A new species of the genus *Heterogen* (Mollusca: Caenogastropoda: Viviparidae) from the Pleistocene Katata Formation of the Kobiwako Group, Shiga Prefecture, central Japan

**Keiji Matsuoka** 1 & **Takahiro Hirano** 2,3,*

1 Toyohashi Museum of Natural History, 1–238 Oana, Oiwa-cho, Toyohashi, Aichi 441–3147, Japan
2 Center for Northeast Asian Studies, Tohoku University, 41 Kawauchi, Aoba, Sendai, Miyagi 980–0862, Japan
3 Graduate School of Life Sciences, Tohoku University, 41 Kawauchi, Aoba, Sendai, Miyagi 980–0862, Japan

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**Abstract:** A new species of viviparid gastropod belonging to the genus *Heterogen* Annandale, 1921, is described from the Pleistocene Katata Formation of the Kobiwako Group in the southern part of Lake Biwa, central Japan. This new species is continuously recorded from the Nijigaoka Clays (1.2 Ma) to the Hiraen Clays (0.8 Ma) of the Katata Formation. This new species, *Heterogen praelongispira* sp. nov. is similar to the extant *H. longispira* in Lake Biwa, but the details of shell morphology are different from those of *H. longispira*, including fine-to-deep suture, flattened whorl side, and oval shape of embryonic shell.

**Key words:** ancient lake, benthos, fossil, Gastropoda

**Introduction**

Ancient lakes often provide excellent case studies addressing processes of speciation and phenotypic diversity because they have high species endemism and diversity (Cristescu et al. 2010). Lake Biwa is the oldest and largest lake in Japan originating in the early Pliocene (ca. 4 Ma: Yokoyama 1984, Kawabe 1989, 1994, Satoguchi 2012) and has been a hotspot of endemic freshwater mollusks since its formation (Strong et al. 2009, Miura et al. 2019, Hirano et al. 2019). Paleo-Lake Biwa is a historical series of lake and marsh environments from 4–0.4 Ma (Tabata et al. 2016), as the topographical and limnological features of Paleo-Lake Biwa successively changed following the Pliocene. The lake basin moved to the current location of Lake Biwa and was refilled about 1.2 Ma, and the enlargement of Lake Biwa to its present volume was estimated to have occurred approximately 0.4 Ma (Miura et al. 2019).

Around the current Lake Biwa, there are some sediments of the Plio-Pleistocene Kobiwako Group bearing fossils of freshwater mollusks (e.g., Matsuoka & Nakamura 1981, Matsuoka 1983, 1986, 1987). The Kobiwako Group consists of lacustrine and/or fluvial sediments divided into seven or eight formations based on their lithofacies: the Ueno, Iga, Ayama, Koka, Gamo, Kusatsu, Zeze, and Katata Formations (Yoshikawa 1984, Satoguchi 2012). The early Pleistocene Katata Formation (approximately 1.3–0.4 Ma) of the Kobiwako Group is mainly distributed in the Katata Hills to the west coast of Lake Biwa (Satoguchi 2012). The early Pleistocene Zeze Formation is sometimes considered to be part of the Katata Formation because both have similar lithofacies and their horizons partly overlap (Yoshikawa 1984, Satoguchi 2012). In this study, we consider that the Zeze Formation is included in the Katata Formation (Satoguchi 2012). Hayashi (1974) divided the Katata Formation into eight members in ascending order: Nijigaoka Clays, Kitahama Sands, Kisen Clays, Takashiro Alternations, Hiraen Clays, Kurihara Alternations, Saka- wa Clays, and Ryuge Sands and Gravels. The lowest horizon of the Nijigaoka Clays was deposited approximately 1.2 Ma (Satoguchi 2012).

The *Heterogen* Annandale, 1921 of the family Vivipari-
A new fossil species of the genus *Heterogen* dae Gray, 1847, was an endemic freshwater gastropod genus in Lake Biwa, with a monotypic species: *Heterogen longispira* (Smith, 1886). Recently, however, Hirano et al. (2015) showed that *H. longispira* is nested within a clade of *Cipangopaludina japonica* (von Martens, 1860) based on mitochondrial DNA sequences. Under these circumstances, an undescribed viviparid species was also recently discovered in the northern part of Lake Biwa (K. Nakai, unpublished data, Hirano et al. 2019: fig. 1, as *Heterogen* sp.). Our population genetic study indicated that these three species are genetically different but monophyletic (Hirano et al. 2019), so we used *Heterogen japonica* instead of *C. japonica* in this study. According to Hirano et al. (2019), the results of statistical analyses of shell morphology and qualitative evaluations indicated that *H. japonica* is clearly distinguished from *H. longispira* by shell morphology, including a round shape and relatively smooth surface, and *Heterogen* sp. is also clearly distinguished from *H. longispira* by shell morphology, including a round shape and the pattern of shell ornamentation.

Fossils of *H. longispira* (including the specimens previously identified) are continuously recorded from the Nijigaoka Clays to the Sakawa Clays of the Katata Formation (Matsuoka 1987). In 2000, we found fossils of *H. longispira* from the Nijigaoka Clays in excellent condition (Hirano et al. 2019). "*Heterogen longispira*" from the Nijigaoka Clays (1.2 Ma) to the Hiraen Clays (0.8 Ma) clearly differs from the fossils of the Sakawa Clays (0.5 Ma) and extant populations of *H. longispira* by the form of the adult and postembryonic shells (Hirano et al. 2019). Therefore, we describe *H. praelongispira*, sp. nov. based on these specimens. The description of the extinct species of *Heterogen* will provide valuable information to understand the ancestry and diversification history of *Heterogen* in the Paleolake Biwa and the current Lake Biwa.

**Materials and Methods**

Study materials, including type specimens, were obtained from Kokubu (locality 1) and Seifu Town (locality 2), Otsu City, Shiga Prefecture, Japan (Fig. 1). Each locality corresponds to Loc. F in Matsuoka and Miura (2013) and Loc. KT6 in Matsuoka (1987). The fossiliferous bed of locality 1 constitutes some horizons of the Ikenouchi II volcanic ash layer interbedded to the Katata Formation, which correlated to the lower part of the Nijigaoka Clays (Yoshikawa 1984, Kobiwako Research Group 1992). The fossiliferous bed of locality 2 also constitutes some horizons of the Biotite II volcanic ash layer interbedded to the Katata Formation, which correlated to the lower part of the Hiraen Clays (Matsuoka 1986). The viviparid gastropod, *H. praelongispira*, sp. nov. is predominant in the fossiliferous bed in each locality.

We measured the shell height and width of the collected fossils and photographed them using a digital camera (EOS Kiss X6i, Canon Inc., Tokyo, Japan) and STYLUS TG-4 Tough (Olympus Co., Tokyo, Japan). The measurements of apical angles were made using angle surveying instruments (Iwamoto Minerals Co., Tokyo, Japan).

Fossil specimens used for this study were deposited in the paleontological collections of the Toyohashi Museum of Natural History (TMNH), Toyohashi City, Aichi Prefecture.

**Systematic Descriptions**

*Family Viviparidae* Gray, 1847  
*Genus: Heterogen* Annandale, 1921  
*Type species: Heterogen turris* Annandale, 1921, original designation [= *Paludina longispira* Smith, 1886].  
*Heterogen praelongispira* sp. nov. (Mukashi-nagatanishi) (Fig. 2)

*Heterogen longispira* (Smith)—Matsuoka (1986): p. 83, pl. 15, figs. 4, 5.  
*Heterogen longispira* — Hirano et al. (2019): p. 5035, fig. 1 [Nijigaoka Clays (1.2 Ma)]

*Material examined:* Holotype. Kokubu, Otsu City, Shiga Prefecture, Japan, lat. 34°58′13″N, long. 135°53′33″E, muddy fossiliferous bed about 20 meters below ground (the Nijigaoka Clays of the Pleistocene Katata Formation), coll. K. Matsuoka, 6 March 2000, [TMNH10245: adult, 44.8 mm (shell height), 26.9 mm (shell width)].

Paratypes. Five individuals: collected with the holotype in the type locality [TMNH10214: adult, 49.2 mm (shell height), 30.1 mm (shell width); TMNH10443: adult, 55.7 mm (shell height), 33.9 mm (shell width); TMNH10635: adult, 48.3 mm (shell height), 28.7 mm (shell height)].
(shell width); TMNH10275: adult, 47.5 mm (shell height), 30.4 mm (shell width), TMNH10573: juvenile, 9.0 mm (shell height), 7.4 mm (shell width).

Two individuals: Seifu Town, Otsu City, Shiga Prefecture, Japan, lat. 35°8′28″N, long. 135°54′30″E, an exposure created by the construction of a housing complex (the Hiraen Clays of the Pleistocene Katata Formation), coll. K. Matsuoka, May 2, 1982, [TMNH10245: adult, 44.0 mm (shell height), 33.5 mm (shell width)].

Other specimens. 12 individuals: collected with the holotype in the type locality [TMNH10225: adult, 49.6 mm (shell height), 30.3 mm (shell width); TMNH10631: adult, 48.0 mm (shell height), 29.8 mm (shell width); TMNH10227: adult, 42.6 mm (shell height), 26.8 mm (shell width); TMNH10256: adult, 39.2 mm (shell height), 28.9 mm (shell width); TMNH10764: adult, 44.0 mm (shell height), 33.5 mm (shell width)].

Fig. 2. Heterogen praelongispira sp. nov. A: Holotype, postembryonic shell (TMNH10245). B: Paratype, postembryonic shell (TMNH10635). C: Paratype, postembryonic shell (TMNH10635). D: Paratype, postembryonic shell (TMNH10635). E: Paratype, postembryonic shell (TMNH10275). F: Paratype, postembryonic shell (TMNH10443). G: Paratype, postembryonic shell (TMNH10214). H: Postembryonic shell (TMNH10264). I: Postembryonic shell (TMNH10510). J: Postembryonic shell (TMNH10488). K: Paratype, early embryonic shell (TMNH10573). L: Paratype, postembryonic shell (TMNH10763). M: Paratype, postembryonic shell (TMNH10764). The specimens of A–K and L–M were recorded from the Nijigaoka Clays (locality 1) and Hiraen Clays (locality 2), respectively. Scale bars for A–I and L–M, and J–K indicate 1 cm and 5 mm, respectively. Each photograph of the individual shows an apertural view (left) and dorsal view (right).
A new fossil species of the genus Heterogen

**Table 1.** Measurements of the new viviparid species *Heterogen praelongispira* sp. nov.

| H      | W  | BWL | AH  | AA  | Clay (Locality in Fig. 1) |
|--------|----|-----|-----|-----|---------------------------|
| TMNH 10245 (Holotype) | 44.8 | 26.9 | 31.5 | 22.1 | 48 | Nijigaoka (Locality 1) |
| TMNH 10214 (Paratype) | 49.2 | 30.1 | 35.4 | 24.8 | 51 | Nijigaoka (Locality 1) |
| TMNH 10443 (Paratype) | 55.7 | 33.9 | 38.5 | 26.0 | 47 | Nijigaoka (Locality 1) |
| TMNH 10635 (Paratype) | 48.3 | 28.7 | 34.3 | 24.1 | 49 | Nijigaoka (Locality 1) |
| TMNH 10275 (Paratype) | 47.5 | 30.4 | 36.0 | 26.1 | 51 | Nijigaoka (Locality 1) |
| TMNH 10573** (Paratype) | 9.0 | 7.4 | 8.1 | 6.5 | 90 | Nijigaoka (Locality 1) |
| TMNH 10225 | 49.6 | 30.3 | 38.0 | 26.5 | 56 | Nijigaoka (Locality 1) |
| TMNH 10631 | 48.0 | 29.8 | 34.9 | 23.6 | 47 | Nijigaoka (Locality 1) |
| TMNH 10227 | 42.6 | 26.8 | 32.6 | 23.0 | 54 | Nijigaoka (Locality 1) |
| TMNH 10256 | 39.2 | 22.6 | 28.7 | 19.1 | 46 | Nijigaoka (Locality 1) |
| TMNH 10264 | 34.3 | 20.1 | 24.5 | 17.9 | 45 | Nijigaoka (Locality 1) |
| TMNH 10270 | 52.0 | 30.7 | 38.7 | 26.9 | 44 | Nijigaoka (Locality 1) |
| TMNH 10279 | 43.6 | 27.7 | 30.4 | 22.8 | 47 | Nijigaoka (Locality 1) |
| TMNH 10510 | 25.2 | 15.8 | 18.6 | 13.6 | 49 | Nijigaoka (Locality 1) |
| TMNH 10511 | 19.3 | 12.9 | 15.4 | 11.5 | 41 | Nijigaoka (Locality 1) |
| TMNH 10568** | 6.4 | 6.6 | 5.6 | 4.5 | 96 | Nijigaoka (Locality 1) |
| TMNH 10570 | 11.8 | 8.8 | 9.6 | 7.1 | 42 | Nijigaoka (Locality 1) |
| TMNH 10649 | 52.5 | 30.2 | 38.2 | 26.2 | 49 | Nijigaoka (Locality 1) |
| TMNH 10763 (Paratype) | 39.4 | 28.9 | — | 20.5 | — | Hiraen (Locality 2) |
| TMNH 10764 (Paratype) | 44.0 | 33.5 | — | — | — | Hiraen (Locality 2) |

H = shell height, W = shell width, BWL = body whorl length, AH = aperture height, AA = apical angle, H, W, BWL, and AH are indicated in mm. AA is indicated in degree. ** embryonic shell. Some morphological traits of the specimens from the Hiraen Clays are not measurable (—). 

22.6 mm (shell width); TMNH10264: adult, 34.3 mm (shell height), 20.1 mm (shell width); TMNH10270: adult, 52.0 mm (shell height), 30.7 mm (shell width); TMNH10279: adult, 43.6 mm (shell height), 27.7 mm (shell width); TMNH10510: juvenile, 25.2 mm (shell height), 15.8 mm (shell width); TMNH10511: juvenile, 19.3 mm (shell height), 12.9 mm (shell width); TMNH10568: juvenile, 6.4 mm (shell height), 6.6 mm (shell width); TMNH10570: juvenile, 11.8 mm (shell height), 8.8 mm (shell width); TMNH10649: adult, 52.5 mm (shell height), 30.2 mm (shell width).

Measurements of the type material and other specimens examined are given in Table 1.

**Diagnosis:** Shell medium to large, thick, broadly conic, about four remaining whorls with eroded apex. Suture deep. Sutural ramp weakly convex with fine growth lines. Embryonic shell oval, early shell turbiniform, with subangular periphery.

**Description:** Shell medium to large, up to approximately 56 mm long (Table 1), elongately conic, moderately thick. Spire elevation consists of five whorls, comprising about half of height in lacking embryonic and postembryonic shells. Apical angle approximately 50° on average (n=16; Table 1). Last whorl rounded periphery with development sutural ramp, ornamented by fine growth lines and their rest marks at irregular intervals: having frequently spiral lirae distinct on convex surface. Subsutural whorl profile weakly convex, rounded periphery, basal part of whorl rounded. Suture fine to deep, impressed. Surface of postembryonic shell ornamented by fine growth lines, their rest marks at irregular intervals, and produce slight carina on last whorl. Width approximately two-fifth of height. Aperture slightly oblique and pyriform, broadly rounded anteriorly and narrowed posteriorly. Outer lip thin, inner lip almost sealing umbilicus. Columellar lip smooth, oblique, visible in growth lines on base. Embryonic shell oval, approximately two-fifth periphery subangular, suture fine, spire whorls rounded. Early embryonic shell turbiniform, body whorl keeled periphery, aperture shape quadrate, umbilicus narrow.

**Derivation of name:** This species is named from prae- (Latin, prefix meaning before) and the specific name of *Heterogen longispira* Smith.

**Remarks:** *Heterogen praelongispira* sp. nov. corresponds to specimens identified as *H. longispira* from the Nijigaoka Clays to the Hiraen Clays, Katata Formation in previous studies (Matsuoka 1986, 1987, Matsuoka & Miura 2018, Hirano et al. 2019). The entire shell outline is similar to that of *H. longispira* from the Sakawa Clays of the Kata-ta Formation (Matsuoka & Nakamura 1981: pl. 41, figs. 2a–b), but it is distinguishable from the fossils and extant populations of *H. longispira* by shell shape (Hirano et al. 2019), including fine-to-deep suture, flattened whorl side, and oval shape of embryonic shell. According to Hirano et
al. (2019), this new species also has a different shell shape from that of Lake Biwa endemic *Heterogen* sp. and the fossil species *Igapaludina stricta* (Araki, 1960). In addition, *I. stricta* appeared at different times (3.4–2.4 Ma: Matsuoka 1985).

**Discussion**

*Heterogen praelongispira* sp. nov. from the Nijigaoka Clays to the Hiraen Clays of the Katata Formation was distinguished from *H. longispira* by the morphologies of the adult and embryonic shells (Hirano et al. 2019). The divergence pattern of shell morphology in viviparid snails may be associated with habitat differences (Hirano et al. 2015, 2019). Although some populations of *H. japonica* were found in the estuary of rivers flowing into the lake in the past (Matsuoka pers. obs.), in general, *H. longispira* is quite isolated from *H. japonica* in Lake Biwa, the latter being restricted to the rice fields and inner lakes (Tomoda 1978). *Heterogen* sp. is found on the 7 m down of the rocky shore of Chikubushima Island in Lake Biwa (Hirano et al. 2019). In addition, shell morphologies of viviparid snails easily change under the influence of the environment even within species [individuals of *Sinotaia quadrata histrica* (Gould, 1859) sampled in the lagoon had thicker and more elongated shells with narrower apertures than those sampled outside the lagoon (Kagawa et al. 2019)].

Lake Biwa was shallower than it is in the present day (Miura et al. 2019). Prey-predator interactions may be associated with the parallel evolution of these shell phenotypes (Hirano et al. 2019). Alternatively, wave action (Yamazaki & Goshima 2012) and calcium content in water could also affect components of shell morphology such as hardness and the existence of ornamentation (Charrier et al. 2012). Although functions of shell morphology of *H. longispira* and *H. praelongispira* sp. nov. and phylogenetic relationships between them are unclear, differences in each habitat might influence shell morphology of the species.

These extant species and fossil species of *Heterogen* have different shell morphologies, but both species seem to adopt the same reproductive strategies because of the sizes of the offspring and the thickness of the shells. In fact, *H. longispira* produces a lower number of larger offspring (k-strategy) with a thick shell, but *H. japonica* produces a higher number of smaller offspring (r-strategy) with a thin shell (Okutani 1986, Kihira et al. 2003). Such changes may have occurred multiple times in the evolutionary history of viviparid snails (Zhang et al. 2015, Hirano et al. 2019). *Heterogen praelongispira* sp. nov. also has relatively larger offspring with a thick shell (Table 1). Therefore, Lake Biwa has affected not only morphological patterns but also reproductive strategies of endemic viviparid snails (Hirano et al. 2019).

The viviparid gastropods from the Pleistocene Katata Formation have been reported to be two extant species, *H. longispira* and *H. japonica* (Matsuoka & Nakamura 1981, Matsuoka 1983, 1986, 1987). The present findings distinguished *H. praelongispira* sp. nov. from Nijigaoka Clays to the Hiraen Clays and/or the Kurihara Alternations, which were deposited about 0.8 Ma. Associated with *H. praelongispira* sp. nov., the following species occur: *Semisulcospira* (Biwamelania) *spinulifera*, *S. (B.) pusilla*, *S. (B.) kokubuensis*, and *Gabbia longicornis*, along with their accompanying unidentified unionid bivalves (Matsuoka & Miura 2018). None of these species were recorded from the Sakawa Clays and other younger layers, suggesting that extinction of these fossil species occurred and the extant endemic molllusks, including *H. longispira*, were extirpated about 0.5 Ma. However, the divergence of fossil species and how malacological fauna of Lake Biwa was changed are still unclear, so further paleontological studies are needed.

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