

The echinoid *Brissopsis lyrifera* from the Danish Upper Miocene Gram Formation

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The irregular echinoid *Brissopsis* is described for the first time from the type locality of the Upper Miocene Gram Formation at Gram, Denmark. The specimens are conspecific with the Recent *Brissopsis lyrifera* Forbes, 1841. Furthermore they show remarkable resemblance to the Danish forms of *B. lyrifera*.

Key words: *Brissopsis lyrifera*, Upper Miocene, Gram Formation, Denmark.

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Until recently only a few echinoids have been collected in the Upper Miocene Gram Formation. The generally bad state of preservation of tests from this period may be the reason that the echinoids have been overlooked by most collectors. In 1996 the waterfilled clay pit north of Gram was drained and opened for fossil hunting by the public. Subsequently, many sea urchins were found and these form the basis of the present communication.

More than 100 tests from the Upper Miocene Gram Formation in Gram Clay Pit were available for this study. The specimens are deposited in the Geological Museum, University of Copenhagen, prefix MGUH. The tests, which are nearly all from the lower fat clay of the pit, are flattened and generally in a poor state of preservation. The best preserved specimens are from the bottom of the pit.

Stratigraphy, geography and distribution

The Gram Formation was deposited on the eastern shelf of the North Sea during the Late Miocene (Rasmussen & Larsen 1989). The formation occurs in the southwestern part of Denmark where it reaches a thickness of up to about 35 m (Rasmussen 1961). It has been divided into three units of varying composition (Rasmussen & Larsen 1989). The present article deals with the uppermost part of the central unit and some of the top unit in Gram Clay Pit, where the matrix is more silty. The sea urchins were mostly

found around two crab-beds near the bottom of the pit. The lowermost crab-bed lies $4.65 \text{ m} \pm 0.05 \text{ m}$ below the lower storm layer of Rasmussen & Larsen (1989), which here will be used as a marker bed. Under and in the lower crab-bed the present authors have encountered a layer of intense bioturbation mostly made by the trace fossil *Chondrites*, but with very few sea urchins. This layer is immediately below the bottom of the present pit. From here and a few m up the section sea urchins are very common, but the number decreases at higher levels. The highest level at which a sea urchin has been encountered is 0.8 m above basis of the storm wave layer. In the clay pit the tests are mostly found lying with the apical system upward, but a few are situated upside down or on their side. They generally occur in distinct horizons.

Brissopsis lyrifera has been described from the Miocene of Italy (Vinassa de Regny 1897), the Pliocene of Italy (Manzoni 1879, Vinassa de Regny 1897, Checchia-Rispoli 1907) and the Holocene of Norway (Brögger 1901). In Denmark it has been collected from the Upper Miocene Gram Formation in Damgård Nord Pit, near FASTERHOLT, and in the Gram Clay Pit. The specimen from Damgård Nord Pit has never been described. Today, this species lives in the North Sea, along the west coast of Norway and seaward to Iceland. From here it can be found all the way to the coast of South Africa and into the Mediterranean (Hayward & Ryland 1995, Mortensen 1927). *Brissopsis lyrifera* is also living along the east coast of North America (Hayward & Ryland 1995, Mortensen 1927).

Depositional environment

The depth of the Gram Sea was approximately between 70 and 100 m (Rasmussen 1966), but was lower at the end of the Miocene. The sea urchin fauna was most numerous before the relative fall in sea level. In the lower to middle part of the pit the palaeoenvironment was dominated by more or less anoxic conditions immediately below the sea floor. This caused a high content of pyrite and organic matter to be preserved and/or precipitated in the clay. However this was not enough to hamper the rich fauna living in the uppermost part of the sediment or on it (Rasmussen & Larsen 1989). Upsection, the clay becomes more silty and was affected by storm currents because of the prograding coast (Rasmussen & Larsen 1989). This resulted in a more restricted benthic fauna (Rasmussen & Larsen 1989).

The relatively small size of the echinoid tests may be due to restricted conditions because of a freshwater influence (Piasecki 1980) and anoxic conditions (Rasmussen & Larsen 1989). The tests usually are found with spines exclusively on the frontal notch; seldom, if ever, are all spines preserved. The echinoderm eating gastropods *Galeodea echinophora* Linné, 1758, and *Phalium miolaevigatum* Sacco, 1890 (Riedel 1995) have been found in association with *B. lyrifera*. It is likely that they are good indicators of where to locate echinoderms in the more restricted parts of the clay. They are fairly common in the echinoderm-rich lower part of the pit, but together with the sea urchins they become increasingly more rare upwards.

Methods

Lovén's system (1874) is used to number the plates of the tests. Where nothing else is noted, the length of the flattened tests is used to calculate the percentages.

Systematic Palaeontology

Family Brissidae Gray, 1855

Genus *Brissopsis* Agassiz, 1840

Brissopsis lyrifera Forbes, 1841

Figs 1A-C, 2A-B and 3A-D.

Figured specimens: MGUH 25628, Fig. 2A; MGUH 25629, Fig. 2B; MGUH 25630, Fig. 3A; MGUH 25631, Fig. 3B; MGUH 25632, Fig. 3C and MGUH 25633, Fig. 3D.

Description – Length varies from 19 to 58 mm and width from 16 to 54 mm, measured on flattened tests. Not all tests have been flattened in the same orientation, and this makes it possible to roughly estimate the original shape. Test height is 55–63% of the original length; test width is between 85 and 98% of the length. The front angle is about 51–53°; the angle between the ventral and periproct side about 75° (measurements from two tests only). Test egg-shaped, rounded oval to oval with an ambulacral front notch.

Apical system about 40% (30–45%) of test length from posterior of deformed test. Originally, before the tests were deformed, the apical system was situated a little anterior to the central part of the tests. Apical system ethmolytic with four genital pores (Figs 1B, 3C). Genital plate 2 (madreporic) intercalates the two posterior genital plates, separating ambulacra I and

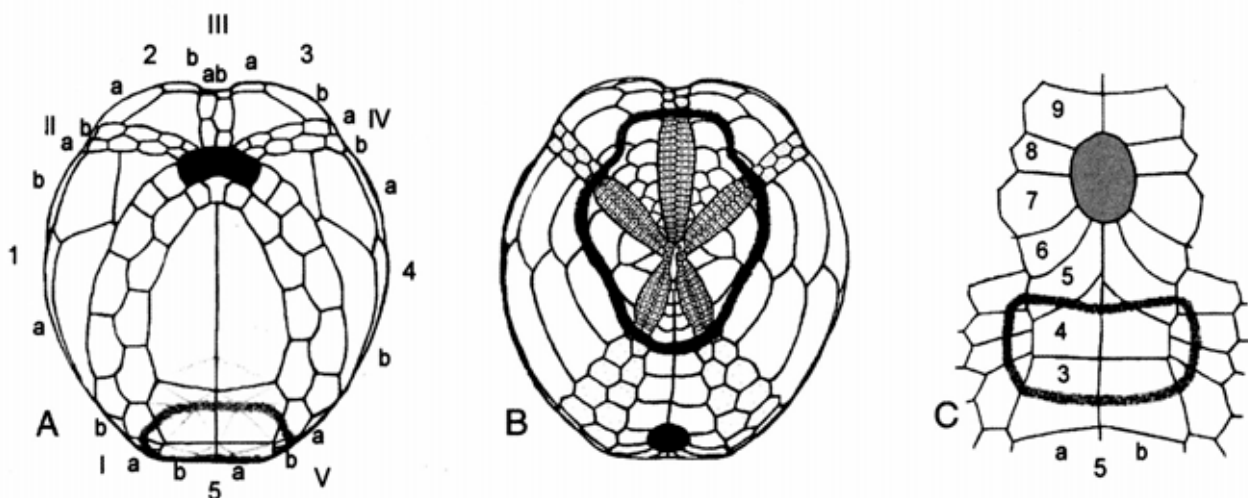
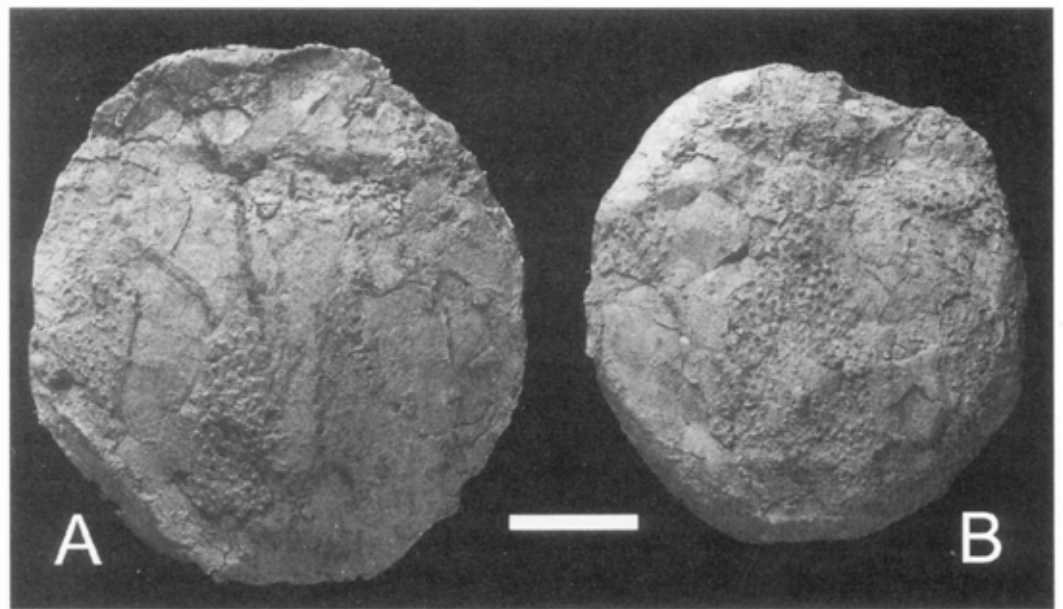


Fig. 1. *Brissopsis lyrifera* Forbes, 1841. A, Reconstructed ventral view of a Miocene Gram specimen with plate numbers according to the Lovénian system (1874); B, Reconstructed dorsal view; C, Subanal fasciole and periproct plate numbers according to the Lovénian system. A and B $\times 1.5$, C $\times 2.5$.

Fig. 2. Ventral view of *Brissopsis lyrifera* (Forbes 1841). Scale bar equals 10 mm.
 A: MGUH 25628.
 B: MGUH 25629.
 Photographs taken by S.B. Andersen.



V. End of madreporic plate smoothly rounded, extending nearly the length again of genital plates 1 and 3 from posterior genital plates (Fig. 1B). Genital plates 1, 3 and 4 more or less hexagonally rounded.

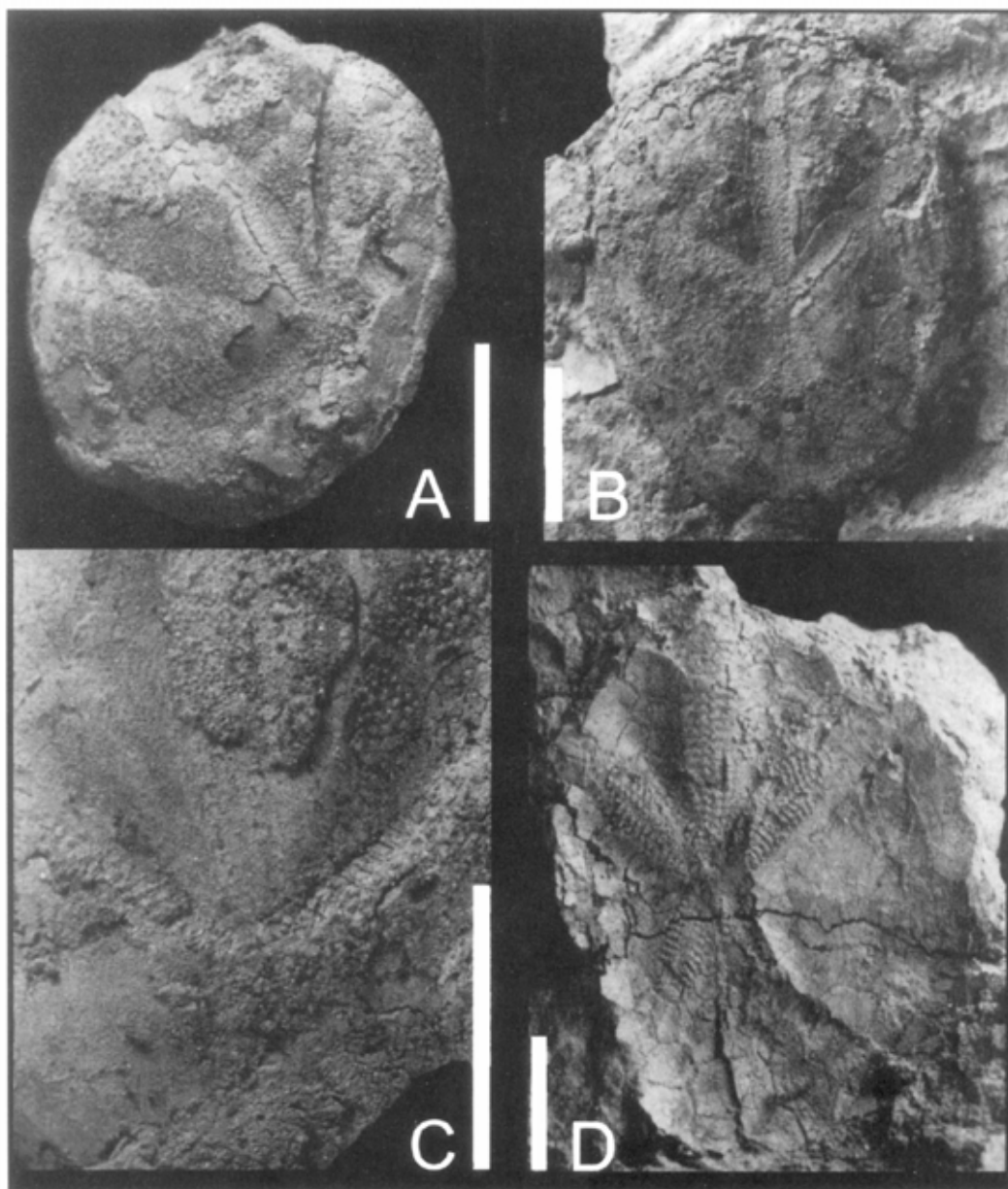
Anterior ambulacrum, between apex and peripetalous fasciole, forms a notch in anterior ambitus (Fig. 1B). Between the peristome and anterior ambulacrum are 5 hexagonal, oblong plates in III.a and III.b. This number does not change with size of the test. Length of anterior ambulacrum is generally between 30 and 45% of test length. Largest width of anterior ambulacrum situated 2/3 of length from apical system, reaching approximately 25% of anterior ambulacral length or about 10% of test length. Anterior ambulacrum has about 32–42 plates (varies somewhat with size), each with 2 almond shaped pores placed a little apart. On many of the tests these features are more or less hidden by a rugged surface, which makes the ambulacrum look more like the surrounding interambulacrum (Figs 3B and C), or they have been worn away. Plates in anterior ambulacrum are generally oblong pentagonal (Figs 3B and D).

Ambulacra II and IV nearly straight from apex to peripetalous fasciole, being about 65% (55–75%) of length of anterior ambulacrum (Figs 3A, B and D). Differences between old and young individuals negligible. The petals start between genital plates 2 and 4, and 1 and 3 respectively, and depart from here at an angle of 44–46° to the symmetry axis of the test. The petals reach maximal widths about 2/3 to 3/4 from apex. They have about 28–36 plates (generally around 85–90% of anterior ambulacrum), looking much like those in anterior ambulacrum with pointed almond shaped pores. Pointed ends, of pores, point toward each other. Plates slightly oblique, the inner-

most pore placed a little above the rearmost. Around the pores are small rises, connected in the middle of the plate, giving it a masklike appearance. A row of tubercles lines the topside of the plate. At least some tubercles form part of the rise over the innermost pore. From petals to peristome the number of plates is 10 (only 9 in some specimens) in II.b and IV.a, and 9 (or sometimes 8) in II.a and IV.b. Variations in number of plates may be due to deformation, hiding some of the plates.

Posterior petals (ambulacra I and V) straight, about 45% of length of anterior ambulacrum. They originate between the rearmost genital plates and the madreporic plate, and extend backwards generally with an angle to the symmetry axis of about 21–24°. Greatest width of petals just over half their length from apex, where their width reaches about 40% of their length. The petals have around 22 plates (generally around 75–80% of anterior ambulacrum), varying between 18 and 32 in the Gram species. They are similar to plates of the other petals. From the end of the petals, ambulacra continue to the mouth, where outer rows end at the side of peristome, inner rows go to labrum (Figs 1A and 2A). In contrast to the other ambulacra, they are broader adorsally of the petals, and have much larger plates. Around subanal fasciole and lower part of anal plates, the plates are much shorter and broader (Fig. 1C). From the episternal plates they become narrower and longer. About 14–15 plates are found from peristome to peripetalous fasciole in row "a" as well as row "b" in I and V.

Peripetalous fasciole lyre-shaped, the end of each petal touching the inside of the outer corners (Fig. 1B). On interambulacrum 5 (I.A.5) the fasciole gently curves over the upper part of plate 5.a.11 and 5.b.11,



Figs 3A-D. *Brissopsis lyrifera* (Forbes 1841).

A (MGUH 25630) and B (MGUH 25631) dorsal view. C (MGUH 25632) apical system.

D (MGUH 25633) dorsal from the inside. Scale bars equal 10 mm.

Photographs taken by S.B. Andersen.

except on one test, where it curves over the upper part of 5.(a,b).10. Peripetalous fasciole curves from ambulacrum I.b.14–15 and V.a.14–15 outwards on the main part of I.A.1 and 4, before it curves slightly in the foremost part in the opposite direction. The fasciole runs over plate 1.a.7 and 1.b.6–7 on the first interambulacrum, and 4.a.6–7 and 4.b.7 on the fourth. On ambulacra II and IV the fasciole crosses plates II.a.9, II.b.9–10, IV.a.9–10 and IV.b.9. In some cases the fasciole seems to pass plate 8 and 8–9 instead, but because of bad preservation it may well be that one of the plates is missing. Interambulacra 2 and 3 are crossed by the fasciole on plates: 2.a.5–4 (angles down) to 2.b.4 and 3.a.4 to 3.b.4–5 (angles up). The fasciole curves on I.A.2 first upwards, but still on the first plate it breaks relatively sharply downwards and then again curves towards the front petal. The fasciole

crosses ambulacrum III on plates III.a.5 and III.b.5. However, one test has 6 instead of 5 plates from mouth to fasciole in ambulacrum III.

Subanal fasciole runs over the bulge on the episternal plates and onto the ambulacral plates I.a.6–9 and V.b.6–9 (Fig. 1C). From plate 9 the fasciole turns to the lower part of the anal-plates I.A.5.(a,b).5 and downwards, where it crosses the subanal plates I.A.5.(a and b).4 just above the bulges. Width of subanal fasciole is between 37–44% of test length.

Peristome peanut shaped, width about 18% (14–23%) and height around 7–9% of test length. It is placed in the front part of the test (Figs 1A and 2A). Periproct higher than wide, encircled by anal plates 5.(a,b).5–9 (Fig. 1C).

Ventral plates: Interambulacral plates 2.1 and 3.1 almost triangular, with I.A.2.1 covering II.b.1–2 and

the lowest part of II.b.3 to one side and III.a.1–2 to the other. I.A.3.1 extends out to III.b.3 and IV.a.3. The slightly hammer shaped labrum is encircled by the first ambulacral plate (ambulacra I and V), sternal plates and mouth (Fig. 1A). It is about 8% (6–8%) of test length. First ambulacral plate short, wider than long. The next are longer than wide, stopping at the edge of the mouth. Ambulacra I.b and V.a start from the side of the mouth. First plate in I.A.1 and 4 almost triangular, extending from the mouth to the middle of the third ambulacral plate in II and IV, and the third plate in I and V. Plate 1.a.2 barely touches plate one (the same for plate 4.b.2 and plate one), while plate 1.b.2 touches plate one along the whole inner boundary. Sternal plate length about 47% (39–57%) of test length, and together the sternal plates generally have a width of about 35% (28–43%) of test length. The two plates are equal sized and together form a relatively big bulge at 80% length from their front end. The sternal plates are surrounded by labrum in the front, ambulacral plates I.a.1–5 and V.b.1–5 to the sides and the episternal plates to the rear. The episternal plates are of equal size, each having a bulge placed 1/3 plate width from the symmetry-axis of the test. Each of the preanal plates (I.A.5.(a,b).4) also have a bulge, although smaller. The bulge is placed 2/3 from the front end of the plate, and 1/4 plate width from the symmetry-axis of the test.

Discussion

Comparison with the Recent species *B. lyrifera* – These Late Miocene specimens appear to be very similar to the recent *Brissopsis lyrifera* now living in the North Sea. Because not all tests of the Gram specimen have been flattened in the same orientation, it is possible to estimate the original shape. The Gram specimens and the recent *B. lyrifera* evidently are of a similar shape, with identical petal angles, an apical system situated a little anterior to the central part and the same outline. The apical system in the Miocene tests is very much like that of the recent *B. lyrifera*, with genital plate 2 passing between the posterior genital plates and out to a tongue like shape. The length and width of the petals are similar to *B. lyrifera*, and there is also no difference in the relation between the amount of plates in the three petals types. The characteristic form of peripetalous fasciole, which gives *B. lyrifera* its name (Mortensen 1927) is also found on the Gram specimens. Its path over the plates of the fifth interambulacrum seems to be different from that described by Chesher (1968); however, the Recent Danish *B. lyrifera* shows much the same variance. As Chesher noted, the fasciole crosses plate III.a.5. In rare

cases there is a sixth plate in front of the front petal, plate 6. On all the tests from the Gram Formation, the fasciole runs across plate 3.a.4 and 3.b.4–5. From there it crosses plate IV.a.9–10 and IV.b.9 (possible it crosses plate 8–9 and 8 in some rare cases), and then 4.a.6–7, in agreement with Chesher. On ambulacrum V the fasciole first passes V.a.14–15, and then somewhere between plates 14 and 15 on b. The exact number on b has not been determined, because of the poor state of preservation of the tests. On 5.a and b the fasciole crosses the upper part of plate 11 instead of plate 10 as Chesher described. The subanal fasciole covers the same plates in the fossils as in the Recent *B. lyrifera*. The peristome, the periproct and the ventral plates look similar to those in the North Sea specimens.

It appears, from the comparison above, that the Miocene specimen is identical to *B. lyrifera*. Another question is whether it is *B. lyrifera sensu stricto* or only a closely similar taxon as Donovan & Veale (1996) discussed for some other heart urchins from the Oligocene and Pleistocene. In the case with *B. lyrifera* the Miocene specimens show the same differences noted by Chesher (1968) between Recent Danish forms from different basins. Additionally the fossil specimens are found within the same region as the Recent form. Therefore it seems most likely it is *B. lyrifera sensu stricto*.

Comparison with other species – The Gram Formation species differs from the Recent *Brissopsis alta* Mortensen in the placement of the fasciole. The fasciole is placed on plate III.b.5 and not III.b.6 as in *B. alta* (Chesher 1968). On I.A.3.b it crosses plate 4 and 5, which is not the case for *B. alta* (Chesher 1968). There are also too few anal plates in *B. alta*. The periproct is only enclosed by I.A.5.b.6–8 (Norlund & Turner 1988), while the Gram specimens have I.A.5.b.5–9.

B. lyrifera capensis Mortensen differs from *B. lyrifera* in the width of the area enclosed by the subanal fasciole, where the mean test width is approximately 40% of test length. The test width of *B. lyrifera capensis* is generally 45–50% of the test length (Chesher 1968). The interval of the mean test height apparently is too low for *B. lyrifera capensis*, but here the possible interval also reaches a little more than that of the Miocene specimens. The main part of the possible interval, however, is in the interval of *B. lyrifera* (50–60%) (Chesher 1968). Another difference is that the peripetalous fasciole only runs across IV.a.9 (Chesher 1968) and not 9 and 10. On V.a it crosses 14 and 15, while on *B. lyrifera capensis* it is 15 and 16 (Chesher 1968).

B. atlantica Mortensen does not have diverging posterior petals as in the examined tests from Gram, and on I.A. 3.a the fasciole passes across plate 4 and 5 (Chesher 1968) and not, as in the Miocene specimens,

across only plate 4. On I.A.3.b it only crosses plate 5 or in some cases bends down from 5 to 4 (Chesher 1968). Another difference from the Miocene tests is that the fasciole on III.b crosses plate 6 (Chesher 1968) and not 5.

B. mediterranea Mortensen has confluent posterior petals (Chesher 1968) rather than divergent petals, and the fasciole goes over III.b.6 (Chesher 1968) and not 5. Furthermore, the peripetalous fasciole crosses plate 3.a.4 and 5 (Chesher 1968), instead of only the fourth, and extends from there over 3.b.5 (Chesher 1968), where in the examined tests from Gram it extends over 4 and 5.

B. elongata Mortensen varies from the Miocene specimens in the placement of the fasciole on III.b, where it crosses plate 6 or 7 (Chesher 1968) and not 5. In the area of I.A.3.a the peripetalous fasciole can be found on plate 4–5 (Chesher 1968). In the Gram Formation specimens it has only been found on the fourth plate. On 3.b it goes over plate 5 (Chesher 1968) instead of 4 and 5. There are 5 (Chesher 1968) and not 4 ambulacral plates in the subanal fasciole as in the Miocene specimens.

Conclusion

In the comparison between the Recent sea urchin *B. lyrifera* and the Gram specimens only one difference from Chesher's description was found, but corresponding variations are also reported amongst Danish specimens living in the North Sea today. Chesher (1968), stated that plate number 5.(a,b).10, is crossed by the peripetalous fasciole, where as the fasciole was found to cross plate 5.(a,b).11 in the Miocene Gram form as well as in the Danish Recent species. The specimens of the genus *Brissopsis*, which were found in the Upper Miocene Gram Formation in Gram Clay Pit, Southwest Denmark, are conspecific with *B. lyrifera*.

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Dansk sammendrag

Gram Formationen fra Øvre Miocæn er blottet i Gram Teglværksgrav. I den nedre del af profilet er der i de senere år fundet et stort antal af et irregulært søpindsvin. Søpindsvinene, der er i en dårlig bevaringstilstand, kan ud fra deres ydre morfologiske træk identificeres som sømusen *Brissopsis lyrifera*, der også lever i danske farvande i dag. Til den sammenlignende anatomi er specielt peripetal og subanal fasciole blevet anvendt. Den nutidige art varierer noget i form fra region til region. Derfor er det bemærkelsesværdigt, at den sen miocæne form fra Gram tilsyneladende fuldstændigt svarer til den nutidige danske form. I sidste del af artiklen bliver den miocæne *Brissopsis lyrifera* yderligere sammenlignet med fem andre arter af slægten *Brissopsis*, der alle lever i europæiske farvande i dag.

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