A new sediment-dwelling pholadid bivalve from Oligocene glaciomarine sediments of King George Island, West Antarctica

KRZYSZTOF HRYNIEWICZ and ANDRZEJ GAŹDZICKI

We present a re-description of the pholadid bivalve from the Oligocene Polonez Cove Formation, King George Island, West Antarctica, previously identified as *Penitella* sp. The study is based on a collection of 210 specimens, preserved exclusively in life position in flask-shaped *Gastrochaenolites* type borings which have been subsequently buried by glaciomarine diamictite. The systematic study showed that this pholadid is a new species belonging to the genus *Pholadidea* rather than to *Penitella* and we name it *Pholadidea gradzinskii* sp. nov. The species is one of very few Late Cretaceous–Paleogene pholadids that we could safely identify as *Pholadidea*. All of them are known exclusively from the southern Pacific and adjacent areas (New Zealand, Antarctica, and Patagonia). We demonstrate that the genus attained its Recent broad distribution before the middle Miocene, when the first species of *Pholadidea* appeared in the Northern Hemisphere. The mass occurrence of *P. gradzinskii* in the Oligocene of West Antarctica results from favourable living condition in a shallow marine environment. Low sedimentation rate allowed the settlement of numerous larvae and their subsequent metamorphosis, growth, and maturity terminated by the mass mortality caused by the burial by marine diamictite. The sediment-boring Paleogene species of *Pholadidea*, among them *P. gradzinskii*, follow the wood-boring Late Cretaceous species *P. (Hatasia) wiffenae*, which reflects a general pattern of evolution of substrate selection among pholadoid bivalves.

Key words: Bivalvia, Pholadoidea, *Pholadidea*, ecology, glaciomarine, palaeobiogeography, Oligocene, Antarctica.

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Introduction

Marine boring bivalves show an ability to excavate dwelling structures in a variety of solid substrates, among them rock, sediment, peat and wood (e.g., Stanley 1970). This large group consists of eight separate superfamilies, among which pholadoids are the most diverse and broadly distributed (e.g., Coan et al. 2000; Coan and Valentich-Scott 2012). They comprise non-xylophagain pholadids, xylophagains, and teredinids (Haga and Kase 2011). The first group consists of wood-, sediment-, and rock-dwelling filter-feeders occurring mostly in shallow marine environments (e.g., Röder 1977) while the latter two comprise specialized wood-borers living with bacterial symbioses (Distel et al. 2011). The trace fossils questionably attributed to pholadoid bivalves are known from the Carboniferous, but the earliest body fossils of unequivocal pholadoid affinity are known from the Middle Jurassic onwards (Skwarko 1972), with major radiations during the Late Cretaceous (Kelly 1988a) and the Neogene (Kennedy 1974). Characteristic feature of pholadoid bivalve morphology are the highly modified shells which are used to mechanically bore into a solid substrate, and accessorial organic and calcareous plates unique to this group (Röder 1977; Ito 1999).

The pholadoid material described in this paper was first introduced and figured by Gaździcki et al. (1982) as *Penitella* sp. The current paper compliments the results of the previous study and shows that the species is in fact a new species belonging to the genus *Pholadidea* Turton, 1819. We discuss the palaeogeographical and evolutionary significance of this new identification and present an interpretation of the ecology of the species in relation to its environmental setting and morphology.

Institutional abbreviations.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

Geological setting and locality

The investigated material comes from the Polonez Cove Formation cropping out on King George Island, West Antarctica (Figs. 1, 2), representing deposits of a shallow shelf influenced by glacial conditions (e.g., Porębski and Gradziński 1987, 1990; Troedson and Smellie 2002; Quaglio et al. 2014). The siliciclastic deposits, chiefly mudstone, sandstone, and diamictite, contain fossils and volcanoclastic material dating them as middle to late Oligocene (Gaździcka and Gaździcki 1985; Birkenmajer 1989, 2001; Dingle et al. 1997; Dingle and Lavelle 1998). The Oligocene glaciation recorded in the so-called Polonez Glaciation is one of the largest Paleogene glaciations in West Antarctica (Birkenmajer et al. 1991; Dingle et al. 1997; Dingle and Lavelle 1998; Troedson and Smellie 2002). The Polonez Glaciation represents part of the general trend of progressive cooling of the Antarctic continent during the Cenozoic (e.g., Kennet 1977; Barrett 2001; Birkenmajer et al. 2005; Beu 2009).

The investigated material was collected at Mazurek Point on the southern shore of King George Island between the Low Head and Lions Rump areas (Fig. 1). The sampled strata belong to the Siklawa Member of the Polonez Cove Formation, composed of fossil-poor marine sandstone, mudstone, and occasional diamictite interbeds (Fig. 2; Porębski and Gradziński 1987, 1990). The pholadids occur exclusively in mudstone intervals (Fig. 3A) containing bivalve dwelling structures of *Gastrochaenolites* type (Gaździcki et al. 1982: fig. 5) buried by marine diamictite with metamorphic, granitoid, and limestone clasts of Antarctic continent provenance (Fig. 3B; Birkenmajer and Weiser 1985; Wrona 1989). All of the investigated specimens were collected by AG, Ryszard Gradziński, Szczepan J. Porębski, and Ryszard Wrona in 1980–1981, as well as by AG in 2006–2007 austral summers.
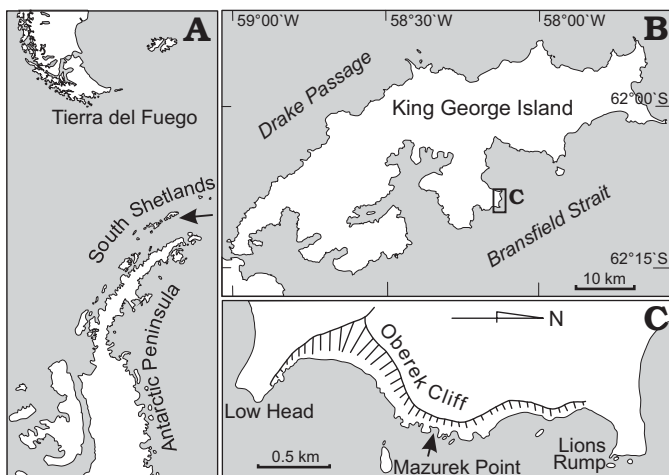

Fig. 1. **A**. Map of Antarctic Peninsula area, arrow shows position of King George Island in South Shetland Islands archipelago. **B**. King George Island showing location of the study area. **C**. Low Head–Lions Rump area, arrow shows position of *Pholadidea gradzinskii* sp. nov. horizons at Mazurek Point (after Gaździcki et al. 1982).
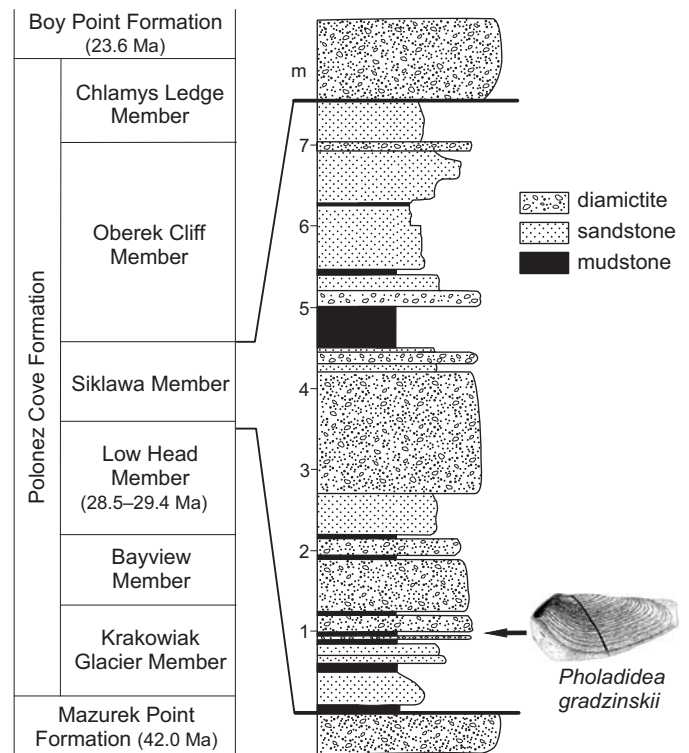

Fig. 2. Simplified lithostratigraphic profile of the Polonez Cove Formation, with lithological profile of the Siklawa Member at Mazurek Point where investigated fossils were collected. The arrow marks the mudstone interval where the majority of the specimens of *Pholadidea gradzinskii* sp. nov. described in this paper was collected. The lithostratigraphy after Birkenmajer (1983), Porębski and Gradziński (1987), Birkenmajer (2001), Troedson and Smellie (2002). Dating of the units after Smellie et al. (1984), Birkenmajer (1989), Dingle et al. (1997), Dingle and Lavelle (1998), and Troedson and Smellie (2002). The lithological profile of the Siklawa Member at Mazurek Point partially adapted from Gaździcki et al. (1982).

Material and methods

The terminology used herein (Fig. 4) follows that of Turner (1969) with respect to the accessorial plates and Kelly (1988a) with respect to remaining parts of the shell morphology. Additionally we introduce the term "rasp" for coarse sculpture on prora and anterior slope. Although the bivalves described in this paper were excavating their dwelling structures within unconsolidated sediment, the term "boring" is used after Röder (1977) and Ito (1999) instead of "burrow" to underline the unique character of pholadoid bivalve motion while penetrating the substrate. Serial thin sections were prepared according to the method proposed by Joysey and Cutbill (1970). As the specimens examined are fairly large, we decided to section them every 1 mm instead of 0.5 mm as proposed by Kelly (1988a).

Systematic palaeontology

Class Bivalvia Linnaeus, 1758
Order Myoida Goldfuss, 1820

Superfamily Pholadoidea Lamarck, 1809
Family Pholadidae Lamarck, 1809
Subfamily Martesiinae Grant and Gale, 1931
Genus *Pholadidea* Turton, 1819

Type species: *Pholadidea loscombiana* Turton, 1819: Recent, eastern Atlantic.

Remarks.—The genus *Pholadidea* is characterized by single umbonal-ventral groove, no protoplax (replaced by a dorsal callum extension), no to incipient metaplax and hypoplax (resulting from calcification of periostracum extending beyond the valve), and by longitudinally divided mesoplax (Turner 1955). The genus is subdivided into two subgenera: *Pholadidea* (*Pholadidea*) Turton, 1819, and *Pholadidea* (*Hatasia*) Gray, 1851. The main criteria of division are the shape and size of the mesoplax, the character of the umbonal reflection and of the siphonal tube. *Pholadidea* (*Pholadidea*) has a small, longitudinally divided mesoplax without basal extension and a raised umbonal reflection, and has no siphonal tube. *Pholadidea* (*Hatasia*) has longitudinally divided mesoplax with basal extension, an appressed umbonal reflection and has a siphonal tube (Turner 1955).

Stratigraphic and geographic range.—Pholadidea ranges from Cretaceous to Recent according to Crampton (1990). Cretaceous occurences of *Pholadidea* are rare and most of them require re-examination according to the revised pholadoid systematics of Turner (1954, 1955, 1969). Crampton (1990) described *Pholadidea* (*Hatasia*) *wiffenae* from the Late Cretaceous (Campanian–Maastrichtian) sunken driftwood from the Maungataniwha Sandstone of North Island, New Zealand. The material is well preserved and shows longitudinally divided mesoplax and other features consistent with the definition of *Pholadidea* (*Hatasia*), and to our knowledge is the oldest confirmed record of the genus. A similar wood-boring pholadoid species was described from the Maastrichtian sunken driftwood from Quiriquina Formation near Concepción, Chile, as *Martesia leali* by Stinnesbeck (1986). The species is slightly larger than *P.* (*H.*) *wiffenae* and has a very similar shape. The description states that meso-, meta-, and protoplax are unknown. These plates are absent on the holotype (Stinnesbeck 1986: 185, pl. 5: 9b, c). As the meso- and metaplax in the genus *Martesia* Sowerby, 1824, are large and robust (e.g., Turner 1955, 1969; Coan and Valentich-Scott 2012), and Quiriquina Formation material is found well preserved in life position within the wood, the absence of mesoplax and metaplax of *M. leali* are unlikely to be caused by taphonomic bias and are most likely a primary feature. The species could therefore potentially belong to *Pholadidea*, but requires re-examination using its type material before it could be formally included into this genus. Stephenson (1923) recorded three pholadoid species from the Upper Cretaceous (Campanian–Maastrichtian) Black Creek Group, North Carolina, which he attributed to *Pholadidea*. The species identified as *Pholadidea*? *subconica* Stephenson, 1923, and *Pholadidea*? *cithara* Morton, 1834,
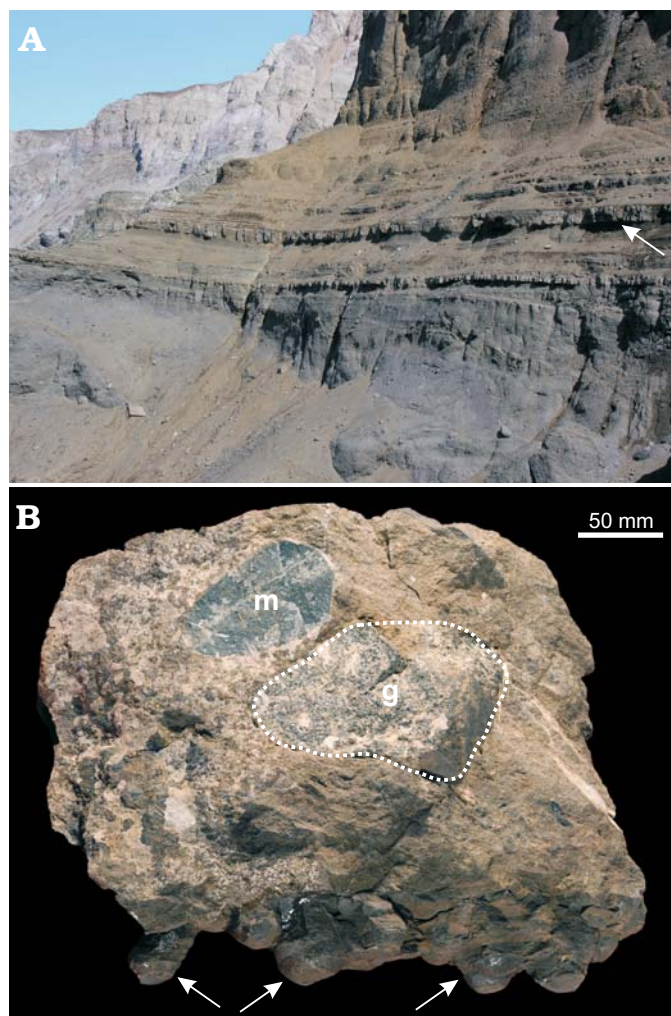
Fig. 3. **A**. Outcrops of glaciomarine strata of the Oligocene Polonez Cove Formation (the Siklawa Member) on King George Island, arrow indicates position on *Pholadidea gradzinskii* horizons at Mazurek Point (photograph by AG, January 2007). **B**. Diamictite from bed in Siklawa Member of the Polonez Cove Formation, with *Pholadidea gradzinskii* bearing moulds at the base (arrowed). The diamictite contains metamorphic (m) and granitoid (g) clasts.

show characteristic radial ornament on the disc (Stephenson 1923: pl. 87: 12–15), unknown in *Pholadidea* and most likely do not belong to this genus. The third species, small (ca. 7 mm long) and shell-boring *Pholadidea fragilis* Stephenson, 1923, does not have such an ornament (Stephenson 1923: pl. 87: 1–11). Stephenson (1923: 348) indicated the species has a double protoplax extending over the beaks. However, the reproduction (Stephenson 1923: pl. 87: 3, 4) does not show protoplax or mesoplax but instead the uncovered dorsal extension of the callum and a calcified periostracum covering the dorsal margin. The species certainly requires revision; in our opinion, it should be rather classified as a member of the genus *Diplothyra* Tryon, 1862. Another Late Cretaceous species in need of revision is *Pholadidea ragsdalensis* Stephenson, 1941, from the Navarro Group, Campbell, Texas (Stephenson 1941). It is a fairly small species (holotype ca. 7.5 mm long), boring within walls of large tubular fossils. Its
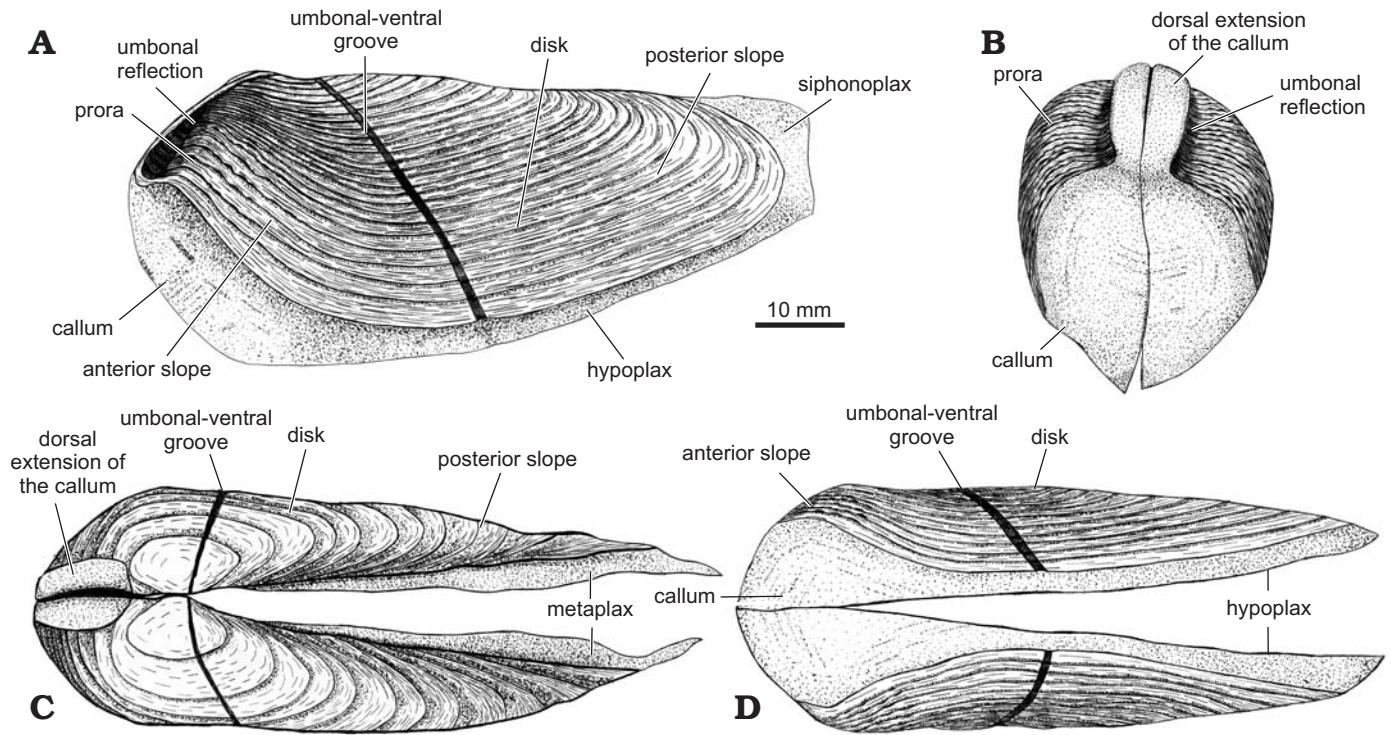
Fig. 4. Schematic illustration of exterior of *Pholadidea gradzinskii* sp. nov., showing main morphological features discussed. Left lateral (**A**), anterior (**B**), dorsal (**C**), and ventral (**D**) views.

callum partially seals the pedal gape, and the shell has two umbonal-ventral grooves (Stephenson 1941: 246, pl. 44: 5), which are not typical of *Pholadidea*. The holotype and the only figured specimen is worn and lacks part of the ventral and posterior margins, so it is difficult to estimate the shell shape based on the figure only. Stephenson (1941) mentioned larger specimens he attributed to yet unidentified species of *Pholadidea,* occurring in a carbonate concretion from the Navarro Group close to Coolidge, Texas. These were poorly preserved and remained unfigured, and we do not comment on their generic affinity. *Pholadidea* has so far not been reported from Cretaceous xylic (Kelly 1988a) and lithic substrates of Antarctica (Wilckens 1910; Zinsmeister and Macellari 1988).

Worldwide Paleogene occurrences of *Pholadidea* are also relatively scarce. The Paleocene *Pholadidea*? sp. nov. from the Red Bluff Tuff of Pitt Island, Chatham Islands, New Zealand (Campbell et al. 1993: 84) is in fact a species of *Jouannetia* Des Moulins in Rang and Des Moulins, 1828, (KH personal observation), an opinion also expressed by Crampton (1990). Two Paleogene species of *Pholadidea* occur in lithic substrates of Patagonia, South America. The older Patagonian species is *Pholadidea frenguellii* from the Eocene shallow marine sediments of Río Turbio Formation in southwestern Patagonia (Griffin 1991). The species is unknown outside of its type area. The second species was introduced by Philippi (1887) as *Pholas patagonica* from Oligocene–lower Miocene rocks cropping out near the mouth of Santa Cruz River, eastern Patagonia (Del Río 2004). These identifications were later commented on by

Ihering (1897, 1899), who attributed it to the genus *Martesia*, and by Ortmann (1902) who classified it in *Pholadidea*. The genus is unkown from Paleogene molluscan faunas of the Seymour Island in West Antarctica (cf. Wilckens 1911; Stilwell and Zinsmeister 1992). The elongate, slender borings from Eocene sunken driftwood from La Meseta Formation (Pirrie et al. 1998) almost certainly have not been made by *Pholadidea*, which forms short, clavate borings similar to other martesiins (Turner 1955; Turner and Johnson 1971; Crampton 1990). *Pholadidea* has also not been reported among the bivalves from the remaining part of the Polonez Cove Formation (Gaździcki and Pugaczewska 1984; Quaglio et al. 2014). To our knowledge, *Pholadidea* has no confirmed fossil record in the Northern Pacific (Kennedy 1974). A possible species of *Pholadidea* from the Eocene of Kamchatka (Krishtofovich 1947) is not sufficiently well described and figured to confirm this generic assignment. A species reported from Oligocene of Hokkaido, Japan (Uozumi and Fujie 1956) does not belong to *Pholadidea* as it has a single, undivided mesoplax.

Since the Neogene *Pholadidea* is broadly distributed in both hemispheres. *Pholadidea patagonica* is known from the lower Miocene of Eastern Patagonia (Del Río 2004) and an undescribed pholadoid species forming mass-accumulations at the base of lower Miocene Chenque Formation (Carmona et al. 2007) could also belong to *Pholadidea*. The latter species is medium sized, fairly short, oval, and has a single umbonal-ventral groove, which is similar to stratigraphically and geographically adjacent *P. patagonica*. The lack of callum reported by Carmona et al. (2007: 334, fig.
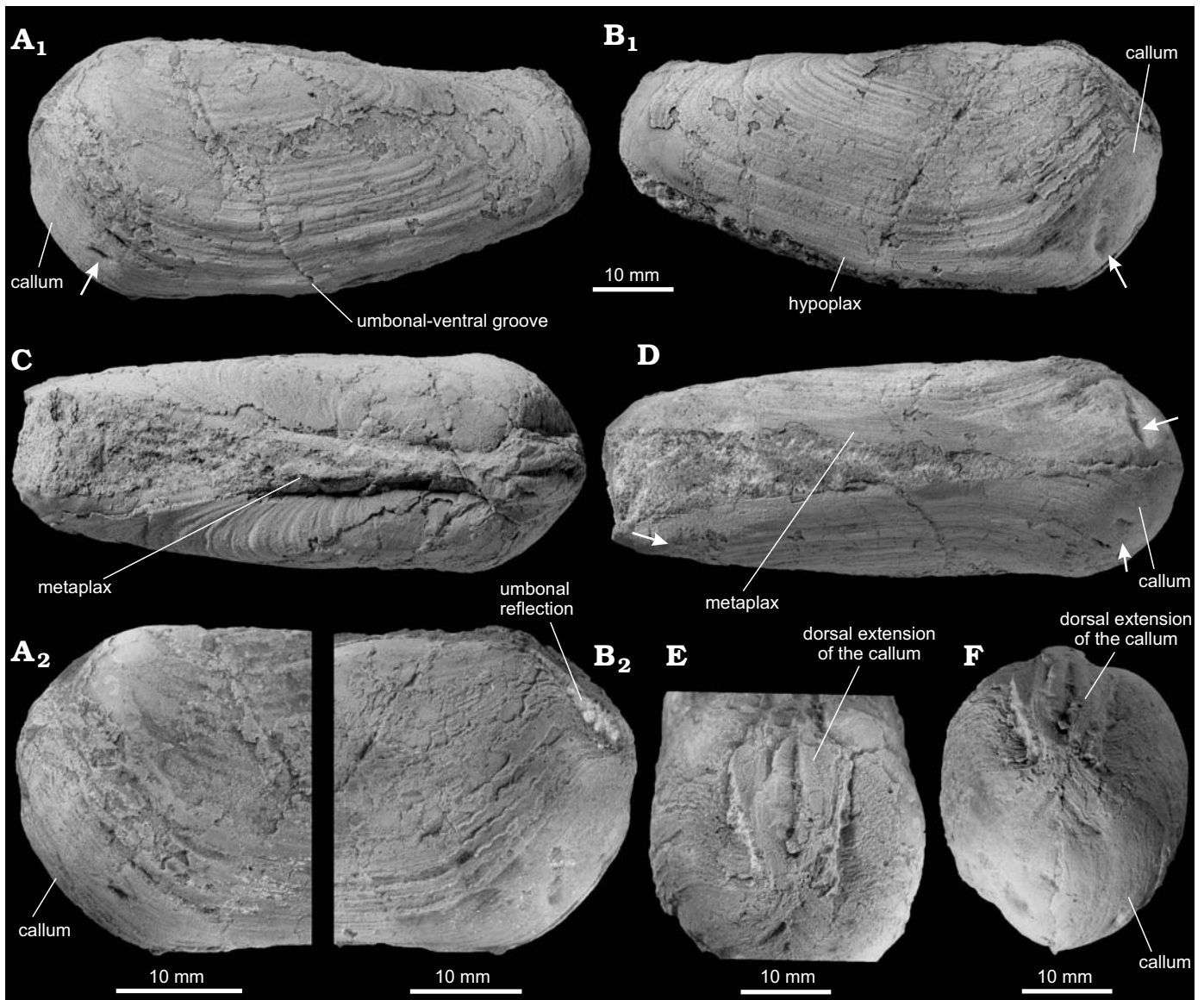
Fig. 5. Pholadid bivalve *Pholadidea gradzinskii* sp. nov. (ZPAL Mo. XVIII/3, holotype) from the Oligocene of King George Island. **A**. Left-lateral view of the complete specimen (A_1), arrow marks deformation of the callum; anterior of the left valve (A_2), showing callum covered with growth lines. **B**. Right-lateral view of the complete specimen (B_1), arrow marks deformation of the callum; anterior of the right valve (B_2), showing umbonal reflection raised anteriorly and appressed on the umbo. **C**. Dorsal view of the complete specimen showing metaplax formed by partially calcified periostracal mantle connecting the dorsal margin of the valves. **D**. Ventral view of the complete specimen showing a hypoplax formed by partially calcified periostracal mantle extending beyond the ventral margin of the shells and connected with the callum; arrows mark deformation of the callum and hypoplax. **E**. Inclined dorsal view of the anterior showing umbonal reflection covered with the dorsal extension of the callum. **F**. Anterior view showing the callum and umbonal reflection covered by the dorsal extension of the callum.

5b) needs to be confirmed. One of the oldest records of the genus in the Northern Hemisphere's Neogene is *Pholadidea loscombiana* Turton, 1819, from the middle Miocene sands of Ukraine (Friedberg 1934) and from the Miocene of Hungary (Csepreghy-Meznerics 1961). The population of *Pholadidea loscombiana* was well established in Europe in the younger Neogene and occurs frequently in the Pliocene and Pleistocene (Malatesta and Zarlenga 1986). The genus is also known from the Plio-Pleistocene of New Zealand (Laws 1936; Beu and Maxwell 1990; Beu 2006). Recent distribution of the genus comprises all of the world's oceans apart from Western Atlantic (Turner 1955) and Northern Pacific (Coan et al. 2000). It bores in a variety of substrates like weakly compacted sediment, soft rock or peat in intertidal to subtidal environments down to ca. 120 m water depth (Turner 1955; Coan and Valentich-Scott 2012).

Pholadidea gradzinskii sp. nov.

Figs. 5–7.

1982 *Penitella* sp.; Gaździcki et al. 1982: 729, figs. 6, 7.

ZooBank LSID: urn:lsid:zoobank.org:act:2C072B3E-3357-4417-B825-8D2FEFC3B2AE

Etymology: In honour of the late Professor Ryszard Gradziński, Kraków (1929–2014), in recognition of his understanding of the sedimentology of the Polonez Cove Formation.

Type material: Holotype: ZPAL Mo. XVIII/3: a well preserved articulated shell with some details of accessory plates visible. Paratypes: ZPAL Mo XVIII/1, an internal mould with traces of pallial line preserved; ZPAL Mo XVIII/4, an articulated shell with rasp visible; ZPAL Mo XVIII/11, a fragment of the prora and anterior slope showing rasp: ZPAL MoXVIII/12/A–W, a set of acetate peels with transverse sections.

Type locality: Cliff at Mazurek Point, King George Island, South Shetland Islands, West Antarctica.

Type horizon: Four mudstone intervals bored by *P. gradzinskii*; capped by diamictite beds; Oligocene, Siklawa Member, Polonez Cove Formation, King George Island, South Shetland Islands, West Antarctica. Three pholadid-bearing beds crop out approximately 20 m above sea level, about a meter above the base of the Siklawa Member. A fourth bed crops out approximately 4.5 m higher in the section.

Other material.—Other borings containing fragmentary preserved specimens used for this work were already figured and referred to by Gaździcki et al. (1982). The material stored in ZPAL comprises 210 boring hosting specimens. These are separate weathered boring traces or accumulations of several in loose blocks.

Diagnosis.—A large, elongate species of *Pholadidea* with commarginal ornament. Prora and anterior slope covered with rasp formed by coarse commarginal ridges with few indentations, the disc and posterior slope with fine commarginal growth lines superimposed on broad commarginal folds. Accessory plates highly simplified and formed by partial calcification of periostracum extending beyond the valve (metaplax, hypoplax, siphonoplax) or artophied (mesoplax, protoplax).

Description.—Shell up to 62 mm in length and 30 mm in height, with virtually all of the available specimens close to the maximum size. Shell elongated, large for the genus, with moderately thick shell anteriorly and thin posteriorly. Umbo located at $1/6^{th}$ of the length from the anterior. Most of the shell features (prora, disc, posterior slope) have no clear boundaries, only clear boundary is the umbonal-ventral groove separating the anterior slope from the disc. Prora short and reduced; anterior slope inflated, representing the widest and highest portion of the shell. Pedal gape large, in adults completely sealed by callum; in juveniles partially opened, as suggested by shape of the growth lines. Callum thin and weakly calcified, often deformed; ornamented with growth lines superimposed on radial striae. Dorsal extension of the callum reaches the beaks and covers the umbonal reflection of the shell. The umbonal reflection raised ante-

riorly, more apressed near the beaks. No protoplax and mesoplax observed in any of the investigated specimens. As all investigated specimens are found articulated in life position, we conclude that lack of protoplax and mesoplax is a primary feature. Metaplax is not a true plate, instead being formed by partial calcification of the periostracum connecting the dorsal margin of both valves; fragments close to the shell margins calcified while median part remained uncalcified. Hypoplax similarly is not a true plate but weakly calcified periostracum extending beyond the ventral margin of both valves. Siphonoplax short, pointed, separate in each valve, composed of calcified periostracum connected with that from the ventral and dorsal margin. Ventral margin gapes, with no ventral condyle observed. The ornament of prora and anterior slope composed of 17–20 coarse, densely spaced coarse commarginal ridges with few weak indentations forming a rasp. On the disc and posterior slope the ornament is finer and formed of low commarginal growth lines superimposed over coarser commarginal folds. Umbonal-ventral groove straight, narrow and moderately deep, impressed on the mould. Posterior margin narrow, truncated but pointed when siphonoplax is taken into account. Pallial line weak and only partially visible. Muscle scars unknown.

Remarks.—*Pholadidea gradzinskii* does not have a mesoplax, but other characters typical for *Pholadidea* are present and we conclude that a lack of mesoplax is caused by a secondary reduction and include this species into *Pholadidea*. However, due to the lack of a mesoplax, which is the most straightforward feature used to separate both subgenera, we restrain from including current species to any subgenus of *Pholadidea*.

Pholadidea gradzinskii differs from *P.* (*Hatasia*) *wiffenae* Crampton, 1990, from the Upper Cretaceous (Campanian–Maastrichtian) of New Zealand by its larger size (< 20 mm in lenght for *P.* (*H.*) *wiffenae*), longer and more slender disc and posterior slope, and lack of mesoplax (Crampton 1990). It is much larger and has finer commarginal ornament than *P. frenguellii* Griffin, 1991, from the Eocene of southwestern Patagonia, which in addition has wider and deeper umbonal-ventral groove (Griffin 1991). *Pholadidea gradzinskii* sp. nov. differs from *P. patagonica* (Philippi, 1887) from Oligocene–lower Miocene of Eastern Patagonia (Del Río 2004) by its more elongate shell and weaker commarginal ornament on anterior slope. Also, *P. gradzinskii* has tapering and truncated posterior of the shell, contrasting with rounded posterior of the shell of *P. patagonica*. The growth lines on the anterior slope of *P. gradzinskii* reach the umbonal-ventral groove at a weakly acute angle (ca. 80°), which is

Fig. 6. Pholadid bivalve *Pholadidea gradzinskii* sp. nov. from the Oligocene of King George Island. **A**. Paratype, ZPAL XVIII/1; right-lateral view of → internal mould showing fragments of the pallial line and the umbonal-ventral groove. **B**. Paratype, ZPAL Mo XVIII/4 complete shell; anterior (B₁) and dorsal (B₃) views, showing umbonal reflection covered by dorsal extension of the callum and prora and anterior slope covered with rasp formed by raised commarginal lamellae; left lateral view (B₂), showing a strongly elongated shape and pointed siphonoplax; enlarged photo of the anterior of the right valve (B₄), showing rasp formed by raised commarginal lamellae. Arrows mark radial striae on the callum, engraved by substrate particles probably during the boring action. **C**. Paratype, ZPAL Mo XVIII/11; SEM photomicrograph of the prora (C₁), showing detailes of rasp formed by coarse commarginal lamellae; detail of coarse commarginal lamellae (C₂), showing signs of wearing.
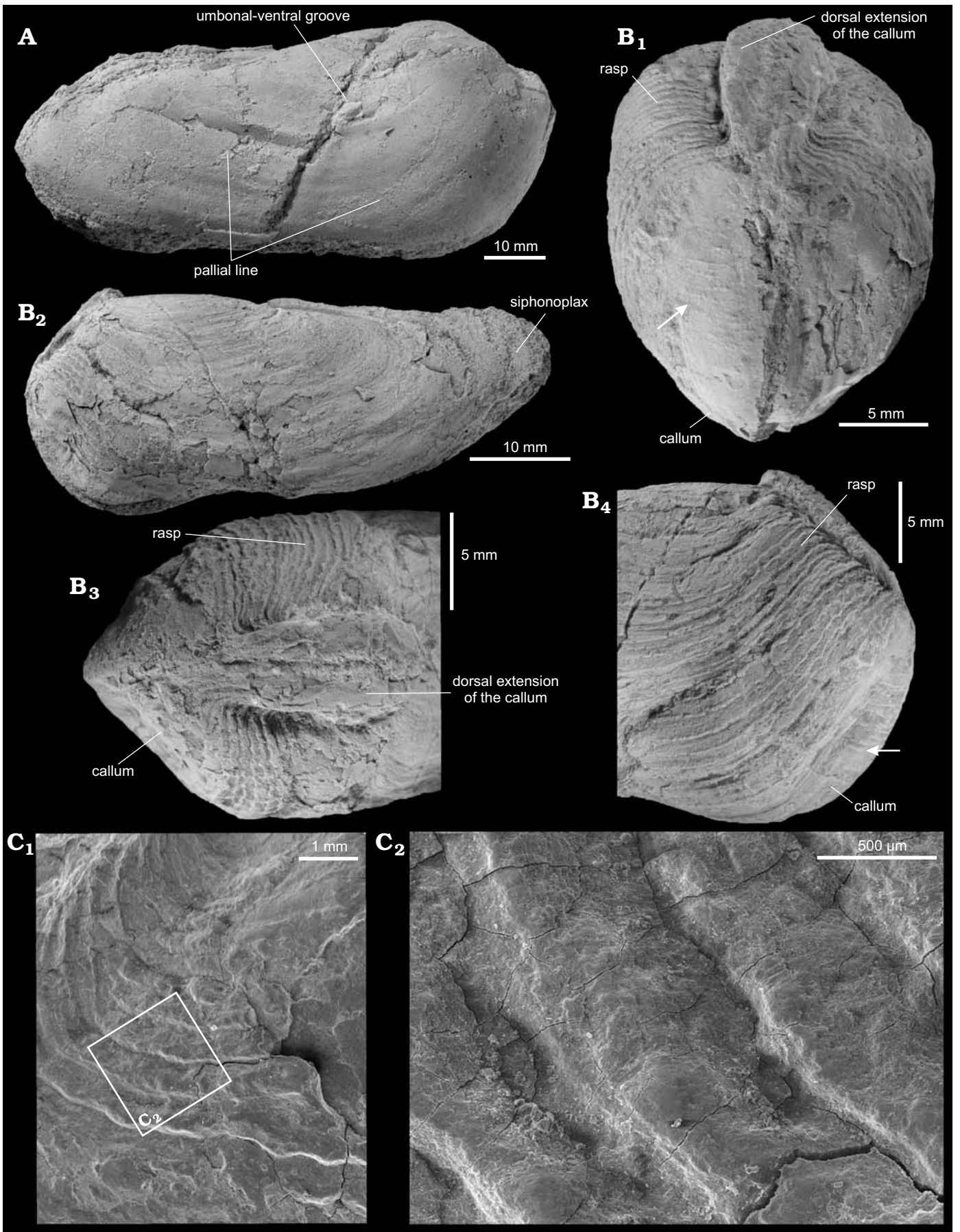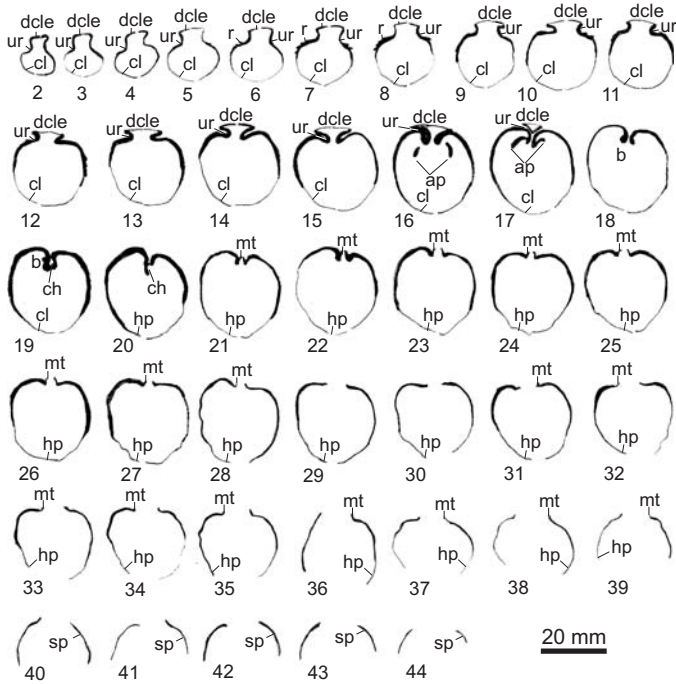
Fig. 7. Vertical transverse sections through pholadid bivalve *Pholadidea gradzinskii* sp. nov. (ZPAL Mo XVIII/12/A–W), preserved in life position within a boring from the Oligocene of King George Island. The numbers refer to distance from the anterior of the shell in milimeters. Abbreviations: ap, apophysis; b, beak; ch, chondrophore; cl, callum; dcle, dorsal extension of the callum; hp, hypoplax; mt, metaplax; r, rasp; sp, siphonoplax; ur, umbonal reflection.

much more acute (ca. 30°) in *P. patagonica* (Del Río 2002). *Pholadidea gradzinskii* is much more elongate than *P. finlayi* Laws, 1936, from the Pliocene of New Zealand (Laws 1936: pl. 11: 41, 42), and has a somewhat less truncated posterior part of the shell. It has also growth lines transecting the umbonal-ventral groove at less acute angle than *P. finlayi*. *Pholadidea gradzinskii* is very similar to *P. suteri* Lamy, 1926, from the Pleistocene of New Zealand with respect of shape, size and no mesoplax sensu Turner (1969) (see Beu and Maxwell 1990). The rasp of *P. suteri* is, however, coarser and has well defined radial ribs, unlike that of *P. gradzinskii* and we prefer to keep both species separate. *Pholadidea tridens* (Gray, 1843) from the Pleistocene of New Zealand is much shorter than the current species, and has wider umbonal-ventral groove (Beu 2006: fig. 38F).

Recent species of *Pholadidea* were discussed by Turner (1955), Beu and Climo (1974) and Coan and Valentich-Scott (2012). *Pholadidea gradzinskii* is more elongated than *P. loscombiana* Turton, 1819, which in addition has anterior slope with growth lines forming an sharp acute angle with the umbonal-ventral groove, and has broad, rectangular posterior margin, unlike the current species. *Pholadidea gradzinskii* is more elongate than *P. acherontea* Beu and Climo, 1974, which has siphonoplax composed of two separate plates, missing in the current species. *Pholadidea* (*Hatasia*) *melanura* (Sowerby, 1834) has much more inflated and broader callum than *P. gradzinskii*, and stronger

radial threads on the anterior slope. *Pholadidea* (*Hatasia*) *quadra* (Sowerby, 1834) has more rectangular shell and more apressed umbonal reflection than the current species. *Pholadidea* (*Hatasia*) *tubifera* (Sowerby, 1834) has similar shape, but has stronger radial threads on the anterior slope and more appressed umbonal reflection. All the above species of *Hatasia* contain a mesoplax, a feature entirely missing in *P. gradzinskii*.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Palaeobiogeography of *Pholadidea*.—Available data suggest that during the Late Cretaceous and the Paleogene, *Pholadidea* did not attain its Recent near-global geographic distribution (Turner 1955). Instead, the genus was largely restricted to the present-day New Zealand and southern South America–Antarctic Peninsula (Fig. 8). During the Late Cretaceous–Paleogene, both areas were located in an embayment of the South Pacific partially isolated from the remaining part of the ocean (Zinsmeister 1982). The relative isolation of this marine basin is reflected by distinctive fauna of the Weddellian Biogeographic Province, extending on the Gondwanan shelves from south-eastern Australia, through New Zealand, Ross Sea shelf and Antarctic Peninsula north to southernmost South America (Zinsmeister 1979). The oldest known species of *Pholadidea*, the Late Cretaceous (Campanian–Maastrichtian) *Pholadidea* (*Hatasia*) *wiffenae* from New Zealand (Crampton 1990) shows that the genus existed in the western reaches of the province, and then dispersed eastward, reaching southern South America in the Eocene (Griffin 1991), where it remained at least until the sea withdrew from the southern Patagonia after early Miocene (Del Río 2004). Interestingly, the genus is unknown in New Zealand from the post-Cretaceous sediments until the Pliocene (Laws 1936). This may be an artifact, but also may be an actual phenomenon associated with latest Cretaceous–earliest Paleogene climate change in New Zealand due to its northward drift (Zinsmeister 1982) and subsequent re-colonization by cool-water fauna in Neogene due to enhanced Antarctic Circumpolar Current (see Beu et al. 1997). Eastward dispersal of early *Pholadidea* within the Weddellian Biogeographic Province is likely to be associated with the west-east offshore water circulation existing in southern Pacific during the Late Cretaceous–Paleogene (Lazarus and Caulet 1993). Similar west-east dispersal patterns within Weddellian Biogeographic Province are characteristic for other fossil invertebrate groups, such as struthiolariid gastropods (e.g., Zinsmeister and Camacho 1980) and some brachiopods (e.g., Craig 2000; Bitner et al. 2009). The paucity of fossil record does not allow to precisely date when *Pholadidea* dispersed outside from the Southern Ocean; it must have happened before the middle Miocene,

when the genus is recorded for the first time in the Northern Hemisphere (Friedberg 1934). It may have dispersed northwards along the coast of South America and then trough the Central American Seaway sometime during the Paleogene as suggested for some Southern Ocean crustaceans and brachiopods (e.g., Feldmann 1986; Bitner 1996) or eastward with palaeo-Antarctic Circumpolar Current trough the Drake Passage during the dissolution of Weddellian Biogeographic Province close to the Oligocene–Miocene transition (e.g., Beu et al. 1997).

Autecology of *Pholadidea gradzinskii*.—Four beds with *P. gradzinskii* contain a macrofaunal life-assemblage of hundreds of thousands of specimens of this bivalve buried in life position by glaciomarine sediment (Gaździcki et al. 1982). The formation of monospecific colonies heavily dominated by a single species is not unusual among rock-, shale-, and wood-boring pholadoids (e.g., Röder 1977; Voight 2007; Carmona et al. 2007), and in this respect the Oligocene occurence from King George Island is comparable to many of its fossil and Recent equivalents. The settlement of pholadoid bivalve larvae is controlled by the type of substrate (e.g., Mann and Gallagher 1984), and the successfull growth of already settled larvae is usually dependent on low sedimentation rate protecting the juveniles from burial (Carmona et al. 2007). In the case of *P. gradzinskii*, the substrate is the glaciomarine mudstone of the Siklawa Member. The entire Polonez Cove Formation is composed of shallow marine clastics with a mixture of clast lithologies, comprising magmatic, metamorphic and volcanic rocks, as well as limestone erratics and recycled stromatolites (e.g., Birkenmajer and Weiser 1985; Wrona 1989; Porębski and Gradziński 1987, 1990; Troedson and Smellie 2002; Gaździcki 2007). The more fine-grained sediments of the Siklawa Member, would provide a good substrate for larval settlement, and the low-sedimentation rate intervals within the member would provide a long-lived colonization surface allowing successful and undisturbed growth of juveniles. The growth must have remained undisturbed for a relatively long time, as all of the specimens found are highly elongated and with gaping ventral margin, suggestive of mature or even gerontic individuals (Röder 1977). Also, the rasp is composed of low and coarse commarginal ridges instead of thin, raised lamellae (Röder 1977: 198, pl. 14: 59–62), suggestive of severe abrasion which could be expected in gerontic individuals. A heavily worn rasp would loose most of it functionality and in effect hamper further anterior boring ability of the bivalve, promoting ventral action and effective widening of the burrow (Röder 1977; Ito 1999) until death and burial of the bivalves beneath the glaciomarine diamictite. The consecutive occurence of similar *P. gradzinskii* assemblages in four successive beds indicates repetative conditions favouring existance of *Pholadidea* colonies at the northern edges of the Antarctic during the Oligocene Polonez Glaciation. Continuing cooling of the Antarctic and the development of large polar ice caps in the
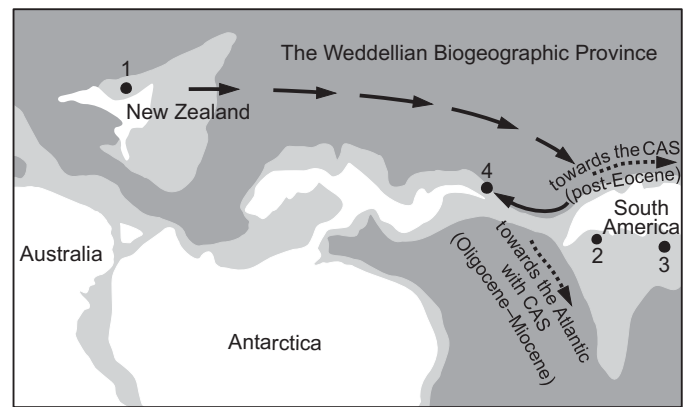

Fig. 8. Paleogene arrangement of Southern Gondwana with distribution of species of *Pholadidea* in The Weddellian Biogeographic Province from the Late Cretaceous–Paleogene. Abbreviations: 1, *Pholadidea* (*Hatasia*) *wiffenae*, Campanian–Maastrichtian; 2, *Pholadidea frenguellii*, Eocene; 3, *Pholadidea patagonica*, Oligocene–early Miocene; 4, *Pholadidea gradzinskii*, Oligocene; CAS, Central American Seaway; full arrows, possible dispersal route of *Pholadidea* from New Zealand to Antarctica/South America during the latest Cretaceous and the Paleogene (in the latest Cretaceous situation, New Zealand was immediately adjacent to Australia and Antarctica); stippled arrows, two possible dispersal routes of *Pholadidea* out from the Weddellian Biogeographic Province. Map adopted after Clarke and Crame (1989).

Neogene effectively removed most of the shallow marine environments from the southern polar seas, contributing to the general paucity of sediment- and rock-boring bivalves in the Antarctic today (Beu 2009).

Evolution of boring strategy among pholadoid bivalves.—Pholadoid bivalves apply two different boring strategies: anterior boring and ventral boring (Nair and Ansell 1968). Anterior boring is typical for species boring in rigid substrates (wood or rock; Röder 1977) and it is used at earlier ontogenetic stages; it may be retained during life or may be largely replaced by ventral boring as the specimen matures (Ito 1999, 2005). So far the oldest known pholadoid bivalve and an anterior borer is "*Teredo*" *australis* Moore, 1870, from the Middle Jurassic (Bajocian) sunken driftwood from Australia (Skwarko 1972). Anterior boring pholadoids re-appear in sunken driftwood several times later during the Late Jurassic and the Cretaceous and are known until Recent (Gerasimov 1955; Kelly 1988a, b; Haga and Kase 2011; Schweigert and Schlampp 2014). Ventral boring, on the other hand, is usually applied by species boring in less rigid substrates (firm sediment). The oldest ventral boring pholadoids are *Pholas*? *scaphoides* from the Upper Cretaceous (Cenomanian) rocks of Texas (Stephenson 1952) and *Barnea* (*Anchomasa*) *saulae* from the Upper Cretaceous (Coniacian–Santonian) rocks of California (Kennedy 1993). Ventral borers are also common in Recent oceans (Röder 1977). The oldest known species of *Pholadidea*, *P.* (*H.*) *wiffenae* from the Late Cretaceous (Campanian–Maastrichtian) sunken driftwood from New Zealand was a wood borer and had relatively well-developed umbonal-ventral groove, suggestive of anterior boring ability (e.g., Röder 1977; Haga and

Kase 2011). However, while the species was preferentially an anterior borer, the ventral boring action must have also taken place, as otherwise the characteristic clavate boring (Crampton 1990: pl. 3: 6) would not be formed. Its younger relative, *P. gradzinskii* from the Oligocene of the Antarctic bored into the firm sediment, which is more typical for ventral borers. The species has a weak umbonal-ventral groove (Figs. 5, 6), which could support a functional ventral condyle and the anterior boring mechanism only at the earlier ontogenetic stages when the shell was still relatively small. We therefore conclude that the *P. gradzinskii* was an anterior borer at earlier ontogenetic stages, and for most of its adult development it was a ventral borer. Interestingly, the evolution of boring strategy in *Pholadidea* proceeded from a predominantly anterior to predominantly ventral borer similar to other pholadoid bivalves (Ito 1999). Our study also suggest that *Pholadidea* originated on xylic substrates and colonized lithic substrates afterwards. This corroborates the observation of Kelly (1988a), who pointed out that the first Mesozoic wood-boring pholadoids appear long before first Mesozoic sediment-boring pholadoids. Whether these observations represent an actual phenomenon or an artifact of the fossil record remains unconfirmed (cf. Hoagland and Turner 1981).

Conclusions

The current study presents the systematic re-description of a pholadid bivalve from the Oligocene glaciomarine sediments from King George Island, West Antarctica. It shows that the new species belongs to the genus *Pholadidea* rather than to *Penitella* as suggested by Gaździcki et al. (1982). The new species is one of a few Late Cretaceous–Paleogene species of *Pholadidea* occurring in the southern Pacific and adjacent areas, which supports the concept of the so-called Weddellian Biogeographic Province (Zinsmeister 1982). The current study also confirms a "wood-before-lithic" pattern of pholadoid substrate adaptation observed by Kelly (1988a) for one more genus.

Pholadoid systematics is still far from being fully understood. This study shows that many fossil pholadoid bivalve species could be misidentified and that a review of Late Cretaceous–Paleogene fossil pholadoids is long overdue. Since Late Cretaceous was a time of a major evolutionary radiation of pholadoids (Kelly 1988a), a proper identification of fossil material could help to understand the dispersal and evolution of this bivalve group and would be important also for neontologists, for example by providing calibration points for molecular clocks.

Acknowledgements

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