

Functional morphology of *Grammatodon inaequalis* (GOLDFUSS) and implications for evolutionary pathways in arcoidean bivalves

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Abstract Secondary soft-bottom dwellers evolved several times in the Arcoidea. These include semi-infaunal endobyssate taxa and free-burrowing species. The Jurassic arcoid bivalve *Grammatodon inaequalis* (GOLDFUSS, 1837) is remarkable for showing different sculptures on its left and right valve. A functional analysis of the shell points to a reclining mode of life on soft bottoms. This interpretation is corroborated by the occurrence of this species in very fine-grained sediments, and by taphonomic patterns such as “butterflied” preservation. It is proposed here that this species was resting on its left valve on the sediment, probably without byssal attachment. This reclining mode of life of *G. inaequalis* was hitherto undescribed from soft-bottom dweller arcoid bivalves.

Keywords Bivalvia · Arcoidea · *Grammatodon* · Opalinuston Formation · Aalenian · Functional morphology

Introduction

The Arcoidea, dating back to the Ordovician, are usually seen as a rather “conservative” group, in shell form and mode of life intermediate between typical Pterioidea and Venerioidea (Thomas 1978a). The Arcoidea are characterized by a simple hinge and a weak duplivincular ligament (both the result of serial repetition of simple structures), the absence of fused mantle siphons, and an unspecialized soft-

part anatomy (Thomas 1978a, b). As a consequence of these inherent constructional limitations, arcoid bivalves could exploit only a limited range of ecospace or substrate niches during their evolutionary history (Stanley 1972; Thomas 1978a, b). Especially the weak ligament and the non-siphonate condition prevented the Arcoidea from colonizing deeper sediment tiers. As a result, modern arcoids are mostly found in unstable habitats, either as epibenthic byssally attached nestlers on hard bottoms and in crevices, or as shallow burrowers in shifting substrates where they are frequently washed out and have to dig themselves into the sediment again (“recovery strategy”; Thomas 1978a).

A survey of extant (and to a lesser degree fossil) members of the superfamily Arcoidea yields an almost perfect correlation between shell elongation and mode of life (Stanley 1970; Thomas 1978a). Epibenthic arcoideans attach themselves permanently with the ventrally emerging byssus and live with the commissural plane vertical. Their elongate shells show a L/H (shell length/shell height) ratio >1.35 . Free burrowing Arcoidea or arcoidean species that attach themselves with a weak and sometimes temporary byssus within soft sediments have shorter shells with $L/H < 1.35$. In addition, epibenthic species usually have a rather flattened venter (Stanley 1970) and, at least species that are exposed to currents, a posterior auricle and sulcus (Kauffman 1969). In burrowing species, the venter is rounded and the oblique posterior margin is truncated (Thomas 1978a).

In this respect, *Grammatodon inaequalis* from the Opalinuston Formation (latest Toarcian to Early Aalenian) of Northern Switzerland and Southern Germany poses several problems. According to the shell outline, this species should have been epibenthic and byssally attached to a hard substrate. Yet this mode of life was hardly possible on this very fine-grained and soft sediment of the Opalinuston

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Formation (see Kobler 1972; Etter 1995, 1996). Byssal attachment to shells of dead ammonites or other molluscs can also be excluded because *G. inaequalvis* shells were never found associated with other mollusc remains. The most striking feature of *G. inaequalvis* is the sculptural pattern, which differs substantially between left and right valve. This is, on the other hand, difficult to reconcile with a burrowing mode of life in which the bivalve was oriented with the commissure vertically. In order to explain this riddle, the taphonomy and functional morphology of *G. inaequalvis* are discussed and a new mode of life for arcoid bivalves is proposed.

Materials and methods

For the present study, well-preserved museum specimens from the uppermost Toarcian to Early Aalenian Opalinuston Formation of Southern Germany (Swabian Alb) and Northern Switzerland (Jura Mountains) were used (see Table 1).

The specimens from the Swabian Alb are deposited in the Staatliches Museum für Naturkunde Stuttgart (SMNS). They were measured, and the compactional patterns were recorded qualitatively. From one specimen a polished cross section was made, and from another specimen a camera lucida drawing was made. The specimens from the Swiss Jura Mountains were collected during a bed-by-bed survey of the fauna and are deposited at the Paläontologisches

Institut, University of Zurich (PIMUZ). These specimens were also measured, and their preservation was analyzed.

Systematic palaeontology and description

Class Bivalvia LINNÉ, 1758

Subclass Autolamellibranchiata GROBBEN, 1894

Pteriomorphia (BEURLEN, 1944)

Order Arcoidea STOLICZKA, 1871

Superfamily Arcoidea LAMARCK, 1809

Family Parallelodontidae DALL, 1898

Subfamily Grammatodontinae BRANSON 1942

Grammatodon inaequalvis (GOLDFUSS, 1837)

Taxonomic remarks

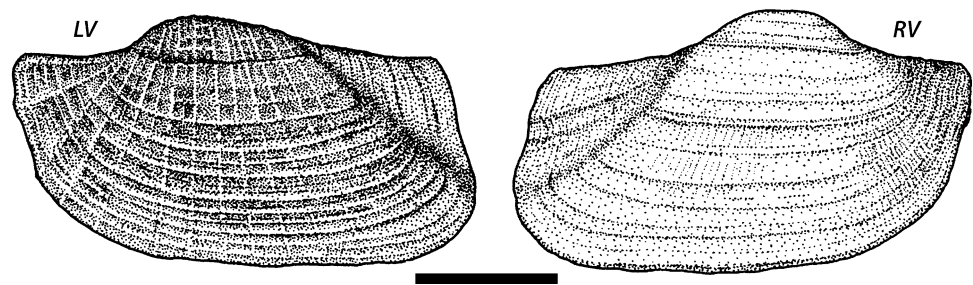
First described as *Arca inaequalvis* (GOLDFUSS 1837), this bivalve was subsequently placed in various genera, including *Cucullaea* LAMARCK, 1801, *Macrodon* LYCETT, 1845, *Macrodon* BEUSHAUSEN, 1895, *Beushausenia* COSSMANN, 1897, and *Cosmetodon* BRANSON 1942. Yet the hinge teeth in this and other Jurassic arcoids differ significantly from those in *Cucullaea*. *Macrodon* and *Macrodon* were preoccupied by a sciaenid fish and a carnivorous mammal, respectively, and *Beushausenia* is a nomen nudum (Driscoll 1961). Some authors placed the species in synonymy

Table 1 Studied specimens of *Grammatodon inaequalvis* (GOLDFUSS) from Northern Switzerland (PIMUZ numbers) and Southern Germany (SMNS numbers)

Museum no	Locality	Length	Height	L/H	Remarks
PIMUZ 6008	Schinznach	22	13	1.69	Double-valved, butterflyed, slightly deformed, cast with periostracum
PIMUZ 6009	Schinznach	26	14.5	1.79	Right valve, undeformed, cast with periostracum
PIMUZ 6246	Schinznach	17	10	1.70	Double-valved, butterflyed, cast with periostracum
PIMUZ 6247	Schinznach	17.5	11	1.59	Left valve, undeformed, cast
PIMUZ 6248	Schinznach	18	11.5	1.57	Right valve, undeformed, cast with periostracum
PIMUZ 6249	Schinznach	16.5	10	1.65	Left valve, undeformed, cast
PIMUZ 6253	Schinznach	13.5	8	1.69	Double-valved, butterflyed, cast with periostracum
SMNS 67137/1	Hohenstaufen	25	16	1.56	Left valve, undeformed, calcite
SMNS 67138/1	Weilerstöffel	33	18	1.83	Double-valved, right valve displaced dorsally, aragonite
SMNS 67138/2	Weilerstöffel	23	12.5	1.84	Double-valved, left valve displaced dorsally, aragonite
SMNS 67139/1	Balingen	27	17	1.59	Double-valved, right valve displaced dorsally, aragonite
SMNS 67139/2	Balingen	25	15	1.67	Double-valved, left valve displaced dorsally, aragonite
SMNS 67139/3	Balingen	23	16	1.44	Double-valved, left valve displaced dorsally, aragonite
SMNS 67139/4	Balingen	N/A	N/A	N/A	Double-valved, strongly deformed, aragonite
SMNS 67140/1	Frickenhausen	25	16	1.56	Double-valved, right valve displaced dorsally, calcite
SMNS 67140/2	Frickenhausen	24	14	1.71	Right valve, undeformed, calcite
SMNS 67140/3	Frickenhausen	23	13.5	1.70	Left valve, undeformed, calcite
SMNS 67140/4	Frickenhausen	18.5	12	1.54	Double-valved, right valve displaced dorsally, calcite

Measurements are in mm. N/A not applicable because specimen strongly deformed

Fig. 1 Left (LV) and right valve (RV) of *Grammatodon inaequalis* (GOLDFUSS) from the Opalinuston Formation of Southern Germany (SMNS 67138/1, Weilerstöffel, Early Aalenian). Scale bar is 1 cm



with *Arca liasina* ROEMER, 1836 (e.g. Oppel 1858) but Goldfuss' species is clearly distinct from all other Jurassic arcoideans (Benecke 1905). It is a central European species with occurrences in the Late Toarcian–Bajocian of Eastern France (Alsace), Southern France (Aveyron), Northern and Southern Germany and Northern Switzerland (Goldfuss 1837; Oppel 1858; Quenstedt 1858; Benecke 1905; Hiltermann 1962).

Based on various characters including the hinge dentition, “*Arca*” *inaequalis* clearly must be placed in the genus *Grammatodon* MEEK & HAYDEN 1861. Within that genus, three subgenera are distinguished in the Jurassic: *Grammatodon* MEEK & HAYDEN 1861, *Cosmetodon* BRANSON 1942, and *Indogrammatodon* COX 1937 (see Newell 1969). Members of the subgenus *Grammatodon* have a rather short and ventrally somewhat rounded shell with a closely spaced costellate sculpture and with a marked posterior carina. Species in the subgenus *Cosmetodon* have more elongate, subrectangular and posteriorly alate shells with the umbo in the first third of the length, and sometimes an umbonal sinus (Branson 1942; Newell 1969). *Indogrammatodon* includes species with a poorly defined posterior carina and with ornamentation, which is on the left valve consistently stronger than on the right valve (Cox 1937; Newell 1969; Gardner and Campbell 1997).

Definitions of bivalve taxa which are based on shell geometry are problematic because convergent evolution among not closely related species cannot be excluded. Especially for the arcoid bivalves, this seems to hold true because homoeoplasia was documented in several instances (Oliver and Holmes 2006). Continued use of the subgenera *Grammatodon* and *Cosmetodon* is thus problematic as these rather represent species with a similar mode of life than monophyletic groups. The subgenus *Indogrammatodon* seems to be better defined, and based on the ornamentation pattern *G. inaequalis* seems indeed to belong to that subgenus. Yet *Indogrammatodon* occurred from Aalenian to Tithonian times in the Tethyan region. The center of dispersion was India, East Africa, Australia and New Zealand, and the Northernmost records are from the Bajocian to Kimmeridgian of Somalia and Arabia (Gardner and Campbell 1997 and references therein). *G. inaequalis* clearly does not fit into that picture. Not only

would it be by far the most northwestern occurrence of the subgenus, it would also be the oldest. Such a disparate history of dispersal seems impossible for a monophyletic group. Therefore *G. inaequalis* does either not belong to *Indogrammatodon*, or *Indogrammatodon* is accepted as a polyphyletic taxon. For these reasons a subgeneric assignment for *Grammatodon inaequalis* is not attempted here.

Morphology

Grammatodon inaequalis attains a maximum length of ~40 mm. It is a moderately inflated species with the broad umbos well in front of the middle but behind the first third of the shell (Fig. 1). The ventral margin is very slightly rounded, and there is no byssal gap. The distinct posterior umbonal ridge is rounded. The posterior border is not alate. The most striking feature is the sculpture of the shell, which differs, as the name implies, between left and right valve. Whereas the right valve is, except for weak concentric growth lines and fine radial striae, almost smooth, the left possesses sharp concentric and radial ribs producing a reticulate ornamentation. The ribs are narrow and symmetrical in cross-section. The original description by Goldfuss (1837) and his figure, based also on material from the Opalinuston Formation of Southern Germany, are quite accurate except for the umbonal sinus, which was never observed in the studied material. Quenstedt (1858) on the other hand confounded left and right valves.

The elongation of the shells, expressed as the *L/H*-ratio averages 1.65 for all the measured specimens from Southern Germany and Northern Switzerland, with the minimum value 1.44 and the maximum 1.84 (Fig. 2; Table 1). The thickness of the valves is considerable and especially pronounced in the ventral part of the shell (Fig. 3). There is no difference between left and right valve thickness, and left and right valve are of equal size.

Preservation and taphonomy

The Opalinuston Formation is a 80–120 m thick succession of dark clayey shales with thin intercalated silty layers and was deposited in a shallow, partially silled epicontinental

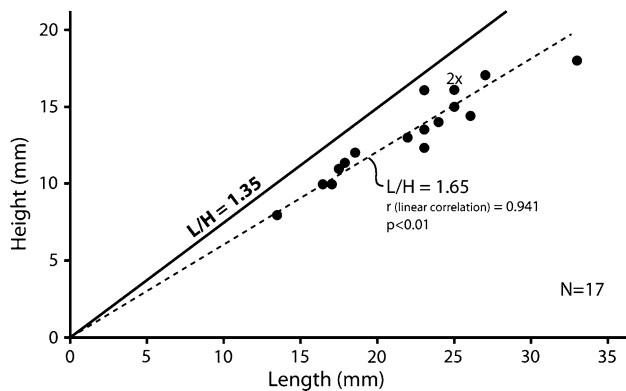


Fig. 2 *L/H*-plot of the studied *Grammatodon inaequivalvis* (GOLDFUSS) specimens from the Opalinuston Formation of Northern Switzerland and Southern Germany (Early Aalenian). Among modern Arcoida, the line indicating $L/H = 1.35$ separates the shorter burrowing taxa from the elongated, byssally attached, epibenthic species

sea, slightly below storm-wave base (Etter 1995, 1996; Wetzel and Allia 2003). The benthic macrofauna of the Opalinuston Formation is of low diversity and low abundance. The most common taxa are small epibenthic bivalves (*Bositra buchi*, *Pseudomytiloides dubius*). Nuculoid bivalves and small trace fossils of the ichnogenus *Planolites* are also fairly common.

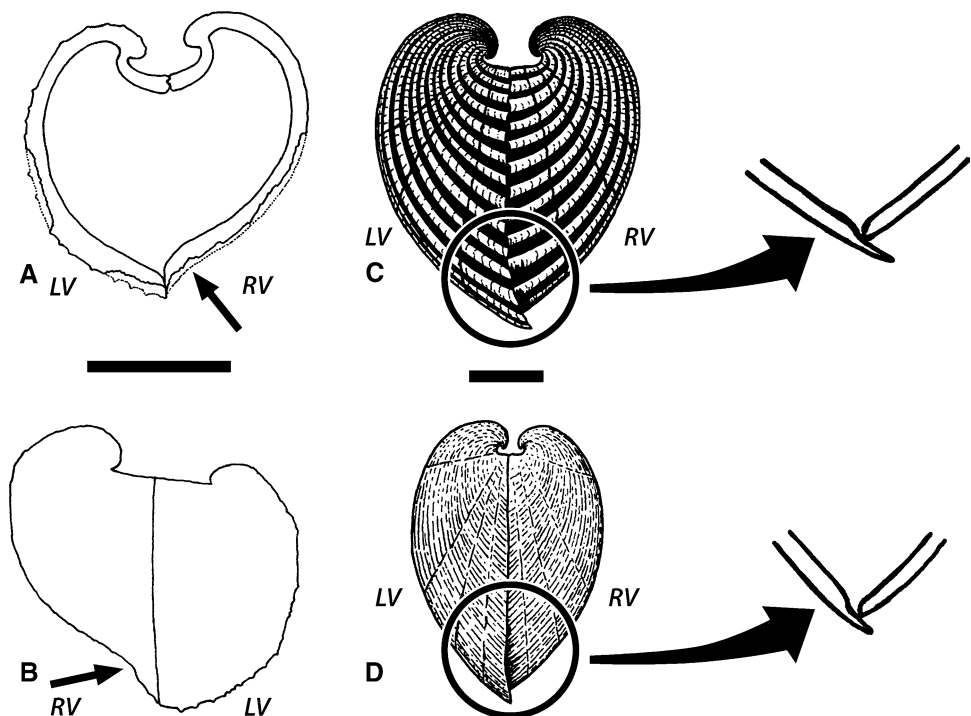
According to the taphonomic signature (no corrosion/abrasion, very low disarticulation rate, no sorting), the benthic fauna of the Opalinuston Formation can confidently be interpreted as autochthonous (Etter 1995, 1996).

Topographic highs were remote, at least during deposition of the lower part of the Formation, and there are no indications that shells were swept into the basin by storms. It is also highly unlikely that *Grammatodon inaequivalvis* lived attached to driftwood or floating algae and that the shells settled from the upper part of the water column. This bivalve was never found associated with logs, and the high proportion of double-valved specimens (see Table 1) contradicts a pseudoplanktonic mode of life (see Wignall and Simms 1990; Etter 1996).

Grammatodon inaequivalvis is a rare species. A bed-by-bed survey of the lower part of the Opalinuston Formation at three localities (Sibilingen, Schinznach, Hägendorf) in Northern Switzerland yielded more than 30,000 macrofaunal specimens (Etter 1990). Only 20 specimens belonged to *G. inaequivalvis*. However, this species is also rare in other geographical regions.

Whereas in Northern Switzerland the aragonitic shells are dissolved (thus leaving only casts with remains of the periostracum), they are preserved either in their original composition or as recrystallized calcite in Southern Germany. Double-valved museum specimens from Southern Germany are preserved with closed shells while those from Northern Switzerland are mostly preserved with the two valves splayed open (“butterflied” preservation; Allmon 1985). This difference is, however, most likely a sampling artifact. The calcareous shells from the Opalinuston Formation of Southern Germany are collected as weathered-out remains, and “butterflied” specimens will therefore be

Fig. 3 *Grammatodon inaequivalvis* (GOLDFUSS) from the Opalinuston Formation of Southern Germany. **a** Cross section (SMNS 67139/1, Balingen, Early Aalenian). **b** Front view (SMNS 67138/1, Weilerstöffel, Early Aalenian). Indentations of the right valve are marked with arrows. **c** Posterior view and cross section of the ventral shell margin of *Scapharca brasiliiana* (LAMARCK) (NMB 1043 1, Los Gallos Pt., Trinidad, recent). **d** Posterior view and cross section of the ventral shell margin of *Cucullaea concamerata* (MARTINI) (NMB 277 b, Macao, China, recent). All scale bars are 1 cm



collected as two isolated valves. In Northern Switzerland, by contrast, the casts of fossils decay completely in surface exposures. Collecting was therefore done by splitting unweathered sediment and the macrofauna was observed on slab surfaces (Etter 1990). In this case, closed double-valved preservation might have gone unnoticed and mistakenly be recorded as single valve.

All the double-valved shells from Southern Germany show a distinct compactional pattern in which one valve is slightly displaced dorsally versus the other valve (Fig. 3a, b) and 40% of the specimens are laterally compressed. By contrast, a displacement of one valve or a compaction of the shell in an anteroposterior direction was never observed. Several specimens showed an indentation of the right valve as a consequence of the compaction (see Fig. 3a, b). A corresponding indentation of the left valve did never occur. A preferred convex-up or convex-down orientation could not be observed.

Discussion

The arcoidean bivalves are usually treated as a group in which the mode of life is intimately correlated with the morphology of the shell (Stanley 1970; Thomas 1978a, b). Especially the distinction between elongate epibenthic byssate hard-bottom dwellers and nestlers and shorter, burrowing but in part still byssate species based on the simple L/H relation has persisted in the literature as a successful example of bivalve functional morphology. This pattern, which is supported by the analysis of numerous modern species is also well corroborated for Neogene members of the genus *Anadara* (Alexander 1993).

There are a few additional shell characters considered useful in constraining the substrate niche of arcoideans: (1) burrowing taxa have a rounded ventral shell margin whereas epibenthic species have a straight or slightly concave venter, usually with a marked byssal gap (Kauffman 1969; Stanley 1970, 1972). (2) Alate posterior borders are only found in epibenthic species, but not all of them have such a winged posterior border (Kauffman 1969). (3) The sculpture is usually commarginal (although sometimes very weak) in endobysate species, radial in non-byssate burrowers, and radial or reticulate in epibenthic byssate taxa (Stanley 1972; Amler 1989).

With a mean L/H ratio of 1.65, *Grammatodon inaequalis* belongs to the elongate taxa among the Grammatodontinae and should have been, according to current practice of arcoid functional analysis, an epibenthic species attached on a hard bottom by a moderately strong byssus, with the commissural plane oriented perpendicular to the substrate. Yet according to the autochthonous occurrences within very fine-grained sediments, this

species was clearly a soft-bottom dweller. This is corroborated by the absence of a byssal gap although this does not automatically imply the absence of a weak byssus (e.g. Morton 1981).

The slightly rounded venter and the truncated non-alate posterior margin would be consistent with a burrowing habit or a semi-endobenthic mode of life. Such a substrate niche was previously assumed for several *Grammatodon* species from the Jurassic of England (Duff 1978; Wignall 1990) and Argentina (Damborenea 1987) despite a L/H ratio >1.35 , thereby expressing discomfort with the simple shell elongation-substrate niche relation. Yet in *Grammatodon inaequalis* the situation is further complicated by the sculptural pattern, which differs strongly between left and right valve. The left valve shows a reticulate ornamentation of sharp ribs. Both radial and commarginal ribs are symmetrical in cross-section. Such ribs certainly hinder during burrowing (Stanley 1981) but they perfectly correspond with the paradigm of a scour-reducing ornamentation and aid in anchoring the shell in the sediment (Stanley 1981).

Members of the subgenus *Indogrammatodon* also show, although to a lesser degree, such a difference between left and right valve sculpture (Cox 1937; Newell 1969). For these species, including the elongated ones, an endobenthic mode of life was proposed (Gardner and Campbell 1997). Because of the greater friction of the left valve an oblique orientation of the shell would result during the process of burrowing, with the right valve inclined towards the substrate (Gardner and Campbell 1997). There are some modern burrowing bivalves in which the commissure is oriented horizontally and which possess a stronger ornamentation on the upper valve (Seilacher 1972, 1984). But these bivalves (members of the superfamily Tellinoidea) possess long siphons, remain buried a considerable distance underneath the surface, and the sculpture consists of asymmetrical ribs. It is hypothesized that this unequal ribbing may become functional when the animal must free itself from a sediment overload (Seilacher 1972). Because siphons are absent in the Arcoidea, the posterior end of a burrowing *Indogrammatodon* species must have been at or near the sediment–water interface. The position of the shell would thus still be with the anterior end pointed downwards albeit in an oblique manner.

As is evident from the compactional patterns observed in *Grammatodon inaequalis*, the long axis of this bivalve must have been horizontal. A compaction in an antero-posterior direction was never noted, whereas the deformation in a dorso-ventral direction is most common. The dorso-ventral displacement of one valve versus the other indicates that the commissure was somewhat tilted but because no preferred left or right valve displacement could be observed, the life position was most likely with

the commissure near-horizontal and the tilting occurred post-mortem. The observation that a compactional indentation was only observed in the right but never in the left valve cannot be used as evidence that the right was the upper valve. Compaction occurred under considerable sediment cover and therefore under equal pressure from both sides (see Seilacher et al. 1976). Probably due to the strong ribbing the left valve was more resistant, thereby producing the deviation from a symmetrical compactional pattern.

Differential compaction could also result from unequal size of the two valves. Inequivalvedness is not uncommon in arcoids, and can attain considerable dimensions as in the twisted ark *Trisidos* (McGhee 1978; Savazzi 1981). In *Cucullaea* and in various species of the genera *Scapharca* and *Cunearca*, the left valve overlaps the right one ventrally (Newell 1969). During compaction, the smaller right valve might perhaps become deformed inwards against the left valve. However, shell overlap is always accompanied by a marginal groove in the larger valve, into which the opposing shell margin fits (see Fig. 3c, d). This is clearly not the case in *Grammatodon inaequalis*, where left and right ventral shell margins are identical.

A novel proposition for the mode of life of *Grammatodon inaequalis*, which reconciles the various functional traits with the taphonomic observations is presented here. It is suggested that *G. inaequalis* had a reclining mode of life and was lying with its left valve on and partially submerged (“iceberg” strategy; Thayer 1975) in the sediment. This explains the unusual sculptural pattern. The reticulate ornamentation of the left valve aided in anchoring the shell in the substrate. Interestingly, in *Trisidos tortuosa* LAMARCK it is also the lower (but here right) valve that shows in its posterior part a slightly stronger ribbing than the overlapping upper left valve. An anchoring sculpture of the lower valve was also reported for a Jurassic bakevelliid from Chile (McGhee 1978).

The position of *Grammatodon inaequalis* on the sediment complies also with the elongate shell, which points to an epibenthic mode of life. Finally, a horizontally oriented long axis and a near-horizontal commissural plane agree with the observed compactional patterns. The “butterflied” preservation of the specimens from Northern Switzerland is also easier to explain when assuming a life position on the sediment. At the moment it cannot be decided whether a weak byssus was present.

The first Arcoidea are now known from the Ordovician and evolved most likely from free-living, soft-bottom dwellers (Rattner and Cope 1998; Cope 2000). By Late Paleozoic times the Parallelodontidae had evolved and were quite common. They included both semi-infaunal soft-bottom dwellers and epibenthic hard-bottom dwellers (Stanley 1972; Amler 1989). Both the Grammatodontinae

and the Cucullaeidae were derived from the epibyssate parallelodontid stock, and in several lines an evolution towards secondary soft-bottom dwellers was documented. Multiple reversions to a secondary soft-bottom dwelling are also known from Late Mesozoic to Neogene Arcidae and the Anadaridae (Stanley 1972; Oliver and Holmes 2006). However, the colonization of the deeper sediment tier was never possible due to the constructional limitations of the Arcoidea (Thomas 1978a, b).

The reconstruction of this evolutionary scenario relies heavily on the distinction of epibenthic byssate taxa and endobenthic burrowers according to the L/H ratio. In the light of the results for *Grammatodon inaequalis* presented here, it cannot be ruled out that in arcoids there were more evolutionary pathways than previously assumed, and that eventually other arcoideans were also recliners. This might especially be true for other Jurassic Grammatodontinae with an elongate shell even if these species lack (species from the Oxford and Kimmeridge Clay; Duff 1978; Wignall 1990; from the Early Jurassic of Argentina; Damborenea 1987) or show only moderate (species of *Indogrammatodon*; Gardner & Campbell 1998) differences in the sculpture between left and right valve. This remains to be tested based on a larger data set and using both morphological and taphonomical analyses.

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