

The genera *Tetrarca* (Subfamily Cucullaeinae), *Arca*, and *Lamarcka*, new genus (Subfamily Arcinae), with special reference to the history of cold adaptation in North Pacific *Tetrarca boucardi* (Bivalvia: Arcidae)

Geerat J. Vermeij

Department of Earth and Planetary Sciences
University of California-Davis
One Shields Avenue
Davis, CA 95616, USA

Kazutaka Amano

Joetsu University of Education
1 Yamayashiki
Joetsu 943-8512, JAPAN

ABSTRACT

Adaptation to cold shallow water characterizes several lineages in the bivalve family Arcidae. One of these, *Arca boucardi* Jousseaume, 1894, differs from *Arca* Linnaeus, 1758 both morphologically and in molecular characters. Here we formally propose that this northwest Pacific species, along with several other fossil and extant species, belongs to the cold-water genus *Tetrarca* Nordsieck, 1969 in the Cucullaeinae. In addition, we re-examine the genus *Arca* and propose the new genus *Lamarcka* for *Arca avellana* Lamarck, 1819 and related tropical species. *Tetrarca* is inferred to have a southern-hemisphere origin. The extant *T. boucardi* is inferred to have migrated to East Asia from the northeast Pacific, where the genus *Tetrarca* became extinct in the early Pleistocene. Cold adaptation in *T. boucardi* and in *Scapharca broughtoni* Schrenck, 1867 took place in the northwest Pacific.

Additional Keywords: Neogene, cold water, temperate

INTRODUCTION

Many clades of primarily warm-water species contain lineages that have become adapted to cold water. The question where, when, and how cold adaptation was achieved is important in light of the fact that thermal tolerances of species tend to be highly conservative, and that many species today must contend with a rapidly changing climate. Most speciation events take place within rather than between climatic zones, indicating that transitions from one thermal regime to another are relatively infrequent, and that most lineages do not make them. In order to answer questions about cold adaptation, it is necessary first to identify the correct phylogenetic position of lineages that have made the transition to cold climates, and then to establish the location and timing of change and the potential for dispersal of the new lineage to other similar climatic regions elsewhere (Vermeij, 2018; Vermeij et al., 2019).

The bivalve family Arcidae is a group in which adaptation to cold conditions can be fruitfully studied. The combination of a rich fossil record and a robust phylogenetic hypothesis for the family (Combosch and Giribet, 2016; Feng et al., 2015; Kong et al., 2020) makes it possible to infer the origins of cold-water lineages. Among shallow-water marine arcids, warm-temperate lineages of Neogene members of the subfamily Anadarinae have already been documented for the North Pacific (Moore, 1983; Noda, 1966), the northwest Atlantic (Ward, 1992), and southern South America (Frassinetti and Covacevich, 1993; del Río, 1991; del Río, 1992). Temperate members of “Arcinae” are known from New Zealand (Beu, 1973), the North Pacific (see below) and southern South America (del Río, 1991; del Río, 1992). Cool-temperate shallow-water species are, however, known only in the northwest Pacific, where *Scapharca broughtoni* became adapted to low-boreal conditions during the middle Pleistocene (Amano and Komori, 2021); *A. amicu-la* (Yokoyama, 1925) in the late Miocene (Amano and Koike, 1993); *Barbatia neozealanica* (Smith, 1915) in the early Pliocene to Recent of southern New Zealand; and “*Arca*” *boucardi* Jousseaume, 1894, may have done so earlier. This paper is concerned with the last species.

The genus *Arca* Linnaeus, 1758 in its traditional sense comprises tropical and subtropical species extending back to at least the middle Eocene (Reinhart, 1943). They are found in all warm seas, where they are members of epifaunal communities and are attached by a byssus. A few northern and southern cool-temperate species have also traditionally been assigned to *Arca*, including late Oligocene to Pleistocene species in New Zealand (Beu, 1973; Beu and Maxwell, 1990), Argentina (del Río, 1991; del Río, 1992; del Río and Camacho, 1998), California (Hall, 1964; Moore, 1983), and *A. boucardi* from northeast Asia. Molecular data on *A. boucardi*, however, indicate that this species is not related to *Arca* but is instead closer to the subfamily Cucullaeinae (Combosch and Giribet, 2016;

Feng et al., 2015). This species was therefore considered to be a member of the genus *Tetrarca* Nordsleck, 1969, whose type species, *Arca tetragona* Poll, 1795, extends to cold waters in the North Atlantic (Oliver and Chesney, 1994; Oliver and von Cosel, 1992). Here we reconstruct the history and taxonomy of *Tetrarca* and comment on the history and taxonomy of *Arca*, with the proposal of the new genus *Lamarcka* for one group of tropical species formerly assigned to *Arca*.

SYSTEMATICS

Family Arcidae Lamarck, 1809

Subfamily Arcinae Lamarck, 1809

Genus *Arca* Linnaeus, 1758

Type Species: *Arca noae* Linnaeus, 1758

Remarks: Species of *Arca* in its traditional sense are characterized by an equivalve, antero-posteriorly elongated shell, a wide cardinal area, beaks placed well anterior to the midline of the hinge and shell, a variably large byssal gape, and usually low radial ribs, as well as by a rather sharp postero-dorsal keel. The posterior or postero-dorsal margin is throughout sinuated. The valves are strongly inflated and the hinge line is very long and straight. The inner edge of the ventral margin is smooth around the byssal gape, and may be smooth or crenulated elsewhere. The hinge teeth are numerous and rather uniform along the length of the hinge line. The adductor muscle scars are not raised on a flange or platform.

Earlier authors identified three or four groups of species in the genus *Arca* (Huber, 2010; Lutaenko and Maestrati, 2007; Oliver and Holmes, 2006; Vermeij, 2013). One group, which contains the type species *A. noae* from the Mediterranean and West Africa, as well as other tropical species, is referred to here as *Arca* in the strict sense. It is characterized by a highly elongate shell, having a protruding posterior wing and sulcus, a pointed anterior end, a vertical posterior margin that is strongly indented, well developed radial ribs, and an inner valve margin that is usually ventrally crenulated on its posterior sector. Lutaenko and Maestrati, (2007) refer to this as their Group II. An extreme version is represented by the taxon *Arcoptera* Heilprin, 1887, containing the single species *A. wagneriana* Dall, 1898 from the early Pleistocene of Florida. In that species, the hinge line extends to a posterior point, below which the posterior margin slopes anterior to the posteroventral corner; the anterior end comes to a long, acute point. We consider *Arcoptera* to be an extreme member of *Arca*, which has assumed a semi-infaunal mode of life instead of the more typical epibyssate habit. We also include in *Arca* in the strict sense the sole member of Lutaenko and Maestrati's (2007) Group III, *Arca koumaci* Lutaenko and Maestrati, 2007. This diminutive species from the Indo-West Pacific, distinguished by a rounded ventral

margin and a sharp posterior keel bearing tiny spines, resembles miniature *A. navicularis* Bruguière, 1798, an undoubted member of *Arca* s. s.

In addition to the species mentioned above, we include the following extant species in *Arca*: *A. bouvieri* Fischer, 1874, from West Africa; *A. pacifica* Sowerby, 1833 from the eastern Pacific; *A. zebra* Swainson, 1833 from the western Atlantic; and *A. symphenacis* Oliver and Chesney, 1994, from the Indo-West Pacific. Additional fossil species include *A. aquila* Heilprin, 1887, from the early Pleistocene of Florida; *A. budoensis* Amano and Kurita, 2020 from the late early Miocene of Japan; *A. noae biangulina* d'Orbigny, 1852, from the early Miocene of France; and *A. paratina* Dall, 1898 and its ancestral subspecies *A. p. tampae* Mansfield, 1937, from the early Miocene of Florida.

A second group (Group I of Lutaenko and Maestrati, 2007), typified by the Indo-West Pacific *Arca avellana* Lamarck, 1819, but also containing other tropical species, is distinct morphologically and in molecular phylogenetic analyses (Combosch and Giribet, 2016; Feng et al., 2015; Vermeij, 2013). Compared with *Arca* in the strict sense, this group is characterized by a less elongate shell in which the posterodorsal margin is obliquely rather than vertically truncated, the radial ribbing is much finer, the anterior end is rounded rather than pointed, and the inner margin of the ventral shell edge is usually smooth throughout. Lutaenko and Maestrati (2007) also included *Arca tetragona* Poli, 1795 and *A. boucardi* in this group, but we exclude them here (see below). Following the recommendation of Combosch and Giribet (2016), and given the differences with *Arca* previously noted by Oliver and Holmes (2006) and Vermeij (2013), we propose a new genus for this second group that was previously attributed to *Arca*.

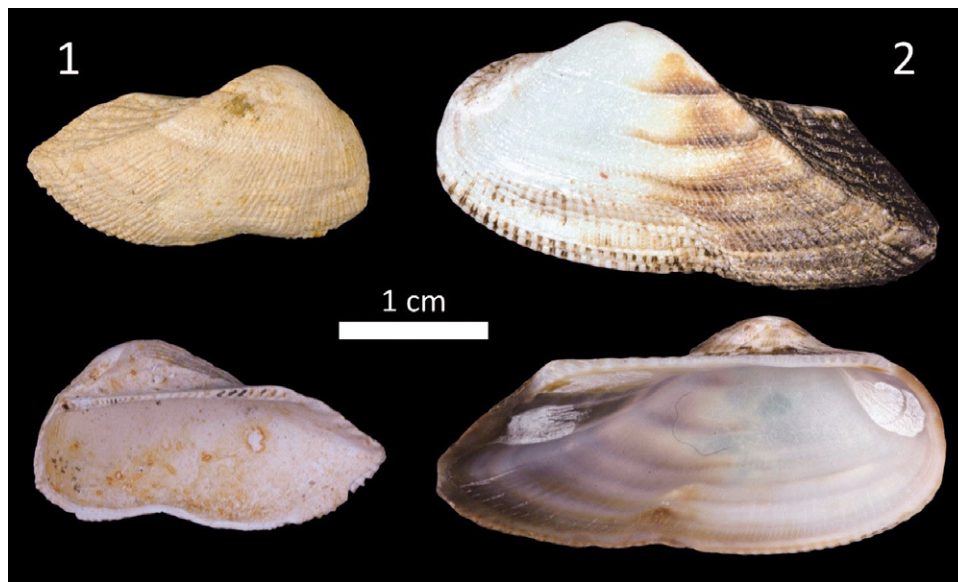
Genus *Lamarcka* new genus

Type Species: *Arca avellana* Lamarck, 1819 (Recent, Indo-West Pacific).

Description: Shell anteroposteriorly somewhat elongate, anteriorly rounded, posteriorly obliquely truncate, with a generally well-marked keel from the umbones to the posteroventral corner, separating the posterior sector from the rest of the shell; sculpture consisting of fine radial ribs and imbricating growth lines, the latter particularly distinct on the posterior keel; ventral margin with a byssal gape, usually smooth throughout on its inner edge.

Etymology: Named for J.B.P.A. de Lamarck, author of the type species.

Other Included Species: RECENT SPECIES – *L. avellana turbatrix* (Oliver and von Cosel, 1992), West Africa; and the Indo-West Pacific *L. ventricosa* (Lamarck 1819); *L. angulata* (King and Broderip, 1831), *L. imbricata* (Bruguière, 1789), western Atlantic; *L. mutabilis* (Sowerby, 1833), eastern Pacific; and *L. truncata* (Sowerby, 1833), eastern Pacific.



Figures 1–2. Two specimens of *Tetrarca boucardi*. **1.** Fossil specimen from the upper Pleistocene Anden Formation in Akita Prefecture, northern Honshu of Japan (outer and inner views). **2.** Recent specimen from Tanihama, Joetsu in Niigata Prefecture, central Honshu of Japan (outer and inner views).

FOSSIL SPECIES—*L. bowdeniana* (Dall, 1898), Pliocene, Jamaica; *L. emiliae* (Dollfus, 1909), early Miocene, France (see Lozouet et al., 2003); *L. subcontracta* (Heilprin, 1882), early Oligocene, Mississippi (see Dockery III, 1982). *L. sakamizuensis* (Hatai and Nisiyama, 1952), Oligocene, Kyushu; ? *L. uedai* (Matsubara, 2002), Paleogene, Maejima, Southwestern Honshu; *L. williamsi* (Olsson, 1967), Pliocene, Florida.

Subfamily Cucullaeinae Lamarck, 1809

Genus *Tetrarca* Nordsieck, 1969

Type Species: *Arca tetragona* Poll, 1795 (Recent, Mediterranean)

Remarks: As noted by Combosch and Giribet, (2016), *Tetrarca* differs from *Arca*, *Lamarcka* and most other Arcidae by having a posterior flange on which the posterior adductor scar is situated. This feature characterizes members of the Cucullaeinae, a group to which *Tetrarca* (as represented by *T. boucardi* (Jousseaume, 1894) (Figures 1, 2) in molecular analyses) is closely related (Combosch and Giribet, 2016; Feng et al., 2015). In addition, the ventral margin of the valves is internally crenulated (see also Vermeij, 2013) and the strong ridge from the beak to posteroventral corner.

Oliver and Chesney (1994) assigned the following extant species to *Tetrarca*: *A. tetragona* from the northeast Atlantic, ranging from West Africa north to 69.5° N (Hørsæter, 1986); *T. acuminata* Krauss, 1848 from southern Africa; *T. a. dayi* Oliver and Chesney, 1994 from the upwelling zone in the Gulf of Oman; and *T. boucardi*. In addition, Oliver in Valentich-Scott et al. (2020) assigned *Arca fernandezensis* Hertlein and Strong, 1943, from the

Juan Fernandez Islands, Chile, to *Tetrarca*. The genus *Tetrarca* therefore occurs in cool waters in both the northern and southern hemispheres.

DISCUSSION

Until now, the fossil record of *Tetrarca* had not been systematically investigated. Marquet (2002) summarized fossil occurrences of *T. tetragona*, and noted that this species is known as early as the Tortonian (late Miocene) of Portugal and also occurs in the Pliocene of the North Sea Basin. In the northwest Pacific, *T. boucardi* is recorded (as *Arca praeboucardi* Sinel'nikova in Gladenkov and Sinel'nikova, 1990) from the lower middle Miocene Kakert and Ilyin horizons of Kamchatka (Gladenkov et al., 1984; Gladenkov and Sinel'nikova, 1990), as well as from the lower Miocene and many younger formations in Japan (Noda, 1966). No earlier species have been recorded from temperate East Asia.

In the northeast Pacific, two definite and one possible species can be confidently attributed to *Tetrarca* from the Cenozoic of western North America. These are *Arca leptogrammica* Hall, 1964 from the Santa Margarita Formation (early middle Miocene; Prothero, 2001) of San Luis Obispo County, California, and *A. sisquocensis* Reinhart, 1937 from the Pliocene and Pleistocene of southern California. Woodring in Woodring and Bramlette (1950) and Hall (1964) had already drawn attention to the similarities of these two species with *T. boucardi* (see also Moore, 1983). Both taxa have the essential features of *Tetrarca*. A possible third member of *Tetrarca* from western North America is the small-bodied *Arca washingtoniana* Dickerson, 1917 from the Gries Ranch Formation (latest Eocene;

Prothero, 2001) of Washington State (see Weaver, 1942, and Durham, 1944 for good descriptions). There is no living species assignable to *Tetrarca* in the northeast Pacific.

We hypothesize that the northwest Pacific *T. boucardi* arose from a lineage that originated in the warm-temperate northeast Pacific. The ancestor of *T. boucardi* would have migrated westward during or just before the early Miocene, when ocean temperatures across the North Pacific were relatively warm. Cold adaptation in *T. boucardi* likely took place soon thereafter given that the early records of this species are what were even then cold-temperate conditions in Kamchatka (Kafanov and Volvenko, 1997). In the northeast Pacific, *Tetrarca* remained in warm-temperate conditions until its regional extinction in the early Pleistocene.

This biogeographical pattern of early Miocene westward migration of lineages from the northeast Pacific to East Asia is consistent with the history of numerous other molluscan groups (for summaries see Amano and Kurita, 2020; Vermeij et al., 2019). Many of these groups, including *Tetrarca*, adapted to cold-water conditions in the northwest Pacific rather than in western North America.

As noted above, *Tetrarca* occurs in the temperate zones of both hemispheres. It is therefore instructive to ask how this distribution was achieved, and in particular how *Tetrarca* came to occupy the North Pacific. A possible southern-hemisphere origin of *Tetrarca* is indicated by several species in the temperate late Paleogene and Neogene faunas of New Zealand and Argentina. In Argentina, two species that were tentatively assigned to the subgenus *Eonavicula* Arkell, 1929 have the hinge and muscle-scar characteristics of *Tetrarca*. These are *Arca* (*Eonavicula*?) *patagonica* von Ihering, 1897 from the Monte Leon Formation (late Oligocene) and *A. (E.?) puntaensis* del Río and Camacho, 1998 from the San Julian Formation (late Eocene) (see del Río and Camacho, 1998). These taxa resemble species assigned to *Arca* from New Zealand, collectively ranging from the late Oligocene to the early Pleistocene (see Beu, 1973; Beu and Maxwell, 1990). Pending examination of these southern-hemisphere species, we suggest that they belong to *Tetrarca* rather than to the primarily Mesozoic taxon *Eonavicula*, and therefore that the genus *Tetrarca* originated from some cucullaeine ancestor in the southern hemisphere during the Paleogene. In this connection it is interesting to note that the Cucullaeinae, a primarily Mesozoic subfamily (Nicol, 1954), persisted to the middle Miocene in Chile (Frassinetti and Covacevich, 1993) and the late Oligocene of Argentina (del Río and Camacho, 1998). The genus *Cucullaea* Lamarck, 1801 is today represented by one or two Indo-West Pacific species, but it has a broader distribution, including the southern (but not northern) hemisphere during the Paleogene. The shells of most cucullaeines are much less antero-posteriorly elongate than in *Tetrarca*, but they share with *Tetrarca* the well-developed posterior adductor flange and the ventrally crenulated margin. If this scenario is correct, *Tetrarca* would represent a strong case of convergence with *Arca* and *Lamarckia*, and would imply a transition

from infaunal to epifaunal habits. Like a number of other lineages with a temperate southern-hemisphere origin, *Tetrarca*'s spread to the North Pacific would have occurred during the latest Eocene, when the eastern Pacific tropics were likely cooler than they are today (Vermeij et al., 2019).

The origin of the North Atlantic *T. tetragona* remains obscure, but may indicate a second northward dispersal in the genus. If *Tetrarca* originated in the southern hemisphere, *T. fernandezensis* and *T. acuminata* would represent relicts of a once more widely distribution that included Argentina and New Zealand. *T. tetragona* would then be the result of dispersal from southern Africa northward. Vermeij (1993) proposed a similar northward dispersal for the extinct muricid gastropod genus *Spinuella* Vermeij, 1993, part of a larger clade of Ocenebrinae with presumed southern-hemisphere origins that also includes a number of North Pacific genera.

ACKNOWLEDGMENTS

We thank Tracy Thomson for technical assistance.

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