>Family CERITHIIDAE | ?*Cerithium* Bruguière, 1789<br><br>Shell elongate, thick and solid, sharply conical with a high many-whorled spire and small aperture. Sculpture variable, usually spiral or nodulosem and with axial ribs or varices. Umbilicus generally absent. Periostracum obsolete. Aperture with a distinct, anterior siphonal canal that may be drawn out, upturned, and often laterally twisted. Outer lip somewhat expanded usually notched posteriorly. Inner lip smooth or twisted. Operculum ovate, corneous, with a few spiral coils and an eccentric nucleus. |
| Family EPITONIIDAE | *Epitonium* Röding, 1798<br><br>Shells are high-spired, deep suture, imperforate, umbilicus narrow, fenestrate, peristome thick, axial ribs thick, partly or completely reflexed, often weakly or not coronated, intervals with axial and spiral microstriae, more or less granulose at the intersection, forming a cancellate sculpture. |
| Family TURRITELLIDAE | *Turritella* Lamarck, 1799<br><br>Shell elongate, sharply conical, with numerous whorls and a small, square to rounded aperture. Umbilicus usually absent. Sides of the whorls sharply keeled. Growth lines arched to sinuous. Outer lip of the aperture thin, often concave. Inner lip smooth. Anterior siphonal canal absent. Operculum corneous, rounded, with many spiral coils and a central nucleus; border of the operculum very thin, often with flexible bristles. |
| | *Turritella terebra* Linnaeus, 1758<br><br>Shell large and solid, with an extremely long and tapering spire, with 25 or more whorls in mature specimens. Whorls strongly convex in outline, with impressed suture and up to six prominent spiral cords and weaker interstitials spiral threads. The apical end of spire invariably missing in adult shells. Aperture is almost circular in outline. The margin of outer lip rather thin, forming a broad, very shallow sinus leaning backward concerning to the direction of growth, continued as a straight line across the base. |
| Order LITTORINIMORPHA<br>Family HYDROBIIDAE | Shell minute to small, usually 1-10 mm in height, dextrally coiled, planispiral to aciculate, phaneromphalous to cryptophalous, with about 2-8 whorls. Body whorl often loosened, shell sometimes partially uncoiling to assume a corkscrew or horn-like shape. Shell thin to fairly solid, transparent to white. Periostracum generally thin, rarely elaborated as hair-like or other projections. |

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| | Aperture holostomatous, sometimes thickened, sinuous deflected or flared, but without notches, canals, siphonal grooves, or denticulations. Shell usually smooth except for collaboral growth-lines, but occasionally with a sculpture of reticulations, carinae, spines, or cords. The protoconch is usually paucipsiral, rarely multispiral, usually dome-like, smooth, or with a sculpture of wrinkles, pits, or spiral lines. The operculum is usually well-formed, rarely rudimentary, corneous, usually paucisliral, rarely multispiral, or conical. Ventral (very rarely dorsal) opercular surface sometimes with elevated corneous or whitened ridges or pegs. |
| Family EULIMIDAE | *Melanella* Swainson*,* 1840<br><br>Shell turreted, white glossy, slippery, straight-sided, and commonly slightly tilted. Spire tall with an acute apex. Aperture drop-like with posterior portion rounded. Outer lip completely convex, forming a symmetrical curve. |
| Family NATICIDAE | *Polinices* Montfort, 1830<br><br>Thick and heavy, pear-shaped, distinctly longer than wide, with a moderately high conical spirem nearly flat-sided whorls and shallow sutures. Outer surface smooth and glossy with only fine lines of growth. Umbilicus closed, entirely filled by a heavy callus (a slight umbilical groove occasionally present anterior to callus in juvenile specimens). Operculum corneous. |
| Family RANELLIDAE | *Cymatium* Röding, 1798<br><br>Shell ovate to fusiform, thick and solid, with a raised spire and strong sculpture composed of nodules, spiral ribs, and axial varices. The periostracum is frequently well developed and fibrous to hairy. Aperture with a short to long siphonal canbal anteriorly. Outer lip prominently thickened, often denticulate inside. Inner lip commonly wrinkled and with a columella callus. Operculum thick and corneous, rounded to trigonal. |
| Order NEOGASTROPODA Family ?MURICIDAE | Shell variably shaped, generally with a raised spire and strong sculpture with spiral ridges and often axial varices (3 or more in number on each whorl), frequently bearing spines, tubercles, or blade-like processes. Periostracum absent. Aperture variable, ovate to more or less contracted, with a well-marked anterior siphonal canal that may be very long. Outer lip often denticulate inside, sometimes with a tooth-like process on margin. The columella is smoothish to weakly ridged. Operculum corneous, thin to thick, with nucleus near the anterior end or at about mid-length of the outer margin. |
| Family COLUMBELLIDAE | *Mitrella* Risso, 1826<br><br>Shell generally small, fusiform to biconical in shape, with a conical, more or less elongate spire. Outer surface without axial varices, ribbed, or smoothish. Periostracum variably developed to absent. Aperture long and narrow, with a rather short, anterior siphonal canal. Outer lip commonly thick, smooth or denticulate inside, sometimes with a shallow groove or slit posteriorly. Inner lip smooth or denticulate, but not folded. Operculum corneous, thin and small to absent with an apical nucleus. |

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| Family FASCIOLARIIDAE | *Fusinus* Rafinesque, 1815<br><br>Shell more or less elongate, fusiform, with a generally elevated spire and a well-developed, sometimes very long siphonal canal. Sculpture variable, often strong and nodular or composed of spiral threads and axial ribs. The periostracum is very thin to thick and fibrous. Aperture long and ovate. Outer lip smooth or with numerous inner spiral lirae. Columella often with a few low basal threads. Operculum thick and corneous, ovate to claw-shaped, with a terminal nucleus. |
| Family MARGINELLIDAE | *Cryptospira* Hinds, 1844<br><br>Shell is oviform to spindle-shaped, with a rather elevated spira. The apertural lip is thin or only very slightly thickened, without crenulations. The siphonal canal is superficial, not distinctly incised. There are four columellar folds, which are thin and narrow, and rather widely spaced. The two basal folds are very oblique, the two adapical ones are more horizontal. |
| Family NASSARIIDAE | *Nassarius* Duméril, 1805<br><br>Shell squat and thick, with a fairly high, stepped spire and inflated body whorl. Early spire whorls with intersecting axial and spiral cords, a granulated pattern. Later whorls smooth, but for a row of prominently rounded nodules on the shoulder and a few spiral cords at the base of the body whorl. Aperture lirate inside, outer lip thickened and often with a few small spines on its anterior outer edge in mature specimens. Inner lip with a prominent tooth-like nodule posteriorly. Columellar callus thick, forming a smooth shield wrapped around the ventral side of the body whorl, and posteriorly connected to the outer lip. Operculum with a serrated margin. |
| Family OLIVELLIDAE | *Olivella* Swainson, 1831<br><br>Shell thick and porcelaneous, elongate ovatem with a short spire, a large body whorl, and usually deeply channeled sutures. Surface smooth, highly polished, and often vividly colored. No periostracum. Aperture elongate, with a wide and short anterior siphonal canal and an indistinct posterior notch. Outer lip slightly thickened in the adult stage, smooth. Inner lip callus reaching almost to the posterior end of the aperture. Columellar callus usually bordered posteriorly by a distinct, calloused spiral band. Operculum absent. |
| Family TURRIDAE | *Drillia* Gray, 1838<br><br>Shell claviform, siphonal canal short, deeply notched, fasciole often strong; anal sinus moderately deep, U-shaped, spout-like, constricted by large parietal pad; and axial ribs strong |
| | *Gemmula* Weinkauff, 1875<br><br>Fusiform in shape, with a high slender spire. The posterior notch of the outer lip on the shoulder. Outer surface composed of axial ribs and nodules. Periostracum often present. Aperture more or less elongate, siphonal canal well marked, short to long. Outer lip generally thin and sharp. A characteristic slit or notch along the posterior part of the outer lip, which is reflected in the growth lines made by the lip. The inner lip is mostly smooth. Operculum corneous. |

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| Order TROCHIDA<br>Superfamily<br>Trochida | *Trochoidea* Rafinesque, 1815<br><br>Shell conical to globose in shape, with a moderately large rounded body whorl with a flattened base. Sculptured spirally with tubercles. The periostracum is sometimes conspicuous. Aperture rounded, without a siphonal canal, nacreous inside. |
| Superorder<br>PYLOPULMONATA<br>Family<br>PYRAMIDELLIDAE | *Chrysallida* Carpenter, 1856<br><br>Shape ovoid-conical, with fairly blunt top. Apex appears immersed in the following whorl. There are nearly three teleoconch whorls, of which the first adult is flat and the others are slightly convex. The body whorl forms more than half of the shell. The sutures are deep and wide; the lowest one is evidently oblique. The axial ribs, narrow and continuing to the base, are well marked and stronger than the spiral cords. The aperture is oval lengthened and there is a hardly visible tooth on the columella. |
| Superorder<br>RINGICULIMORPHA<br>Family<br>RINGICULIDAE | *Ringicula* Deshayes, 1838<br><br>Shell minute, ovate to the subglobose, medium-height spire, convex whorls with seven incised spiral grooves, thickened outer lip with thick parietal callus, markedly curved inner lip with two folds, siphonal canal broadly open. |
| Unranked clade<br>CAENOGASTROPODA<br>informal group<br>ARCHITAENIOGLOSSA<br>Family VIVIPARIDAE | *Bellamya javanica* (von dem Busch, 1844)<br><br>The shell is conical and globular in shape, with a sharp apex and relatively higher spire and distant body whorls. The aperture is oval. |
| Unranked clade<br>Heterobranchia/<br>Euthyneura/<br>Panpulmonata/<br>Hyrophila<br>Family PLANORBIDAE | *Planorbis* Müller, 1773<br><br>Rounded body whorl. Whorls regularly increasing in size, suture deep with close transverse growth lines, aperture oval, body whorl rounded, the first whorl on both sides depressed. |

B. Class Bivalvia

| Taxonomy | Taxon and its description |
|---|---|
| Order ARCIDA<br>Family ARCIDAE | *Anadara* Gray, 1847<br><br>Shell solid, inequivalve. Umbone in front of the midline, prosogyrate on top of a wide cardinal area. Ligament external, stretching across the cardinal area, with V-shaped grooves. About 28 radial ribs at each valve; radial ribs without a narrow median groove. Hinge elongate, almost straight, with numerous small transverse teeth which increase in size towards anterior and posterior ends. Interior of shell porcelaneous. |
| | *Arca* Linnaeus, 1758<br><br>Subrectangular, markedly inequilateral outline. Ligamental area-wide and almost flat, meeting the commissural plane of valves nearly at the right angle with the hinge line. Posterior margin sinuates, beak at the anterior, broad dorsal area with evidence of anterior ligament, blunt umbonal keel, sculpture of numerous radial riblets made beaded by crossing commarginal ridges. Umbo non-ventral keep sharply angulated. |

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| Family ARCIDAE/ NOETIIDAE | *Arcopsis* Koenen, 1885<br><br>Shell solid equivalve, subtrigonal trapezoidal to elliptical in shape, generally inequilateral and longer than high. Umbones often opisthogyrate, set apart from the dorsal margin by a trigonal cardinal area. Ligament external, stretching across the cardinal area, with oblique grooves and transverse striations. Outer surface with radial sculpture. Periostracum conspicuous, generally pilose. Hinge elongate, straightish to slightly arched with numerous small transverse teeth which somewhat increase in size towards anterior and posterior ends. Interior of shell porcelaneous. Two subequal adductor muscle scars, with a ridge or a shelf present along the inner margin of one or both scars. A pallial line without sinus. Internal margins of valves smooth or crenulated. |
| Family GLYCYMERIDIDAE | *Glycymeris* da Costa, 1778<br><br>Shell rounded-subquadrate in outline, moderately inflated slightly inequilateral with rounded anterior and obtusely pointed posterior margin. Umbones not very prominent, slightly opisthogyrate and in front of the midline of valves. External sculture weak, with very low rounded radial undulations and fine grooves, crossed by numerous, small concentric marks. |
| Order OSTREIDA Family OSTREIDAE Rafinesque, 1815 | Shell solid, often irregularly shaped, inequivalve, cemented to the substrate by the left (lower) valve which is generally larger and deeper. Right (upper) valve quite flat, often with thin, concentrically arranged, imbricating plates of horny material tending to make a protruding fringe beyond the shell margin. Outer surface commonly, at least on the left valve, with radial folds or ribs which may affect the shell margin. Ligamental area with a shallow median groove and two lateral thickenings. Hinge without teeth. Interior of shell porcelaneous, sometimes with irregular chalky deposits or with a subnacreous tinge. |
| Order PECTINIDA Family PECTINIDAE | *Amusium pleuronectes* (Linnaeus, 1758)<br><br>Shell thin, medium-sized (commonly attaining 8 cm in length), laterally compressed, almost circular in outline, gaping anteriorly and posteriorly. Nearly smooth externally, but with distinct internal radial ribs. |
| | *Amusium* Röding, 1798<br><br>Shell more or less inequivalve, usually with one valve more convex than the other; ovate to subcircular in outline with median low, orthogyrate umbones and a straight dorsal margin forming wing-like ears at both ends. |
| | *Mimachlamys* Iredale, 1929<br><br>Shell solid, medium-sized, higher than long and rounded-ovate in outline. Both valves are convex and subequal. Ears markedly unequal in size. |

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| Family PLACUNIDAE | *Placuna* Lightfoot, 1786<br><br>Shell thin and more or less translucent, almost circular in outline. Dorsal margin somewhat flattened to widely curved, sometimes faintly protruding anteriorly and posteriorly. Valves greatly compressed laterally, the lower (right) valve flat, the upper (left) valve with slight convexity. Commissural plane flat. Outer surface nearly smooth, excepting numerous, minute radiating threads forming tenuous wrinkles on the finely lamellate concentric lines of growth. |
| Family PLICATULIDAE | *Plicatula* Lamarck, 1801<br><br>Valve small, ostreiform, slightly curved, equivalved, slightly inequilateral, with the same degree of low convexity; right valve showing a relatively large area of attachment in the dorsal posterior beak region; shell sculpture of very broad fold-like radial ribs. |
| Order CARDITIDA<br>Family CARDITIDAE | *Cardites* Link, 1807<br><br>Shell subtrapezoidal in outline, not strongly expanded posteroventrally; sculpture of about 20 broad radial ribs. |
| Family CRASSATELLIDAE | *Bathytormus* Stewart, 1930<br><br>Small, elongate, sharply carinate. Sculpture of sharp relatively widely spaced concentric lamellae. |
| Order LUCINIDA<br>Family LUCINIDAE | *Cardiolucina* Sacco, 1901<br><br>Outer sculpture of narrow, rounded radial ribs and concentric cords, forming distinct nodules at the points of intersection all over the surface of the valves; hinge with well-developed cardinal and lateral teeth. |
| | *Myrtea* Turton, 1822<br><br>Shell ovate in outline and the surface is smooth and radial ribs forming a granulose surface. The umbones are centrally located and anteriorly curved, the ligament is external or partially internal, the hinge line smooth with weak cardinal and lateral teeth. |
| Order MYIDA<br>Family CORBULIDAE | *Corbula* (Aniscorbula) Iredale, 1930<br><br>Shell small, thick, ovate, more or less rostrate; valves unequal, the usually smaller and flatter; umbones prominent, prosygrate or erect, the right usually higher than the left; hinge line of right valve fitted with a single prominent tooth in front of the resilial pit; left valve with a chondrophore and a deep cardinal socket; surface sculpture usually concentric; adductor scars distinct; pallial line indistinct; sinus feeble or obsolete. |
| | *Varicorbula* Grant & Gale, 1931<br><br>Shell trigonal, rather thin but sturdy, bluntly truncated posteriorly, strongly inequivalve; left valve smaller, flatter, less rostrate; right valve larger, more inflated. Both valves concentrically sculptured, but discreptantly so; right valce with coarser, higher ridges; left valve with finer concentric ridges, crossed by radial ridges. Umbones prosogyrous, higher and more inflated in right valve, without nepionic caps. |

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| | Periostracum on the left valve forming overlapping foliations and radial lines, overhanging shell edge substantially. Right valve with a large knob-shaped tooth, articulating with a deep socket in the left valve. Elongated plate posterior to the socket of the left valve, including resilium-bearing chondrophore; complimentary right chondrophore on a shelf within embayment posterior to the tooth. Resilium oriented dorsoventrally; external ligament very small. Lateral teeth absent. Interior shell margins smooth. The deep interior groove running parallel to the ventral edge of the right valve, and continuing into lateral lamellae on either side of the hinge, into which margin of left valve inserts. Anterior muscle scar moderately large and crescent-shaped; posterior muscle scar oval and slightly larger. Pallial line entire; pallial sinus shallow but distinct. |
| Order VENERIDA Family KELLIELLIDAE | *Alveinus* Conrad, 1865<br><br>Equivalved, smooth; anterior, posterior, and ventral margins channeled within; hinge of right valve emarginated under the apex, and having one pyramidal tooth anteriorly; hinge of the left valve with a pit under the apex, and two compressed diverging teeth anteriorly; pallial line entire. |
| Family VENERIDAE Rafinesque, 1815 | Shell mostly solid, obliquely rounded in outline; with prominent umbones. Sculpture only concentric. Ligament external, behind the umbones, often inserted in a deep groove. Hinge with 3 usually radially disposed of cardinal teeth in each valve. Interior of shell porcelaneous. Two or more or less equal adductor muscle scars. Pallial sinus usually present. Internal margins smooth to denticulate. |
| | *Circe* Schumacher, 1817<br><br>Shell is more roundly trigonal and lacks the roundly truncated anteroventral margin. Very compressed laterally, about as long as high; umbones submedian and flattened. Pallial sinus very shallow hardly extending forwards beyond the posterior adductor scar. |
| | *Timoclea* T Brown, 1827<br><br>Shell very small, very inflated, obliquely trigonal. Anterior end broadly rounded, posterior one subangulate; ventral border broadly convex, somewhat being concave near the posteroventral corner. Beaks small and pointed. Hinge small and narrow consisting of two cardinal teeth and two thin lateral teeth on the right valve. Pallial sinus broad, shallow, triangular and pointed at the end. Surface sculptured with radial ribs and growth lines and becomes weaker or absent at the anterior part. |
| | *Venus* Linnaeus, 1758<br><br>Trigonal-ovate, subequilateral, compressed shell, anterior side oval, posterior one truncate, flattened umbonal area, lunule and escutcheon narrow, lanceolate, the former bounded by a distinct angulation, hingle with 3 elongate, radiating cardinals and 1 approximate, prominent anterior lateral in each valve, pallial sinus obsolescent, the sculpture of even commarginal cords that are are weaker over the umbonal area. |

| | |
|---|---|
| Order VENEROIDA<br>Family<br>CORBICULIDAE | *Corbicula gerthi* (Oostingh, 1935)<br><br>Shell has a rounded triangular shell with a clear asymmetry. The shell umbo is very robust, situated above the ligament, slightly rotated and directed to the front of the shell. The periostracum is glossy and covered with tightly spaced ribs. |
| | *Corbicula pullata* (Philippi, 1851)<br><br>Shell is a trigonal, subequilateral species with the ventral margin greatly arched, rounded anteriorly, and with a subtruncated posterior margin. The most single left valve is much higher than long and very inequilateral, while a few are more elongate. The sculpture consists of very regular, rather narrow but well-impressed ridges. |
| | *Corbicula* Megerle, 1811<br><br>Shell has an oval-triangular outline with prominent, more or less centrally located umbo. The sculpture is prominent with raised, regular concentric ribs. |
| Order UNIONIDAE<br>Family UNIONIDAE | *Elongaria orientalis* (Lea, 1840)<br><br>Shell oval-elongated, rounded at the front, and often pointed behind. Striated concentrically according to the growth lines. The dorsal and ventral margin is almost parallel, rather accurate in the dorsal margin, particularly old shell, the lower margin straight or slightly concave. The ligament is between the apex and the meeting point between the dorsal and posterior margin. Muscle scar in the upper half of the shell, connected by a fine pallial line without sinus. |
| Superorder<br>ANOMALODESMATA<br>Family<br>MYOCHAMIDAE | *Myochama* Stutchbury, 1830<br><br>Shell inequivalve, trigonal with small posteriorly inclined beaks, sculpture with strong rather widely spaced rounded concentric ridges, occasionally anastomosing. Pallial sinus of moderate depth. Hinge with a deep narrow wedge-shaped resilifer, flanked irregular ridges confluent with the hinge-plate. |
| Superoder<br>IMPARIDENTIA<br>Family<br>MESODESMATIDAE<br>Gray, 1840 | Shell equivalve, usually thick and heavy, more or less compressed laterally, inequilateral, elongate ovate or subtrigonal to wedge-shaped in outline. Umbones opisthogyrate. Outer surface smooth or mostly concentrically sculptured, with a well-developed and often glossy periostracum. External ligament short and not prominent, communicating with a strong internal ligament fitting in each valve in a deep pit of the hinge plate. Hinge with 1 or 2 cardinal teeth and more or less developed lateral teeth in each valve. Interior of shell porcelaneous. Two adductor muscle scars, subequal in size. Pallial line with a rather short sinus. Internal margins smooth. |

namely, *Myrtea, Amusium, Placuna, Plicatula, Timoclea* for bivalves and ? *Calliostoma, Polinices, Ringicula for gastropods* and *hard bottom dwellers, Arca* and *Arcopsis of Arcidae, Myrtea, Myochama, Placuna for bivalves* and *Vaceuchelus, Mitrella, Diodora,* and *Cymatium* for gastropods. They are mostly characterized as a near-shore, shallow marine environment. The genus *Anadara sp*. and other taxa from family Arcidae suggests the development of a wetland environment. The assemblages also imply that some areas in Sangiran were submerged while other parts started to develop shores at that time.

The diversity and ecological requirements of taxa identified in Kalibeng indicate a sublittoral soft substrate. They all live underwater, which suggests a submersion event. Deposition of *Placuna sp., Varicorbula sp.* and shell fragments from family Veneridae confirm this point, which is also supported by the presence of *Turritella sp.* They all lived in the neritic zone where the water is considered as shallow.

### 3.2 Bivalves and Gastropods Assemblage in the *Corbicula* Bed and Lower Pucangan

The shell assemblages from the *Corbicula* Bed and in the Lower Pucangan were recovered from the topmost level of Kalibeng layer and the Lower Lahar and the Black Clay layers of Sangiran dome. There are 27 mollusc taxa, 14 bivalves, and 13 gastropods from the marine and freshwater environments. Marine molluscs are present along with the freshwater molluscs in the Corbicula Bed. There are 10 marine bivalve taxa identified: *Amusium pleuronectes, Bathytormus sp., Cardites sp., Circe sp., Corbula sp., Glycymeris sp. Myrtea sp., Timoclea sp.,* and from the family Mesodesmatidae and Ostreidae (fragmented, juvenile, and unidentified species). Two marine gastropods were found in this formation, a fragmented *Diodora sp. and Trochoidea s.l.*

The lower lahar consists of gray andesitic volcanic tuff with rounded pebbles. It has freshwater fossils. The black clay conformably overlies the lower lahar and is widely distributed in the Sangiran dome. Freshwater mollusc taxa that are present both in the lower lahar unit and black clay layers have four bivalves and eleven gastropods. Freshwater bivalves are mostly composed of the Family Corbiculidae (Corbicula gerthi, Corbicula pullata, Corbicula sp.) and one from Family Unionidae, Elongaria orientalis. Gastropods in the Sangiran formation are represented by several taxa from the family Pachychilidae (Sulcospira testudinaria, Sulcospira sp. and ? Pachychilidae) and family Thiaridae (Tarebia granifera, Tarebia aff. granifera, Tarebia sp. Thiara winteri and Thiara sp.). The rest of the gastropods are Bellamya javanica and Planorbis sp., and one from the family Hydrobiidae.

Molluscan associations were verified through taphonomic analysis that reveals changing environments within the Lower Pucangan formation, from near-shore marine environments to freshwater continental sedimentation with lahar-infilled lagoons. Analogous associations were supported by the vast *Corbicula* that occurred in the *Corbicula* Bed.

Shell assemblages inhabited subsequent streams distributed in the central part of the dome during the early Pleistocene. The presence of shell species in lower Pucangan layers are positively correlated with the aquatic ecological diversity and habitat association (Table 3). The layers show an open environment with *Corbicula*, consistently present in all sampled sites. They are living in quiet streams and between sand and mud. The species richness indicates a landscape transformation with marine and freshwater molluscs especially with the presence of *Trochoidea* that can live in different zones and substrates. Endemic bivalve, *Elongaria*, lives in forest streams and present midden-like characteristics in the Lower Lahar and Black Clay deposits that may posit an aquatic mollusc consumption. These two facies have also terrestrial mammals living in a coastal marine or freshwater habitat in Sangiran. With the richness of *Elongaria* in the assemblage, considered as medium to large-sized shells and shell meat, and presence of terrestrial predators may lead to a symbiosis of aquatic exploitation (Joordens *et al.*, 2009). On the other hand, species abundance and richness of Thiariadae in the layer depicts shallow fast-flowing streams. They are widely distributed in Java and eat algae, rotted plant parts, carrion, and diatoms. Diatoms are evident in the Pucangan layer in Sangiran. Massive incidence of diatoms was observed in the Pablengan area where five species of Thiaridae were identified. This suggests another symbolic relationship and supports the sediment pattern and shell deposits in Sangiran.

**Table 2.** Ecological Distribution and Characteristics of Mollusc Taxa Recovered from the Kalibeng Layer

A. The Kalibeng Bivalve Molluscs

| Family | Taxon | Sublittoral Zone | | Substrate | | Habitat |
|---|---|---|---|---|---|---|
| | | Nearshore | Offshore | Soft | Hard | |
| Arcidae/ Noetiidae | | x | | x | x | Sedentary animals, nestling in rock crevices, or unattached and more or less buried in the soft-bottom. |
| Arcidae | *Anadara* Gray, 1847 | x | x | x | | On muddy bottoms, intertidal and sublittoral to a depth of 25 |
| Arcidae | *Arca* Linnaeus, 1758 | x | | | x | Fixed on rocks, corals, or under stones. Littoral and sublittoral waters to a depth of 20 m. |
| Arcidae | *Arcopsis* Koenen,1885 | x | | | x | Shallow water, under stones. Littoral and sublittoral to a depth of 25 m. |
| Corbulidae | *Corbula* (Anisocorbula) Iredale,1930 | x | x | x | | Lives on subtidal and intertidal mudflats, partially buried in soft sediment. Occasionally on the lower shore as well as in muddy sand and gravel and most are in abundant offshore. |
| Corbulidae | *Varicorbula* Grant & Gale, 1931 | x | | x | | Shallow water |
| Crassatellidae | *Bathytormus* Stewart,1930 | x | | x | | Shallow water in the littoral zone with soft and sand-mud bottoms. |
| Glycymerididae | *Glycymeris* da Costa,1778 | | x | x | | In sublittoral muddy-sand bottoms |
| Kellielidae | *Alveinus* Conrad, 1865 | x | | x | x | Sandy level-bottom in pelitic sample |
| Lucinidae | *Cardiolucina* Sacco, 1901 | | x | x | | Buried in sandy bottoms, often in coral reef areas, from shallow sublittoral waters to a depth of 20 m. |
| Lucinidae | *Myrtea* Turton, 1822 | | x | | x | Deep, offshore habitats with cohesive sandy mud (>20% mud) |
| Myochamidae | *Myochama* Stutchbury, 1830 | x | | | x | Intertidal sand flats to 20m, cemented to other shells or to rocks |
| Pectinidae | *Amusium* Röding, 1798 | | x | x | x | On sand and mud bottoms, sublittoral, from depths of 10 to 80 m. |
| Pectinidae | *Mimachlamys* Iredale, 1929 | x | x | x | | On a sand or muddy-sand bottoms with gravel, coral rubble, shell debris, or rocks. Littoral and sublittoral zones |
| Placunidae | *Placuna* Lightfoot, 1786 | x | x | | x | On the surface of soft muddy to sandy-mud bottoms, from low tide levels to a depth of about 100 m. |
| Plicatulidae | *Plicatula* Lamarck,1801 | x | x | x | | Intertidal and shallow subtidal waters, offshore on gravel bottom, 1 to 50 m, on hard substrates |
| Veneridae | *Timoclea* T. Brown,1827 | x | x | x | | Intertidal. Found in sand, muddy-sand, and gravel offshore, at depths ranging from 3 m to 180 m. |
| Veneridae | *Venus* Linnaeus,1758 | x | | x | | In shallow sandy areas |

| | | | | | | |
|---|---|---|---|---|---|---|
| Veneridae | | x | | x | | Inhabit muddy or sandy water just below the water surface and live in shallow to deep water. |
| Calloistomatidae | ?*Calliostoma* Swainson, 1840 | | x | x | x | Intertidal zone to mid-bathyal depths. Deep water, found mainly on hard substrates, although Japanese species have been found on sandy bottoms. |

B. The Kalibeng Gastropod Molluscs

| Family | Taxon | Sublittoral Zone | | Substrate | | Habitat |
|---|---|---|---|---|---|---|
| | | Nearshore | Offshore | Soft | Hard | |
| Cerithiidae | ? *Cerithium* Bruguière, 1789 | x | | x | x | Living on sandy to muddy bottoms of marine and estuarine environments, though small species may abound under rocks or on marine vegetation |
| Chilodontidae | *Vaceuchelus* Iredale, 1929 | x | | | x | Intertidal, living on the rocky substrate near shore |
| Columbellidae | *Mitrella* Risso, 1826 | x | | | x | Among stones and weed, common in coral reef areas. Intertidal and shallow subtidal waters. |
| Epitoniidae | *Epitomium* Röding, 1798 | x | | x | x | Subtidal to 29 m |
| Eulimidae | *Melanella* Swainson, 1840 | x | | Parasitic | | Sublittoral, muddy sediments |
| Fasciolariidae | *Fusinus* Rafinesque, 1815 | x | | x | | On sandy bottoms, intertidal and sublittoral zones |
| Fissurellidae | *Diodora* JE Gray, 1821 | x | | | x | Subtidal on rocks |
| Marginellidae | *Cryptospira* Hinds, 1844 | x | | x | | Shallow water, in mud |
| ?Muricidae | | x | | x | | On muddy littoral rocks |
| Nassariidae | *Nassarius* Duméril, 1805 | x | | x | | On clean sand bottoms, often associated with coral reefs. Intertidal and shallow subtidal zones |
| Naticidae | *Polinices* Montfort, 1830 | x | x | x | | On sandy to muddy bottoms. Intertidal to shelf zones, to a depth of about 100 m. |
| Olivellidae | *Olivella* Swainson, 1831 | x | | x | | Burrowing in sand bottoms, at shallow subtidal depths. |
| Pyramidellidae | *Chrysallida* Carpenter, 1856 | x | | x | | Shallow water, sand |
| Ranellidae | *Cymatium* Röding, 1798 | x | | | x | In coral reef areas, low tide marks and shallow sublittoral waters to a depth of about 15 m. |
| Ringiculidae | *Ringicula* Deshayes, 1838 | x | x | x | | Soft bottoms |
| Solariellidae | *Solariella* SV Wood, 1842 | x | | x | | Infralittoral and circalittoral and estuary |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Turridae | *Drillia* Gray, 1838 | x | | | x | x | Mostly living in soft substrates, but some species also occurring in r ock and coral reef habitats. May abound in sublittoral and shelf zones. |
| Turridae | *Gemmula* Weinkauff, 1875 | x | | | x | | Deep water, mostly living in soft substrates, but some species also occurring in rock and coral reef habitats. May abound in sublittoral and shelf zones. |
| Turritellidae | *Turritella* Lamarck,1799 | x | | | x | | On soft bottoms, from shallow sublittoral zones to a depth of about 30 m. |
| Turritellidae | *Turritella terebra* Linnaeus,1758 | x | | | x | | On soft bottoms, from shallow sublittoral zones to a depth of about 30 m. |

Distribution and species richness of molluscs within habitats in various facies of Lower Pucangan are controlled by complexly interrelated physical factors namely, basin size, water depth, energy levels, substrate, and sediment influx that varied in time and space during their deposition. The twenty-seven molluscan taxa from the *Corbicula* Bed and the Lower Lahar and Black Clay deposits in Lower Pucangan layer of the dome significantly picture low to high-energy flowing waters due to volcanic activity and oscillations that changed the hydrological courses, and to the nature of the basin that headed to landmass development. This is also in relation to elevation, highland or lowland, and the impact of sediment and water run-off in terms of gravity and soil contact to water movement at that time. Furthermore, the environment evolved into shallow, sublittoral lotic ecosystems that can tolerate disturbance in the environment concealed of emergent wetland vegetation.

## 4. Conclusion

A collection of molluscs preserved in Krikilan, Ngampon, Pablengan, Pondok, and Puren in Sangiran enables updating of palaeoecological and palaeoenvironmental data. For more than half a century, no data has been published on Sangiran fossil shells. The identified shells in this paper may be utilized as a reference for Sangiran and molluscan taxonomic representative in Kalibeng and Pucangan layers of Solo Basin in Central Java. Moreover, marine and freshwater shells examined can be deduced for the palaeoaquatic ecology of Sangiran of 2 Ma. They explored quantitative patterns recorded in mollusc assemblages to elucidate the palaeoenvironment and the relationship between the established palaeodatasets of analysis and the levels of variability in palaeontological data.

The Kalibeng mollusc assemblage exhibits generally similar overall composition and ecological marine structure with those that inhabited the soft bottom sublittoral zone. Species from the *Corbicula* Bed assemblages, characterized by the presence of numerous *Corbicula*, contained shell species that originated from both freshwater and marine environment. Mollusc assemblages from the Lower Lahar and Black Clay Pucangan were pure freshwater shells.

The studied samples do not contain mangrove shells, which is problematic to confer that the assemblage lived in an estuarine environment as compared to the previous studies conducted in Sangiran. Based on the pollen analysis in the first two lithographic units of Sangiran, the blue clay facies are dominated by mangrove forests and the black clay unit shows a decline of mangrove taxa (Sémah AM, 1982, 1984). However, the shell habitat and substrates inform us that it was a wetland environment, a land consisting of marshes or swamps.

**Table 3.** Ecological Distribution and Characteristic of Mollusc Taxa Recovered from the Pucangan Layer

A. The Marine Shells in Pucangan Formation

| Family | Taxon | Littoral zone | Sublittoral Zone | | Substrate | | Habitat |
|---|---|---|---|---|---|---|---|
| **Class Bivalvia** | | | **Nearshore** | **Offshore** | **Soft** | **Hard** | |
| Carditidae | *Cardites* Link, 1807 | x | x | | | x | On various littoral and shallow sublittoral bottoms. |
| Corbulidae | *Corbula* (Anisocorbula) Iredale, 1930 | | x | x | x | | Lives on subtidal and intertidal mudflats, partially buried in soft sediment. Occasionally on the lower shore as well as in muddy sand and gravel and most are in abundant offshore. |
| Crassatellidae | *Bathytormus* Stewart, 1930 | | x | | x | | Shallow water in the littoral zone with soft and sand-mud bottoms. |
| Glycymeridae | *Glycymeris* da Costa, 1778 | | | x | x | | In sublittoral muddy-sand bottoms. |
| Lucinidae | *Myrtea* Turton, 1822 | | | x | | x | Deep, offshore habitats with cohesive sandy mud (>20% mud). |
| Mesodesmatidae Gray, 1840 | | x | | | x | | Intertidal. In sandy bottoms and beaches. |
| Ostreidae Rafinesque, 1815 | | x | x | | x | x | Intertidal and shallow subtidal water. Attached to various hard substrates or objects, and on soft bottoms |
| Pectinidae | *Amusium pleuronectes* (Linnaeus, 1758) | | | x | x | x | On sand and mud bottoms. Sublittoral, from a depth of 10 to 80 m |
| Veneridae | *Circe* Schumacher, 1817 | x | x | | x | x | Shallow water in low intertidal to subtidal depths. Active burrowers in various soft bottoms, sometimes nestling in rock crevices or among marine growths. |
| Veneridae | *Timoclea* T. Brown, 1827 | | x | x | x | | Intertidal. Found in sand, muddy-sand, and gravel offshore, at depths ranging from 3 m to 180 m. |
| **Class Gastropodia** | | | | | | | |
| Fissurellidae | *Myochama* Stutchbury, 1830 | | x | | | x | Subtidal on rocks |
| Trochoidea (Superfamily) | *Amusium* Röding, 1798 | x | x | | x | x | Mostly littoral and shallow sublittoral, occurring in large numbers on hard substrates like rocky shores or coral reefs and in muddy-sand bottoms. |
| Mesodesmatidae Gray, 1840 | | x | | | x | | Intertidal. In sandy bottoms and beaches. |

B. The Freshwater Shells in Pucangan Formation

| Family | Taxon | Ecosystems | | Water Energy | | Habitat |
|---|---|---|---|---|---|---|
| Class Bivalvia | | Lotic | Lentic | Low | High | |
| Corbiculidae | *Corbicula gerthi* (Oostingh,1935) | x | | x | | In inland quiet rivers and streams |
| Corbiculidae | *Corbicula pullata* (Philippi, 1851) | x | | x | | In inland quiet rivers and streams to occasionally brackish water |
| Corbiculidae | *Corbicula* Megerle, 1811 | x | | x | | In streams and between sand and mud |
| Unionidae | *Elongaria orientalis* (Lea, 1840) | x | | | | Forest streams and sandy, shallow areas in lakes and rivers |
| **Class Gastropodia** | | | | | | |
| Hydrobiidae Stimpson, 1865 | | x | x | | | In lakes, ponds, rivers, and streams. Some found in brackish water or at the borders between freshwater and brackish water. A few occur in marine environments on sandy or muddy bottoms between algae and seagrass. |
| Pachychilidae | *Sulcospira* Troschel, 1857 | x | x | x | x | Rapid waters, eurytopic (able to tolerate a wide range of habitats or ecological conditions) |
| Pachychilidae | *Sulcospira testudinaria* (Köhler & Dames, 2009) | x | x | x | x | |
| ?Pachychilidae P Fischer & Crosse, 1892 | | | x | | x | In fast-flowing oxygenated water on hard substrates |
| Planorbidae | *Planorbis* Müller, 1773 | | x | x | | Vegetation-zone in stagnant water |

The changing environment has resulted in significant shifts in the density and distribution of Sangiran molluscs as revealed by the assemblages that were deposited on the different facies of Kalibeng and Pucangan layers. The approach provides a narrative of the relevant transformation of the aquatic ecology and elucidates the sources of variability on palaeontological patterns in Sangiran.

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