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Aquilofusus klugorum n. sp. (Gastropoda, Buccinidae) from Late Miocene of the North Sea Basin and stratigraphical implications of the genus *Aquilofusus* Kautsky 1925

KARL GÜRS & KAI INGEMANN SCHNETLER

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Aquilofusus klugorum n. sp. (Gastropoda, Buccinidae) is described from five localities in Jutland (Denmark) and northern Germany. The entire material is derived from the Gram Formation and the Gramian regional stage. The new species seems to be a descendent from the Middle Miocene *Aquilofusus tricinctus* and as *Aquilofusus semiglaber* to be an index fossil for the Gramian. A new method for taxonomical research within the *Aquilofusus* genus is developed and preliminary results for species definition of Middle and Upper Miocene species is discussed using high resolution *Bolboforma* and pteropod biostratigraphy for age control. A biostratigraphic scheme of the genus for the entire Miocene including a biozonation is presented.

Dr. K. GÜRS, LANU Schleswig-Holstein, Hamburger Chaussee 25, D-24220 Flintbek, Germany, kguers@lanu.landsh.de.

K.I. SCHNETLER, Fuglebakken 14, Stevnstrup, DK–8870 Langå, Denmark, schnetler@teliamail.dk.

Zusammenfassung

Die neue Art *Aquilofusus klugorum* n. sp. (Gastropoda, Buccinidae) wird von fünf Lokalitäten aus Jütland (Dänemark) und Norddeutschland beschrieben. Sämtliche Stücke stammen aus der Gram Formation sowie aus dem Gramium der Nordseebecken Regional-Stufen. Die neue Art scheint ein Abkömmling des mittelmiozänen *Aquilofusus tricinctus* zu sein und wie *Aquilofusus semiglaber* Leitwert für das Gramium zu besitzen. Ein neuer taxonomischer Ansatz zur Artdefinition innerhalb der Gattung und vorläufige Ergebnisse für die mittel- und obermiozänen Arten werden im Rahmen der hochauflösenden *Bolboforma* und Pteropoden Biostratigraphien diskutiert. Es wird ein biostratigraphisches Schema für die Gattung für das gesamte Miozän inklusive Zonierung vorgestellt.

Introduction

During its Neogene history, the fauna of the North Sea Basin was influenced by varying connections to the Atlantic (via the southwest and the northwest) and the climatic development during this period. As can be seen in the plankton record (MÜLLER 1986; SPIEGLER 1986), the southwestern connection of the North Sea Basin to the Atlantic broke down during the early Middle Miocene, and the North Sea Basin was isolated from warmer seas. Somewhat later, a severe cooling stressed the fauna inhabiting the basin (GÜRS 2001) and lead to stronger endemic developments especially in the molluscan fauna. Despite the closure of the southwestern pathway, a strong sea level rise occurred within the North Sea Basin leading to a far eastern extension of even deeper marine conditions with clay sedimentation in eastern parts of Germany (BÜLOW 2000) until the late Middle Miocene. A high biostratigraphic resolution for this time-span is achieved by using the *Bolboforma* biostratigraphy (SPIEGLER 1999) or the pteropod biostratigraphy (GÜRS & JANSSEN 2002), which can be used for correlation to the international time scale.

The early Middle Miocene was the climate optimum of the Neogene. Mainly subtropical species inhabited the basin (GÜRS 2001). During the following cooling event, the proportion of species and individuals of mollusca from temperate waters increased. Cold water species remigrated into the basin, as *Drepanocheilus speciosus* (SCHLOTHEIM 1820) and *Eopaziella octonarius* (BEYRICH 1854), which were displaced by the warm climate during late Early Miocene to early Middle Miocene.

In this setting, the abundance of *Aquilofusus* is very striking, and it was applied very early for biostratigraphic purposes (HINSCH 1952).

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Material and Method

RASMUSSEN (1968) figured and described *Aquilofusus* sp. from the clay-pit of Strandgård brickworks at Måde, east of Esbjerg, and from the Karlsgårde Canal at Hodde from an unspecified horizon of the Gram Formation. One specimen of this *Aquilofusus* sp. was found recently in the sediments of the Gram clay pit, a very

famous locality for Upper Miocene marine fossils in Jutland, Denmark. The Upper Miocene Mica-Clay locality of Tiste in Lower Saxony, Germany, yielded three additional specimens as well. Together with two further specimens from the Enderupskov sand-pit, which were glacially redeposited, a total of eight specimens could be studied.

These eight specimens were compared to other Miocene and Pliocene *Aquilofusus* species. Criteria were shell shape, number of visible primary spirals (i.e. spiral ridges developing on the protoconch of the shell and lying above the base), development of secondary spirals, development of axial sculpture. For comparison, the following *Aquilofusus* material was investigated:

Gramian: Strandgård brickworks at Måde, Jutland, Denmark (9 specimens).

Gram brickwork, Jutland, Denmark (c. 600 specimens).

Pinneberg sands of several boreholes in the vicinity of Pinneberg, Schleswig-Holstein, Germany (16 specimens).

Wienerberger brickworks at Tiste, Lower Saxony, Germany (4 specimens).

Langenfeldian: *Limacina wilhelminae* Zone: Strandgård brickworks at Måde, Jutland, Denmark (9 specimens).

Limacina ingridae Zone, *Bolboforma laevis/capsula* Zone: Ohle clay pit, Groß Pampau, Schleswig-Holstein, Germany (10 specimens).

Limacina ingridae Zone, *Bolboforma fragori/subfragoris* Zone: Ohle clay pit, Groß Pampau, Schleswig-Holstein, Germany (25 specimens).

Limacina gramensis Zone, *Bolboforma compressispinosa* Zone Ohle clay pit Groß Pampau, Schleswig-Holstein, Germany (1 specimen).

Limacina gramensis Zone, *Bolboforma badenensis* Zone: Hohen Woos clay pit, Mecklenburg, Germany (27 specimens).

Limacina gramensis Zone, *Bolboforma danielsi* Zone: Bockup brickwork pit, Mecklenburg, Germany (9 specimens).

Syltian: No material was available.

Localities

The clay-pit of Strandgård brickworks at Måde

RASMUSSEN (1966) described the clay pits of the brickworks of Strandgård and Bramminge where the Gram Clay is overlain by meltwater sands, sandy boulder clay or moraine sands. In the extended clay pits, the Gram Clay cropped out only at the northernmost corner and dipped away steeply towards ESE. In 1947, 1949, and 1954, RASMUSSEN collected Miocene molluscs from the Gram Clay and from the overburden, with supplementary collections from the latter in 1962 (a total of 379

specimens belonging to 28 species of molluscs). The holotype of *Aquilofusus klugorum* n. sp., described in this paper comes from these collections that are housed in GEUS (Danmarks og Grønlands Geologiske Undersøgelse, Geological Survey of Denmark and Greenland). Judging from the list of RASMUSSEN (1968) from the new pit north of the brickworks, containing *Astarte gleuei* (in RASMUSSEN as: *Astarte radiata*) (45.4%), *Archimediella subangulata* and *Uromitra wirtzi*, it is evident that clays of Langenfeldian Stage were exposed in this clay-pit as well. This is also supported by collections of HINSCH (1958), who separately sampled the lower and the upper part of the pit. From this material *Aquilofusus* populations of the Gramian as well as of the Langenfeldian could be studied, although they are badly affected by pyrite deterioration.

Karlsgårde Canal at Hodde

RASMUSSEN (1966) described the localities Grøde and Hoddemark near the Hodde village with Miocene layers excavated during the construction of the Karlsgårde Canal from 1941 to 1943.

In both localities, the sequence from dark grey Gram Clay through dark green Glauconitic Clay to black Hodde Clay with a ca. 30 cm thick shell bed containing an assemblage typical of the Arnum Formation was encountered. The fauna of the Gram Clay contains *Aquilofusus* sp.sensu RASMUSSEN (1968), whose exact location and stratigraphic position in the sequence is however unknown. The molluscs listed are typical Gramian fauna except for *Aquilofusus luneburgensis* and *Uromitra wirtzi*. These two species indicate the presence of the Langenfeldian.

Gram clay-pit

This locality has been described in detail by RASMUSSEN (1956, 1966). The production of the brickwork ceased in 1986, and for almost 10 years, the water-logged clay-pit was inaccessible. Since 1996, however, the clay-pit was made accessible again by the Midsønderjyllands Museum, but only about six meters of the uppermost Gram Clay are exposed permanently. The clay pit as well as the neighboured Gram I borehole form the type locality of the Gram Formation (RASMUSSEN 1956). The geology and paleontology of the pit are currently investigated in an interdisciplinary project (ROTH & HOEDEMAKERS 2004, in press), in which the mollusc fauna of the pit and the Gram I borehole will be treated by the second author (SCHNETLER 2004, in press), while the first author is involved in investigations on the bolboforms of a section from the pit (SPIEGLER & GÜRS 2004, in press).

Enderupskov sand-pit

In the neighbourhood of the small village of Enderupskov (ca. 5 km west of Gram), many reworked molluscs have been found that originated mostly from layers of the Arnum Formation. Occasionally, typical Gram Clay molluscs were also encountered,

e.g. *Aquilofusus semiglaber* and *Astarte reimersi*. Material is present in the collections of Midtsønderjyllands Museum (Gram) and in several private and public collections in Denmark and Germany. During a study of the collections of the Museum Naturalis, Leiden (The Netherlands), the second author found a single specimen of *Aquilofusus klugorum* n. sp. Messr. A.C. JANSE from Brielle, the Netherlands (pers. comm., 2003) reported another single fragmentary specimen in his collection.

Wienerberger brickwork pit at Tiste/Freetz

The Wienerberger brickwork pit is situated about 300 m east of Tiste village, Lower Saxony, Northern Germany, immediately north of the motorway A1 (Hamburg to Bremen) at the Ostetal resting place. It is cited several times in literature, for example, for its whale bones (ROTHAUSEN 1986, KLUG & KLUG 1997), or its molluscan fauna (KLUG & KLUG 1999). When visited in the early 1990's, the pit was about 13 m deep. The beds dipped gently towards SW, and the lower 10 m consisted of dark grey silty clay containing some mica. There is a conspicuous boundary to the upper 3 m of clay in the southwest of the quarry, resulting from a larger fine sand content of the upper clay package leading to a higher potential of erosion.

The lower clay has a scarce fauna. Only very rarely, bones of whales or sharks teeth (especially *Macrorhizodus hastalis*) can be found. This part probably belongs to the Langenfeldian of regional North Sea Basin stages, according to KLUG & KLUG (1999, from unpublished data of Hinsch 1985-89) to the Langenfeldian and Lüneburgian sensu HINSCH (1987). The upper part of the clay bears a rich carbonate fauna. The microfauna contains *Bolboforma metzmacheri* and *Uvigerina pygmaea langeri*, indicating an age of Late Miocene or more precisely Gramian. The same also holds true for the pteropods with the only species observed being *Limacina atlanta*. The presence of *L.* aff. *wilhelminae* referred to in the list of KLUG & KLUG (1999) could not be confirmed, but would not contradict the stratigraphic assignment. The mollusc fauna bears *Astarte reimersi* and *Aquilofusus semiglaber*, and thus an age of Gramian is supported by its index species as well.

Neither the existence of reverse bedding due to glacial tectonics nor the occurrence of *Astarte vetula* in the upper part of the clay as reported by KLUG & KLUG (1999) could be confirmed by our own observations.

Groß Pampau clay pit

The Ohle gravel and clay pit at Groß Pampau is situated about five km northeast of Schwarzenbek. It is described in detail in MOTHS (1994) and SPIEGLER & GÜRS (1996). The exposed clays range in age from *Bolboforma compressispinosa* Zone (lowermost pale grey clay) to *B. laevis/capsula* Zone (uppermost clayey silts to fine sands).

Hohen Woos brickwork pit

The clay exposure of Hohen Woos is an erratic thrust body of dark grey to brown micaceous clay. Fossils were collected in the 1950's and 1960's when the clay was exploited by a brickwork. Hohen Woos is situated between Boizenburg and Ludwigslust in Mecklenburg-Vorpommern, Germany. The exposure is treated in detail in BÜLOW (1959). The clay is assigned by GÜRS & SPIEGLER (2000) to the *Bolboforma badenensis* Zone.

Bockup brickwork pit

Dark grey to brown silty micaceous clay was exploited by a brickwork near Bockup village 1.5 km north of Dömitz (Mecklenburg-Vorpommern, Germany). The pit was abandoned for more than 40 years, but new collections come from clay excavated in the pit for reconstruction works on the local waste dump. The history of this and the former site is elucidated by BÜLOW (2000). The age of the clay was determined by GÜRS & SPIEGLER 2000 as *Bolboforma danielsi* Zone.

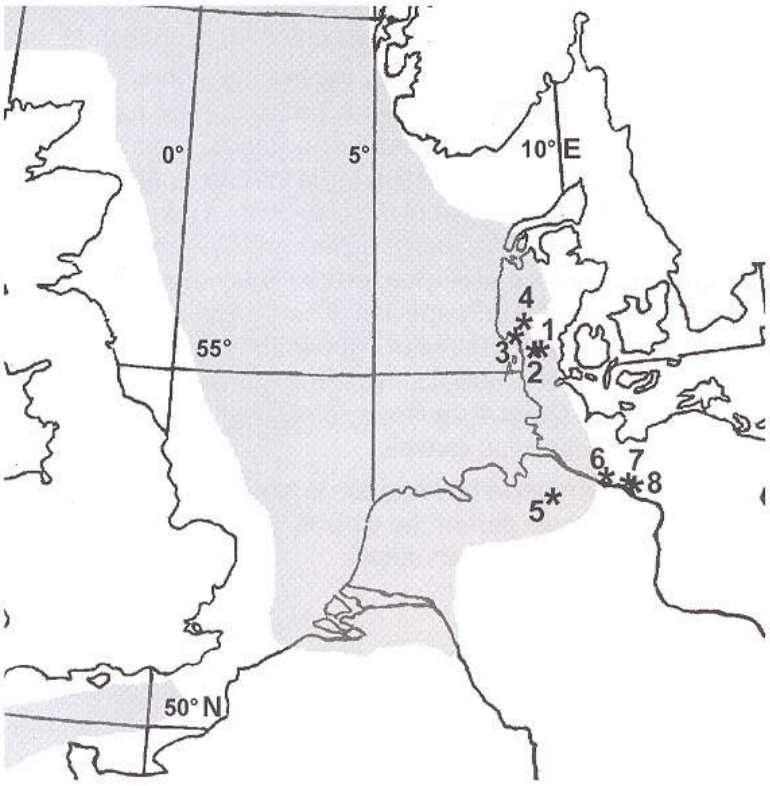

Fig. 1: Paleogeography of the North Sea Basin during early Gramian (shaded grey = sea) and localities: 1 Gram, 2 Enderupskov, 3 Strandgård brickworks at Måde, 4 Karlsgårde Canal at Hodde, 5 Tiste/Freetz, 6 Groß Pampau, 7 Hohen Woos, 8 Bockup.

Systematics

Mollusca

Gastropoda

Orthogastropoda

Neogastropoda

Buccinidae

Aquilofusus KAUTSKY 1925

Type species: *Fusus waeli* NYST 1845

Aquilofusus klugorum *n. sp.*

plate 1, figures 1-3

v 1968 *Aquilofusus* sp.- RASMUSSEN, p. 159, pl. 13 fig. 1

v 1999 *Aquilofusus alveolatus* – KLUG & KLUG, p. 81

v 2004 *Aquilofusus* n. sp.- SCHNETLER, p. 7, pl. 7, fig. 4, pl. 10, fig. 7

Holotypus: GEUS No. 1968–LBR–76, plate 1 figure 2.

Locus typicus: clay-pit of Strandgård brickworks, Måde.

Stratum typicum: dark grey silty fine sandy clay of the Gram Formation, Gramian, Upper Miocene.

Derivatio nominis: after BIRGIT and GÜNTHER KLUG in honour of their work on the fauna of the Tiste/Freetz brickworks pit.

Diagnosis: An *Aquilofusus* with two prominent spiral rows on the early teleoconch whorls, and a very conspicuous shoulder below the suture on the later whorls.

Differential diagnosis: This species differs from

- the contemporaneous *Aquilofusus semiglaber* by having only two spirals instead of three on the early teleoconch whorls, by its conspicuous shoulder, and by its lack of secondary spirals above the first prominent spiral;

- *A. festivus* by having a stronger and more widely spaced axial sculpture on the first teleoconch whorls, and less convex whorls;

- *A. tricinctus* by the two spiral rows instead of three on the early teleoconch whorls, the prominent shoulder, and the weakening sculpture on the last teleoconch whorls; and

- the Pliocene *A. alveolatus* in having a more pronounced shoulder, and a broader shell, and in developing secondary spirals earlier on the teleoconch.

Material: Holotype: GEUS No. 1968–LBR–76; Paratypes: Hodde, Karlsgårde Canal 1 specimen GEUS (not registered); Gram clay-pit 1 specimen coll. Midtsønderjyllands Museum 1629 x1 (plate 1 figure 1a-b); Enderupskov sand-pit 1 specimen coll. Naturalis Leiden (Rijksmuseum van Geologie en Mineralogie, Leiden, former name of Museum Naturalis, Leiden, the Netherlands, RGM 456222), 1 fragmentary specimen coll. A. C. JANSE, Brielle, the Netherlands; Tiste/Freetz, Wienerberger brickworks pit 1 specimen (Landesamt für Natur und Umwelt, State Agency for Natur and Environment of the State of Schleswig-Holstein, Germany, LANU) (plate 1 figure 3a-b), 2 fragments coll GÜRS.

Description: Shell approximately 30 to 40 mm high, spindle shaped, height/width ratio 2.2. Protoconch not known. Teleoconch of 5 to 6 whorls built by a concave shoulder below the suture and a convex part below this shoulder meeting perpendicularly, height/width ratio of last whorl 1.5. Sculpture solely of 2 primary spiral ridges, rectangular in intersection, overrun by sharp growth lines at right angles on the first whorl, afterwards 20 to 22 broad conspicuous axial ribs develop per whorl. They build knobs with the spirals. Axial ribs most prominent in the middle part of the whorls between the spirals, less prominent below, and nearly invisible above. A secondary spiral below the second primary spiral develops at the third to fourth whorl, while in two individuals, a second secondary spiral develops between the two primary spirals; growth lines visible all over the shell; axial sculpture weakens and smoothes on the last half whorl. Base has 4 prominent spirals alternating with 3 weak spirals, and nine additional spirals on the neck of the siphonal canal. Aperture subcircular with a straight, broad, moderately long to long, strong siphonal canal, outer and inner lips not thickened, without any teeth or folds.

Historical outline

The first *Aquilofusus* species of the North Sea Basin Miocene were described and figured by PHILIPPI (1847) from a clay pit at Lüneburg (Lower Saxony, northern Germany). He named them *Fusus luneburgensis* and *F. glabriculus*. His descriptions and figures are poor, and do not define the species well enough for identification. BEYRICH (1856) described additional species, such as *A. eximius*, *A. tricinctus*, *A. semiglaber*, *A. puggaardi*, and *A. festivus*. He gave detailed descriptions and good figures of his species as well as of those of PHILIPPI, although it is probable that his interpretation of *A. glabriculus* differed from that of PHILIPPI. SEMPER (1862) added *A. meyni* to the list of species, and NYST (1861) described *A. beyrichi* from the Edegem Sands of northern Belgium.

KAUTSKY (1925) erected the *Aquilofusus* genus with *Fusus waeli* NYST 1845, a species from the Boom Clay of northern Belgium with a stratigraphic range from Early Oligocene to Early Miocene, as type species. He described 5 new species (*A. hemmoorensis*, *A. siebsi*, *A. oppenheimi*, *A. lategradatus*, and *A. grippi*) from the erratic sands of Hemmoor that mainly belong to the Hemmoorian regional stage. Only *A. lategradatus* was derived from late Middle Miocene sediments. He was the first to recognise the importance of the protoconch of this group of gastropods.

HINSCH (1952) demonstrated the stratigraphical importance of this genus for the North Sea Basin Miocene and regarded *A. festivus* as an index fossil for the Reinbekian, *A. luneburgensis* for the Langenfeldian, *A. semiglaber* for the Gramian and *A. eximius* for the Syltian. He saw a main phylogenetic trend in the reduction of the primary spirals from three to two in these species. Furthermore, he restricted the *A. eximius* species of BEYRICH (1856) to the form with two primary spirals of the Syltian Mica Clay, and excluded older forms with three primary spirals, which he synonymized with *A. luneburgensis*. He also synonymized *A. tricinctus* with *A. luneburgensis*.

KAUTSKY (1962) developed a phylogenetical scheme of the *Aquilofusus* species. He adopted the ideas of HINSCH (1952) concerning the Langenfeldian to Syltian development. Unfortunately, he confused the stage names and swopped Langenfeldian and Syltian.

His assumption that *Aquilofusus* is an offspring of an unknown *Streptochetus* species was revised by TEMBROCK (1968), who was the first to recognize that the characteristic protoconch of *Aquilofusus* is typical for some Buccinidae. Her unification of all these Buccinidae in only one genus, the Lower Miocene *Scalaspira* genus of the eastern USA is however excessive. In contrast to HINSCH (1952), TEMBROCK (1968) chose a specimen from Gühlitz as lectotype of *A. eximius*, belonging to the lowermost Langenfeldian, thus denying the phylogenetical interpretation of HINSCH with a lineage from *A. luneburgensis* (Langenfeldian) via *A. semiglaber* (Gramian) to *A. eximius* (Syltian). She also took *A. tricinctus* as a subspecies of *A. eximius* rather than of *A. luneburgensis*. Her species concept contrasts the former phylogenetical interpretations. In her paper, *A. alveolatus*, *A. imperspicuus* and *A. consocialis* all have ranges from middle Miocene to Pliocene, and *A. eximius* ranges from earliest Langenfeldian to Syltian. Furthermore, she interpreted *A. meyni* as a good species, being descendant from *A. waeli*.

RASMUSSEN (1968) united all *Aquilofusus* from Middle and Upper Miocene with three primary spirals in one species: *A. luneburgensis*. He divided this species into four subspecies: *A. l. tricinctus*, *A. l. luneburgensis*, *A. l. meyni* and *A. l. eximius*. He doubted the statement of Hinsch that *A. eximius* has two primary spirals, and figured a specimen from the Morsum Cliff at Sylt with three primary spirals. He further mentioned that all his specimens from Sylt show this feature. He also described the new species published here under the name *A. klugorum* as *A.* sp., but could not decide whether it is a separate species or a subspecies of *A. semiglaber*.

SPIEGLER & GÜRS (1996) discussed the phylogeny of the *Aquilofusus* genus at the vicinity of the Reinbekian/Langenfeldian boundary and believed *A. luneburgensis* and *A. tricinctus* to be closely related species originating from the Reinbekian *A. festivus*. A model of the phylogeny of *A. festivus*, *A. tricinctus* and *A. luneburgensis* was presented in GÜRS & SPIEGLER (2000).

Discussion

The research history on the *Aquilofusus* genus shows that infraspecific variability of many shell characters makes species identification very difficult. There is a lot of confusion not only on the separation of species, but also in the assignment of species to names from literature. During taxonomic work for description of the new *Aquilofusus* species, a large number of specimens from several outcrops and drillings from the upper Middle Miocene to Upper Miocene were scrutinised. It appeared that classical characters such as shell outline, sculpture and microsculpture, and protoconch morphology did not provide enough information for species identification.

Therefore, the order of appearance of spiral chords on the shell surface was tested. This method is new for the genus, but well established for Turritellidae (ANDERSON 1960).

Aquilofusus klugorum n. sp. has two primary spiral chords (PSC = spiral chords developing on the protoconch). The first secondary spiral (SSC) always appears below the second PSC after 3.5 to 4 teleoconch whorls. All other specimens from Gramian deposits develop the first SSC on the first or second teleoconch whorl above the first PSC. This is also true for three specimens with three primary spirals all originating from the early Gramian Pinneberg sands. These specimens are all referred to *A. semiglaber*. They may develop up to two further SSC between, below or above the PSC, but at least one teleoconch whorl after the first SSC.

The significance of sculptural development of *Aquilofusus klugorum* is shared by *A. alveolatus* from the Pliocene (one beach specimen from Sheppey, UK and figures in literature) and by three specimens from Hohen Woos and Bockup. The latter have three PSC and develop the first SSC between the PSC, but not before the fourth teleoconch whorl. They may develop even more secondary spirals after the fifth teleoconch whorl. These specimens have a protoconch very different from other specimens of the same localities in having a higher spire, no axial ornamentation and evenly spaced PSC. This is *A. tricinctus* in the sense of BEYRICH 1856 but not of RASMUSSEN (1968) or SPIEGLER & GÜRS (1996).

The significance of the sculptural development of *Aquilofusus semiglaber* is the same as in five specimens from Måde. These specimens however differ in having three PSC. Additionally most of them develop more (up to six) SSC on the younger whorls. However, the distance from the beginning of the first SSC to the next is more than one and a half whorls. This is what RASMUSSEN (1968) called *A. luneburgensis luneburgensis* and *A. l. eximius*. Some very similar specimens were determined as *A. tricinctus* by RASMUSSEN (1968) and SPIEGLER & GÜRS (1996). They are stratigraphically slightly older and all have three PSC. Their first SSC appears also above the first PSC, but not before the end of the third teleoconch whorl. About one whorl thereafter, several SSC may develop. The same feature is shown by the majority of specimens from the older deposits of Hohen Woos and Bockup. TEMBROCK chose such a specimen from Gühlitz (Mecklenburg, Germany) as lectotype of *A. eximius*.

A third group within the Hohen Woos material shows a protoconch with three PSC similar to the first group. Immediately after the protoconch, one SSC develops above the first PSC, followed in a short distance by up to 9 other spirals resulting in a very fine striation. This species was described by TEMBROCK (1968) as *A. multicostatus*, which is most probably a junior synonym of *A. glabriculus* (PHILIPPI 1847).

The majority of specimens from Groß Pampau and *Aquilofusus luneburgensis meyni* in the sense of RASMUSSEN (1968) have three PSC. Most of them develop their first SSC on the first or early second teleoconch whorl. In most of the specimens, it lies between the first and second PSC, only in a few above the first PSC. They

differ from *A. eximius* specimens in the fact that the following SSC develop immediately after the first PSC. These specimens belong to typical *A. luneburgensis*.

In this respect, *A. luneburgensis* and *A. glabriculus* have a similar development, but the latter has more axial ribs per whorl (15-22 instead of 10-16 in *A. luneburgensis*), and loses its axial sculpture very early.

Stratigraphical Results

Aquilofusus klugorum is a widelyspread, but very rare species so far observed from Måde in Jutland to Tiste near Sittensen in Lower Saxony over a distance of more than 300 km. It is restricted to the Gramian regional stage, and can be an additional marker species to the more common *A. semiglaber*. In the Gram clay-pit (SPIEGLER & GÜRS 2004) as in the Tiste/Freetz Brickworks pit, it is associated with *Bolboforma metzmacheri* (CLODIUS 1922) and *Limacina atlanta* (MØRCH 1874). It therefore belongs to the *B. metzmacheri* zone according to SPIEGLER (1999) and the pteropod zone 21 = *Limacina atlanta* zone (GÜRS & JANSSEN 2002).

In Figure 2, a spreadsheet for the Miocene *Aquilofusus* species is shown. The *Aquilofusus* zones coincide mainly with the regional stage boundaries,due to the definition of the stages being based mainly on the *Aquilofusus* and *Astarte* stratigraphy. Unfortunately, the zone boundaries are not very precise as the occurrence of *Aquilofusus* species is rare in the late Hemmoorian and in the late Reinbekian. The upper boundary of the lower Langenfeldian or Levensauian as defined by HINSCH (1987) does not coincide with the upper boundary of the *A. tricinctus* zone as *A. luneburgensis* already exists in the upper part of the lower Langenfeldian, as observed in the Pampau clay-pit. This boundary is defined by the first appearance date of true *A. luneburgensis*.

Conclusions

Aquilofusus klugorum n. sp. is a good biostratigraphic tool in addition to *A. semiglaber* to detect the Gramian Stage. Investigations on the development of spiral ornamentation, especially in the succession of the spirals, show that there is a good potential for further phylogenetic studies within this genus, which is in bad need of revision. Nevertheless, the high biostratigraphic potential of this genus is shown in Figure 2. The planned revision of this genus may lead to an even better resolution as used today, especially as high resolution *Bolboforma* and pteropod biostratigraphy can be applied for age control of the investigated faunas.

A weak point of this study is the lack of material from the Syltian. This has to be studied within the scope of the revision now underway.

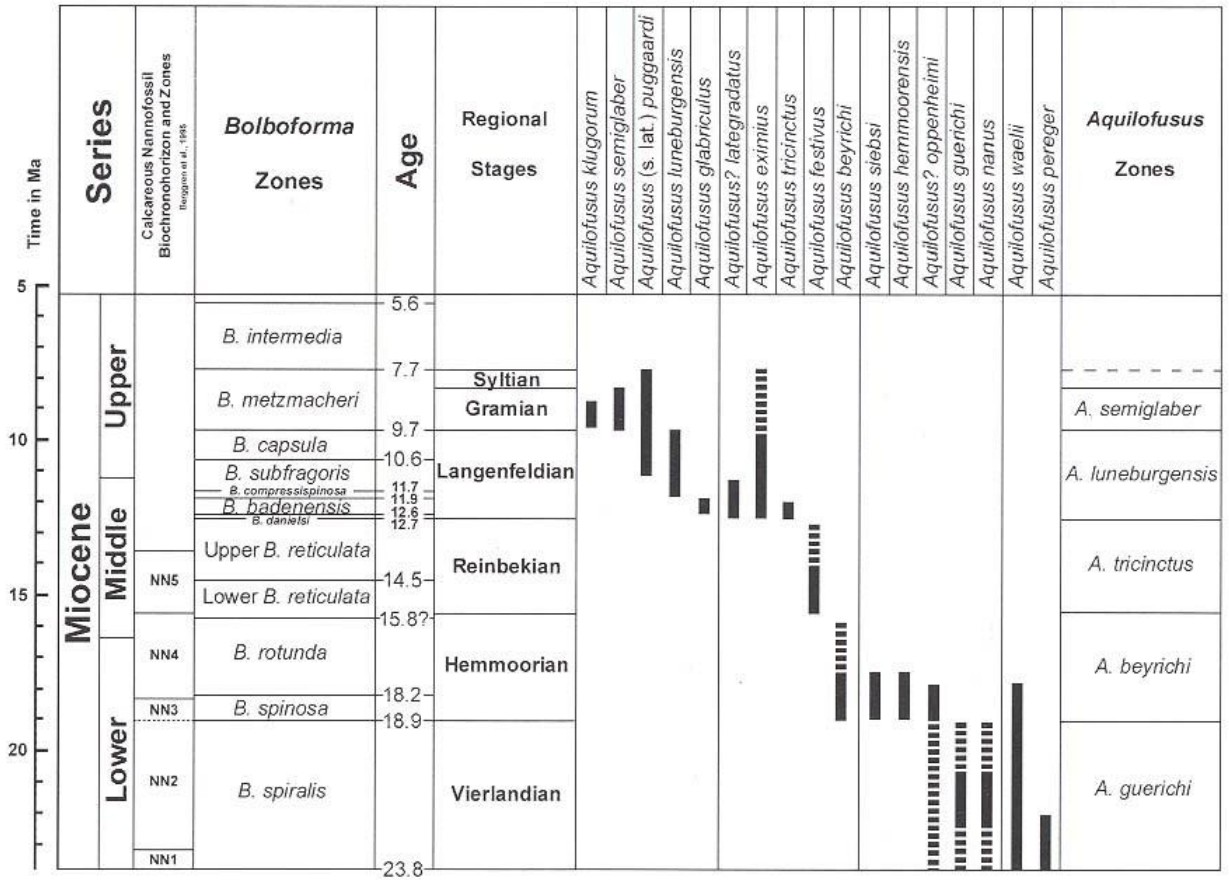

Fig. 2: Zonation for the Miocene based on the *Aquilofusus* gastropod genus. Calibration points are NN3 for the basal Hemmoorian and first occurrence date (FOD) of *A. beyrichi*, NN4/NN5 boundary for FOD of *A. festivus*, *Bolboforma danielsi* Zone for the FOD of *A. tricinctus*, *B. compressispinosa* Zone for the FOD of *A. luneburgensis*, *B. capsula/B. metzmacheri* Zone boundary for the FOD of *A. semiglaber*. The zone boundaries are mainly identical with the regional stage boundaries as these are defined mainly on the *Aquilofusus* distribution.

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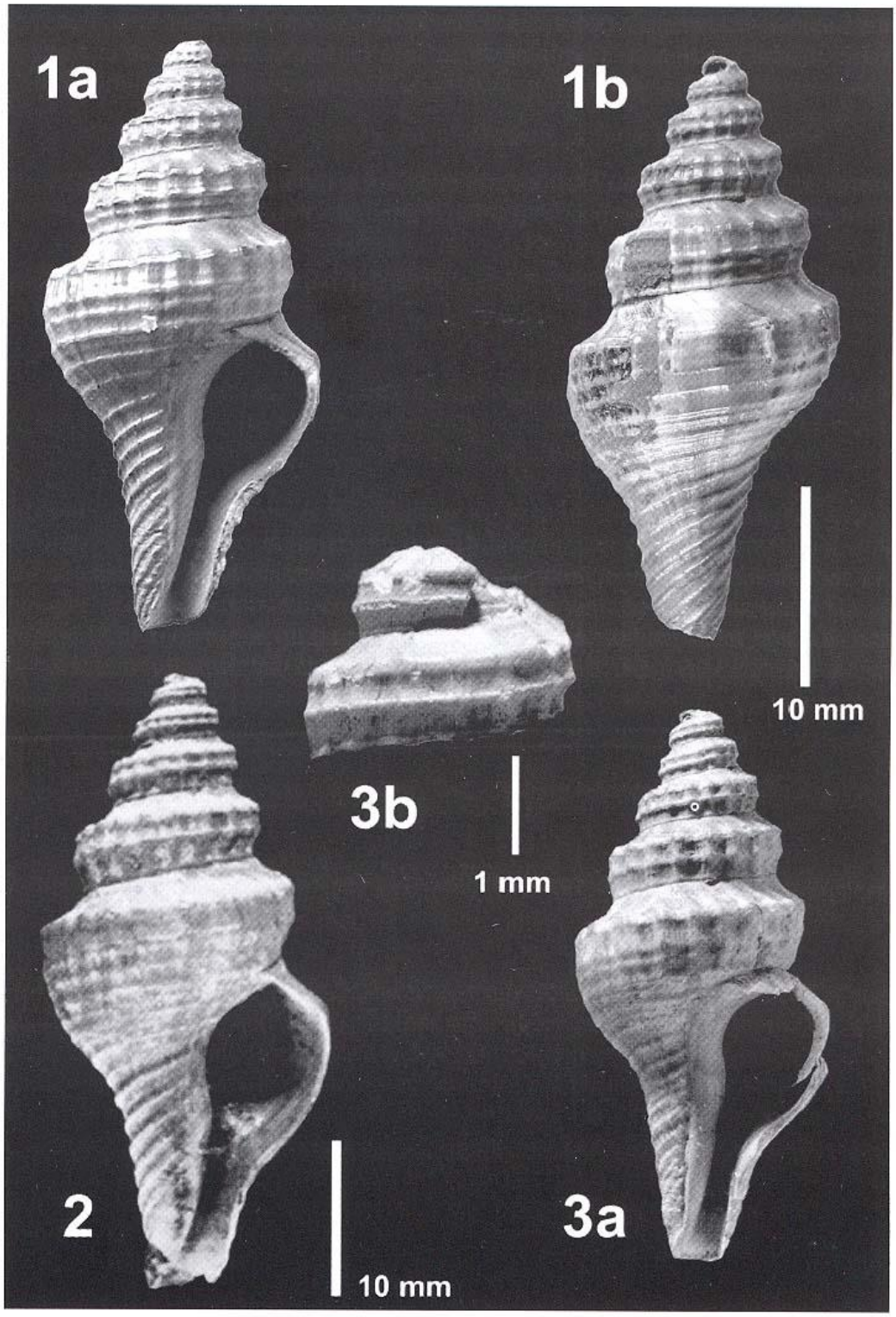
1a
1b
10 mm
3b
1 mm
2
10 mm
3a

Plate 1: *Aquilofusus klugorum* n. sp.

Figure 1: Paratype, Gram clay-pit, 29,5 mm, Midtsønderjyllands Museum, reg. no. 1629 x1, a: front view, b: dorsal view

Figure 2: Holotype, Strandgård brickworks, Måde, 39,6 mm, GEUS, reg. no. 1968–LBR–76

Figure 3: Paratype, Tiste/Freetz, Wienerberger brickworks pit, 28,0 mm, LANU (not registrated), a: front view, b: detail of early teleoconch whorl