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Ecology, Shell Morphology, Anatomy and Sperm Ultrastructure of the Caenogastropod *Pyrgula annulata*, with a Discussion of the Relationship between the ‘Pyrgulidae’ and Caspian and Baikalian Rissoidaeans

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With 6 Figures and 3 Tables

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Abstract

The composition of the Pyrgulidae and its relationships to other member families of the caenogastropod superfamily Rissoidae are examined after a consideration of new anatomical (including gross anatomy, sperm ultrastructure), conchological (including protoconch features), ecological, biogeographical and palaeontological data and a re-evaluation of existing literature. Pyrgulidae can be distinguished from hydrobiids unequivocally only with the aid of the radula. Sperm ultrastructural features suggest a very close relationship between the Pyrgulidae, the Hydrobiidae and the Bithyniidae (in fact no family-diagnostic sperm characters can be found to separate these three taxa). Based upon neontological and fossil evidence it is likely that pyrgulids represent a Miocene offshoot from a paratethyal hydrobiid lineage. Pyrgulids may also represent the stock from which the baicaliids arose, in which case the Pyrgulidae must be considered a paraphyletic group. The huge biogeographic gap between the Caspian Sea and Lake Baikal is to some extent bridged by the finding of a Neogene pyrgulid from the Altai Mountains. An alternative scenario for the origin of baicaliids is presented.

Introduction

RADOMAN's (1983) conclusion that *Pyrgula* JAN & CRISTOFORI, 1882 should be regarded as monotypic was largely the result of his earlier taxonomic decisions (RADOMAN 1955, 1973) to create new genera to accommodate many species formerly included in *Pyrgula*. Certainly there are examples of species incorrectly assigned to *Pyrgula*, as in the case of *Pyrgula barroisi* DAUTZENBERG, 1894 which was originally described on the basis of empty shells from Lake Kinneret. Drawings of the radular teeth by TCHERNOV (1975) clearly demonstrate that this species should be attributed to a different genus if not family of rissoidaeans. The problem as to

which species truly belong to *Pyrgula* is compounded by a lack of detailed, comparative data on the ecology, anatomy and shell morphology of species nominally included in that genus.

What then is so special about *Pyrgula* and what is the precise nature of its relationship to other freshwater Rissoidae? To begin to answer these questions it is first important to briefly outline the somewhat convoluted systematic history of *Pyrgula* throughout the various proposed classifications (see Table 1).

THIELE (1929) placed *Pyrgula* in the hydrobiid subfamily Truncatellinae together with *Oncomelania* GREDLER, 1881 and *Truncatella* RISSO, 1826 while *Chilopyrgula* BRUSINA, 1896 and *Ginaia* BRUSINA, 1896 were assigned to the Micromelaniidae, a family based upon a fossil type *Micromelania* BRUSINA, 1874 (from the Lower Pliocene of Croatia). The protoconch of *Micromelania* has not, unfortunately, been documented. THIELE (1929) also placed among the Micromelaniidae, *Baicalia* MARTENS, 1876, a genus endemic to Lake Baikal and *Turricaspia* DYBOWSKI & GROCHMALICKI, 1917, a taxon endemic to the Caspian Sea. THIELE (1929) regarded *Turricaspia* as a subgenus of *Micromelania*. WENZ (1938–1944) used Pyrgulinae to house *Pyrgula* but listed this subfamily next to Truncatellinae within the Hydrobiidae. In respect of *Turricaspia*, *Chilopyrgula* or *Baicalia* WENZ generally followed THIELE's (1929) concept of Micromelaniidae. RADOMAN (1973, 1983) recognized a superfamily Hydrobioidea (containing Hydrobiidae, Orientalinidae, Pyrgulidae, Micropyrgulidae, Turricaspiidae, Emmericiidae, Lithoglyphidae, Lithoglyphulidae, Bythinellidae, Baicaliidae) and used the family name Pyrgulidae to accommodate *Pyrgula*,

Table 1. Contrasting classification schemes of authors with regard to *Pyrgula*, *Turricaspia* and *Baicalia*.

Author	<i>Pyrgula</i> Family Subfamily	<i>Turricaspia</i> Family Subfamily	<i>Baicalia</i> Family Subfamily
THIELE, 1929	Hydrobiidae Truncatellinae	Micromelaniidae Micromelaniinae	Micromelaniidae Micromelaniinae
WENZ, 1938–1944	Hydrobiidae Pyrgulinae	Micromelaniidae Micromelaniinae	Micromelaniidae Baicaliinae
RADOMAN, 1983	Pyrgulidae Pyrgulinae	Turricaspiidae Turricaspiinae	Baicaliidae not indicated
VAUGHT, 1989	Micromelaniidae ?Pyrgulinae	Micromelaniidae ?Pyrgulinae	Baicaliidae not indicated

Chilopyrgula, *Ginaia* and some other genera. For unknown reasons RADOMAN (1983) chose to ignore the name Micromelaniidae. PONDER & WARÉN (1988) regarded Micromelaniidae as a younger synonym of Pyrgulidae (without indication of reasons). VAUGHT (1989) included *Pyrgula*, *Ginaia* and *Chilopyrgula* tentatively within the subfamily Pyrgulinae of the Micromelaniidae. She also attributed *Turricaspia* to the Pyrgulinae, which is in contrast to RADOMAN (1983) who established the Turricaspiidae, following DYBOWSKI & GROCHMALICKI (1917) who coined Turricaspiinae. With regard to *Baicalia* and relatives, RADOMAN (1983) and SITNIKOVA (1991, 1994) pointed out that the Baicaliidae, which are endemic to Lake Baikal, are deserving of their family status, and must be treated as distinct from hydrobiids or pyrgulids (compare KOZHOV 1951). This is also supported by additional investigations on baicaliid ecology, anatomy, reproduction, embryogeny and protoconchs (SITNIKOVA et al. 2001; RÖPSTORF, RIEDEL & SITNIKOVA, unpubl. data) as well as by comparative sperm ultrastructure (RÖPSTORF et al., in press).

The supposed biogeography of *Pyrgula annulata* (LINNÉ, 1767), type species of *Pyrgula* and of the Pyrgulidae, includes the northern Italian lakes Garda (the type locality), Idro, Iseo and Eudine (GERMAIN 1931, personal observation FR), Lake Bacina and the Zrmanja River in Croatia, the lower course of the Neretva River in Herzegovina and Lake Skutari in Montenegro (RADOMAN 1983). In the Caspian Sea, 72 species of rissooideans assigned to the Pyrgulidae have been reported (KOSAREV & YABLONSKAYA 1994) with species of *Turricaspia* also found in the Wolga delta (MITROPOLSKI 1979). However, it is still not clear what taxa truly constitute the Pyrgulidae and what the relationships of this family (if it should be considered as such) are to other rissooideans. Does the Pyrgulidae really include taxa from the Caspian Sea and do these possibly represent a stock from which baicaliids arose? This also raises the question as to how to bridge such a huge biogeographic gap between the Caspian Sea and Lake Baikal.

The aim of this study is to clarify the relationships between the Pyrgulidae and other rissooideans based on a consideration of new data (gross anatomical, radular, spermato-

logical and protoconch data) and a re-evaluation of existing literature. As *Pyrgula annulata* is the type species of *Pyrgula* CRISTOFOR & JAN, 1832 and also the species on which the Pyrgulidae BRUSINA, 1881 was based, we believe that a detailed study of the anatomy and shell morphology of this species would provide a logical starting point for any re-examination of pyrgulid systematics. In addition to neontological information we recognize a need to scrutinize what is known of Cenozoic palaeogeography in order to better assess possible fossil relatives. As only the shell portion of gastropods survives fossilization, it is necessary to examine anatomical information of all ontogenetic stages to test the consistency of shell characters as indicators of taxonomic identity, especially in groups such as the Rissooidea where similar teleoconchs recur. Only then is there a reasonable chance to identify possible fossil precursors (see e.g. BANDEL 1988; RIEDEL 1993; BANDEL & RIEDEL 1994). *Pyrgula*-like teleoconchs, for example, can be found in several rissooidean groups such as the Pomatiopsidae (see e.g. BRANDT 1974) or the hydrobiid subfamily Cochliopinae (see e.g. HERSHLER & THOMPSON 1987, 1992; see Discussion).

For comparison with *Pyrgula annulata*, ecological, anatomical and conchological data are also presented for *Turricaspia turricula* (CLESSIN & W. DYBOWSKI, 1888) (type species of *Turricaspia* CLESSIN & W. DYBOWSKI, 1888), and *Turricaspia dimidiata* (EICHWALD, 1841). Both species are extant in the Caspian Sea. Additionally, fossil shells from Mio-Pliocene outcrops of the Chuya basin located in the Altai Mountains have been examined of which *Aenigmapyrgus steklovi* POPOVA & STAROBOGATOV, 1970 is described and documented here.

Materials and Methods

Several hundred living and several thousand dead specimens of *Pyrgula annulata* were collected in the beginning of May 1998 by snorkeling off the southeastern coast of Lake Garda near the village of Placengo (45° 28.936 N, 10° 43.284 E - coordinates determined with the aid of a Garmin GPS II Plus). Most specimens (live and dead) were obtained by sieving the substrate. Approximately 40 liv-

ing specimens were picked by hand from the surface of the substrate. The majority of living specimens were kept in a cool box and transported to Berlin. The maximum water temperature reached during the transport was 18 °C but this did not result in high mortalities. In order to obtain egg capsules of *Pyrgula annulata*, specimens were maintained for several weeks in aquaria but without success. Living animals were photographed using a Wild M 400 microscope (with Photoautomat MPS 55).

Turricaspia dimidiata (station 100; 9396) and *T. turricula* (station 99; 9525/938) were dredged from soft bottom (by B.M. LOGVINENKO) of the Caspian Sea (21 August, 1956) in 74 m and 37 m water depth respectively and preserved in ethanol. The specimen of the fossil *Aenigmapyrgus steklovi* (paratype N. 2 borrowed for this study from the Zoological Institute in St. Petersburg, Russia) originates from Mio-Pliocene sediments of the Chuya depression of the Altai mountains.

For transmission electron microscopy (TEM) of mature spermatozoa, sperm-filled genital ducts of males were fixed in 3% glutaraldehyde (prepared using water from Lake Garda) for 48 hours. Subsequently the fixed material was washed three times in cacodylic buffer, then osmicated in 1% osmium tetroxide (in cacodylic buffer), washed again in cacodylic buffer, dehydrated using ethanol and embedded in Spurr's low viscosity epoxy resin. Ultrathin sections were cut at about 70 to 80 nm using a Reichert Ultracut E ultramicrotome, and stained with uranyl acetate and lead citrate. The sections were examined and photographed using a Philips transmission electron microscope; additional observations were made using a Hitachi 300 transmission electron microscope. The length of the spermatozoan midpiece was measured from alcohol fixed material with the aid of a Cambridge Scanning Electron Microscope (SEM).

Radulae and opercula were extracted from fresh and ethanol-fixed material respectively, and cleaned in KOH and H₂O₂ respectively. Radulae, opercula and shells with preserved protoconchs were mounted on stubs, sputter-coated with gold and examined using a SEM. Morphometric data on teleoconchs were obtained with the aid of a binocular microscope while protoconchs were measured under the SEM. The anatomical sketches are camera lucida drawings.

Voucher material of all species examined is deposited in the Institute of Geological Sciences, Freie Universität Berlin.

Results

Ecology of *Pyrgula annulata*

Lake Garda, with a surface area of 370 km², is the largest body of freshwater in Italy (RAMA 1995). The northern part is comparatively narrow due to a tectonic encroachment of the southern margin of the Alps, while the southern part of the lake is much wider, filling a basin of the foothills of the Alps and being more or less connected to the huge Po depression (see Fig. 1). Due to this geological setting, the banks of Lake Garda are much steeper in the north than in the south. The maximum depth of 346 m has been measured at the transition from the narrow to the wider part of the lake. The lake level is about 65 m above sea level (RAMA 1995). Accumulation of fine sediments in shallower water occurs mainly in the south. The Mincio River, which opens into the Po River, represents the outflow of Lake Garda.

In this study *Pyrgula annulata* was found in southern Lake Garda living on and in soft sediments at a water depth of 2 to 7 m. It possibly also lives in depths greater than 7 m but this remains to be determined using SCUBA, dredging or grab-sampling. The water temperature of the lake (on the 5th of May 1998) was 14 °C at 2 m, 13 °C at 3 m, 12 °C at 4 m and about 10 °C at 7 m. The densest population of *P. annulata* (estimated at 150–200 individuals per m²) was found at 3–4 m where the upper 4–12 cm of the substratum consisted - apart from occasional stones and portions of sandy grains - almost exclusively of gastropod faecal pellets (in particular of *P. annulata*). The pellets are more or less ellipsoidal, having a length of 0.3–0.4 mm and consisting of fine silty grains wrapped in mucus. Some larger pellets were determined to be those of *Viviparus ater* (CRISTOFORI & JAN, 1832), which occurs sympatrically with *P. annulata*, but pellets of *V. ater* also occur on hard substrata such as pebbles. Other identifiable pellets from the collection site were those of *Valvata piscinalis* (MÜLLER, 1774) and *Bithynia tentaculata* (LINNÉ, 1758). These two species were only sporadically found deeper than 2 m. The unionid bivalve *Anodonta cygnea* (LINNÉ, 1758) was restricted to sandy areas and probably has not contributed significantly to the pellet sediment.



Fig. 1. Airplane view from the North, demonstrating that the narrow northern part of Lake Garda is located within the alpine relief while the wider, southern part stretches on the foreland and is more or less connected to the Po depression. The Po river flows to the east and empties into the northern Adriatic Sea. The outflow of Lake Garda, the Mincio river, empties into the Po. Not to scale.

Following a 60 m transect from the beach down to 3 m, the substrate changes substantially. Down to about 1 m pebbles of different sizes are characteristic. Further down to 2 m, patchy areas of coarse sand are intercalated with the pebbles and the pebbles are covered more densely by algal growth. Going deeper, patches of water plants appear on the soft substratum, which consists of coarse to fine sand and partly even silt particles. Here the first individuals of *Pyrgula annulata* could be found. Deeper than 3 m there are almost no more pebbles and the faecal pellet sediment becomes characteristic.

Pyrgula annulata live only in the upper oxygenated 1 to 2 cm of the pellet sediment, with only a minority of individuals dwelling in the uppermost 1–2 mm. In the latter group population could be observed. Judging from the observed be-

haviour of *P. annulata*, filter-feeding can be excluded as a means of obtaining nutrition. A closer examination of the uppermost dwelling specimens revealed that they actually feed on the sediment, most probably living on detritus accumulated between the pellets and on pellet surfaces respectively or on bacterial films.

Shell features of *Pyrgula annulata*, *Turricaspia dimidiata*, *T. turricula* and of the fossil *Aenigmapyrgus steklovi*

Teleroconchs of *Pyrgula annulata* are turriciform, about 6 to 7 mm high (see Table 2) and more or less bicarinate. Morphological differences between some specimens are obvious (Figs. 2A–D) and superficial comparison could at first suggest that these individuals are not conspecific. However examination of a range of material showed that there are no consistent shell features to support this impression and that any observed conchological variation is truly intraspecific. Data on intact shells are presented in Table 2, and these specimens are referred to in the following text as T2-n.

Specimen T2–30 with lowest maximum height of 6.1 mm is wider (2.7 mm) than T2–1 with highest maximum height of 7.2 mm having a maximum width of 2.6 mm. The seven specimens having 7.7 whorls range in maximum height from

Table 2. Data compilation of shells of adult specimens of *Pyrgula annulata* from Lake Garda, starting with the highest total number of whorls. SN = number of specimen, NW = total number of whorls, H = maximum height, W = maximum width, PK = onset of primary keel at number of whorls. Data obtained with the aid of a light microscope.

SN	NW	H	W	PK
1	8.7	7.2 mm	2.6 mm	1.9
2	8.7	7.0 mm	2.6 mm	2.4
3	8.4	7.0 mm	2.5 mm	2.5
4	8.4	6.8 mm	2.3 mm	2.2
5	8.2	7.0 mm	2.4 mm	2.3
6	8.2	6.6 mm	2.3 mm	2.1
7	8.2	6.5 mm	2.5 mm	2.3
8	8.1	6.9 mm	2.5 mm	2.3
9	8.1	6.6 mm	2.3 mm	2.0
10	8.0	7.0 mm	2.5 mm	2.0
11	8.0	6.6 mm	2.4 mm	2.1
12	8.0	6.5 mm	2.2 mm	2.8
13	8.0	6.4 mm	2.3 mm	2.1
14	7.9	6.8 mm	2.5 mm	2.0
15	7.9	6.7 mm	2.8 mm	2.0
16	7.9	6.4 mm	2.5 mm	2.0
17	7.9	6.3 mm	2.6 mm	2.4
18	7.9	6.2 mm	2.5 mm	2.3
19	7.7	6.9 mm	2.4 mm	2.1
20	7.7	6.8 mm	2.5 mm	2.2
21	7.7	6.5 mm	2.7 mm	2.9
22	7.7	6.5 mm	2.7 mm	2.2
23	7.7	6.4 mm	2.6 mm	2.5
24	7.7	6.3 mm	2.6 mm	2.1
25	7.7	6.2 mm	2.4 mm	2.1
26	7.6	6.1 mm	2.7 mm	2.4
27	7.6	6.1 mm	2.6 mm	2.6
28	7.5	6.5 mm	2.4 mm	2.3
29	7.5	6.3 mm	3.0 mm	2.1
30	7.2	6.1 mm	2.7 mm	1.9

Mean	7.9	6.6 mm	2.5 mm	2.2
Deviation	0.3	0.3 mm	0.2 mm	0.3

Table 3. Data compilation of the protoconch of *Pyrgula annulata* from Lake Garda, starting with the highest number of whorls. SN = number of specimen, NW = number of whorls, D = maximum diameter, H = interpolated maximum height, NS = width of nonspiral. Data obtained with the aid of a scanning electron microscope.

SN	NW	D	H	NS
1	1.65	0.43 mm	0.39 mm	60 µm
2	1.6	0.44 mm	0.44 mm	95 µm
3	1.6	0.42 mm	0.43 mm	115 µm
4	1.6	0.42 mm	0.40 mm	115 µm
5	1.6	0.42 mm	0.40 mm	115 µm
6	1.6	0.42 mm	0.43 mm	110 µm
7	1.6	0.42 mm	0.42 mm	110 µm
8	1.6	0.42 mm	0.41 mm	110 µm
9	1.6	0.42 mm	0.39 mm	100 µm
10	1.6	0.42 mm	0.41 mm	100 µm
11	1.6	0.42 mm	0.43 mm	95 µm
12	1.6	0.41 mm	0.43 mm	115 µm
13	1.6	0.41 mm	0.44 mm	110 µm
14	1.6	0.41 mm	0.42 mm	90 µm
15	1.6	0.39 mm	0.43 mm	110 µm
16	1.6	0.39 mm	0.39 mm	80 µm
17	1.55	0.41 mm	0.44 mm	110 µm
18	1.55	0.40 mm	0.42 mm	120 µm
19	1.55	0.40 mm	0.40 mm	105 µm
20	1.55	0.40 mm	0.39 mm	90 µm

Mean	1.6	0.41 mm	0.42 mm	103 µm
Deviation	0.02	0.01 mm	0.02 mm	15 µm

6.9 mm to 6.2 mm, which is more than 10% difference. The lowest height/width-ratio of 2.1 can be found in specimen T2-29, the highest ratio of 2.95 in T2-4. T2-19 with 7.7 whorls has a higher shell than T2-4 with 8.4 whorls. In most shells the onset of the primary (upper) keel can be recognized at 0.3–0.5 whorls after the protoconch/teleoconch-transition. In T2-12 it is 1.2 and in T2-21 1.3 whorls. Strength of the spiral keels (carinae) varies significantly, particularly in the secondary (lower) one, which may be very weakly developed.

In respect of the early ontogenetic shell the situation is quite different from that seen in the teleoconch. Intraspecific variation is relatively low. Data on the protoconchs are compiled in Table 3, specimens of which are referred to as T3-n.

In summary, *Pyrgula annulata* has a protoconch consisting of about 1.6 whorls, which amount to an average maximum diameter of about 0.42 mm and an almost equal height. The width of the nonspiral (sensu RIEDEL 1993) is comparatively variable, ranging around 0.1 mm. Sculptural elements are very inconspicuous except for growth increments, which commence already on the nonspiral and increase in strength at the transition to the teleoconch. The initial whorl exhibits a somewhat wrinkled to malleate surface while the remaining portion of the protoconch shows very weak striae (Figs. 2E-I).

Variation and correlation of protoconch parameters can be exemplified. Specimen T3-1 with the maximum number of whorls is second in maximum diameter. T3-2 in direct com-

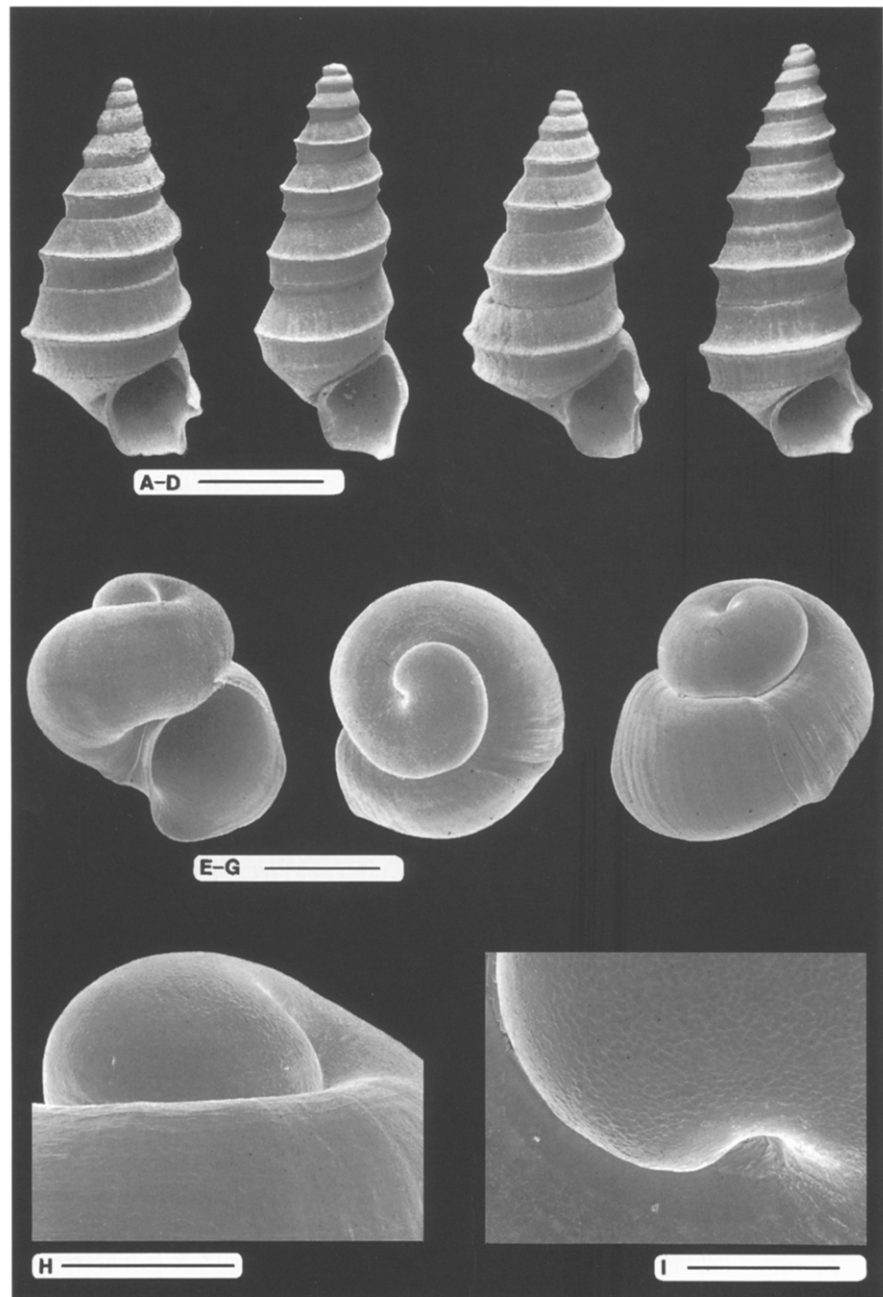


Fig. 2. *Pyrgula annulata* - features of the shell. **A-D:** Differences in adult shell shape and sculpture demonstrate intraspecific variation. Scale line = 2 mm. **E-G:** Early juvenile shell in apertural, apical and lateral view. Dense growth increments indicate the terminal embryonic shell. Scale line = 0.2 mm. **H:** Same specimen as in E-G - magnification of embryonic shell exhibiting the development of delicate spiral lirae. Scale line = 0.1 mm. **I:** Same specimen as in E-H - malleate microsculpture of the initial embryonic shell. Scale line = 50 µm.

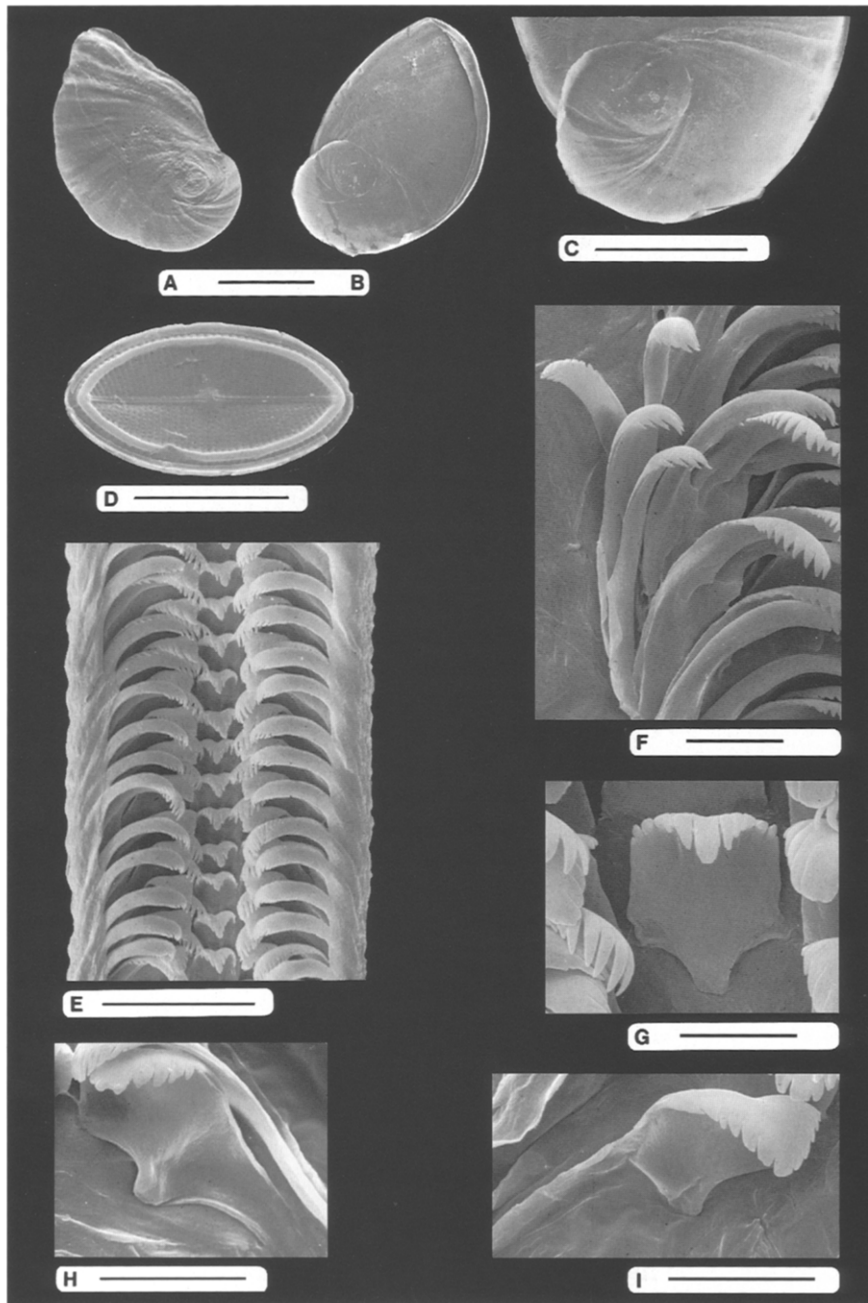


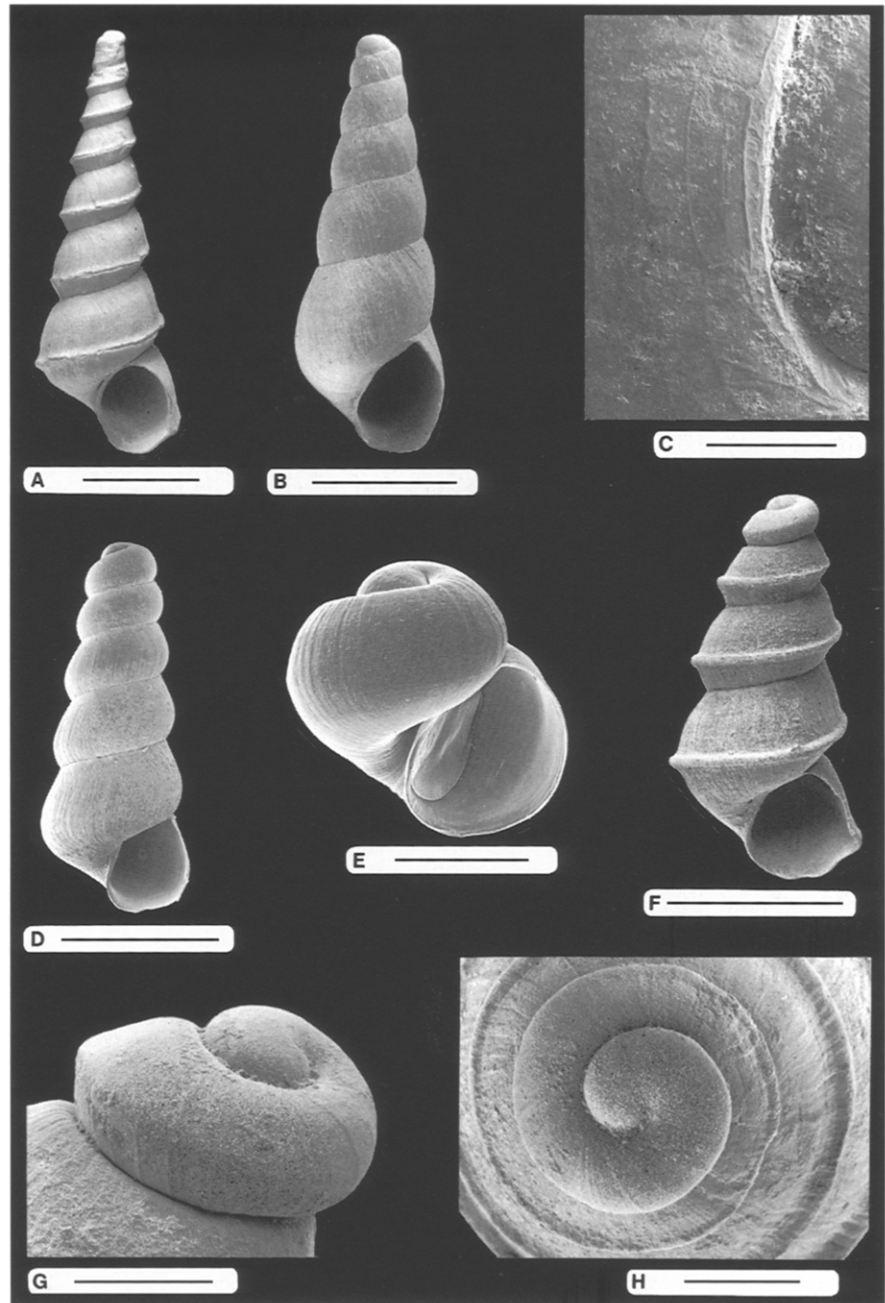
Fig. 3. *Pyrgula annulata* - features of the operculum and the radula. **A:** Internal view of the operculum. Scale line = 0.5 mm. **B:** External view of the operculum. Scale as in A. **C:** Magnification of external opercular nucleus. Scale line = 0.4 mm. **D:** Pennate diatom which was attached to the nuclear region of the external operculum. Scale line = 10 µm. **E:** Section of the radular ribbon. Scale line = 50 µm. **F:** Marginal radular teeth. Scale line = 20 µm. **G:** Central radular tooth. Scale line = 10 µm. **H-I:** Lateral radular teeth. Scale line = 20 µm.

parison has a wider nonspiral and exhibits the largest diameter. The height/diameter-ratio ranges from 0.9 in T3-1 to 1.1 in T3-15 and there is a rough negative correlation with the number of whorls. There is apparently no correlation between the width of the nonspiral and other protoconch parameters (see Table 2).

Two assumed pyrgulids from the Caspian Sea are briefly described with regard to their shells. The shell of *Turricaspia dimidiata* is coiled to about 8.5-9 whorls (Fig. 4A), giving a total length of 7.5-8 mm. The maximum diameter (or width) of 2.5-3 mm can be measured at the terminal whorl. The height/width-ratio thus lies between 2.7 and 3. The initial 1.5

whorls constitute the protoconch or the embryonic shell respectively, the apical maximum diameter of which is 0.5 mm. The nonspiral portion of the protoconch is 0.19 mm wide. Although the specimen at our disposal is apically corroded as well as encrusted, remains of spiral striae on the embryonic shell can still be recognized. The transition from the protoconch to the teleoconch is characterized by the onset of a peripheral spiral keel, which becomes prominent during the course of the first teleoconch whorl. The keel continues to the holostomous, more or less egg-shaped aperture, where it produces a minute triangular furrow on the inner side of the outer lip. The increase in diameter decreases with construction of

Fig. 4. *Turricaspia dimidiata*, *T. turricula*, *Godlewskia pulchella*, *Parabaikalia florii* and *Aenigmapyrgus steklovi*. **A:** *Turricaspia dimidiata* - shell of an adult specimen. Scale line = 2 mm. **B:** *T. turricula* - shell of a juvenile specimen. Scale line = 1 mm. **C:** *T. turricula* - same specimen as in B, magnification of the embryonic whorl showing delicate spiral lirae. Scale line = 50 μ m. **D:** *Godlewskia pulchella* (juvenile specimen) as an example for a highly turriiform baicalioid. Scale line = 1 mm. **E:** *Parabaikalia florii* - shell of a hatchling. Scale line = 0.5 mm. **F–H:** Shell features of the fossil *Aenigmapyrgus steklovi*. **F:** Adult shell. Scale line = 1 mm. **G:** Lateral view of apex with transition from protoconch to teleoconch. Scale line = 0.2 mm. **H:** Apical view of early whorls. Scale line = 0.2 mm.



the first teleoconch whorl, but increases again on the second teleoconch whorl. Whilst the upper flank of the earlier teleoconch whorls is more or less straight, it later becomes clearly convex (compare DYBOWSKI 1888).

The shell of *Turricaspia turricula* shows only superficial similarity to baicaliids such as *Godlewskia pulchella* (DYBOWSKI, 1875) (see Fig. 4D) and much more closely resembles those of certain Eulimidae (see Fig. 4B), which, however, are marine ptenoglossans. In adult specimens shell consists of 11 whorls, which give a total length of approximately 7 mm. The maximum diameter of 2 mm can be measured through the last whorl. The height/width-ratio of 3.5 (7 mm :

2 mm) is thus significantly higher than in *T. dimidiata*. The initial 1.4–1.5 whorls represent the protoconch (or embryonic shell), which measures 0.35 mm across. The nonspiral portion of the protoconch is about 0.12 mm wide. The embryonic shell is sculptured by delicate spiral striae (Fig. 4C), which partly continue across the transition to the teleoconch. The increase in diameter decreases with construction of the first teleoconch whorl, but increases again on the second teleoconch whorl. All teleoconch whorls are well rounded and do not exhibit sculpture except for growth increments. The holostomous aperture is more or less egg-shaped but triangulated posteriorly (compare DYBOWSKI 1888).

The shell of the fossil *Aenygmapyrgus steklovi* (Fig. 4F) is similar to that of *Turricaspia dimidiata*, but significantly smaller. The specimen of *A. steklovi* examined in this study has 5 whorls and measures 2.3 mm in length (height). The maximum diameter (or width) is 1.1 mm, thereby giving a height/width-ratio of approximately 2.1. The transition from the protoconch to the teleoconch appears to correlate with the onset of a spiral keel and a corresponding diameter change between the embryonic and the juvenile aperture (Fig. 4G). The 1.2–1.3 protoconch whorls measure 0.38 mm across and do not show sculpture (possibly due to some surface corrosion of the shell) except for some growth increments. The nonspiral portion of the protoconch is 0.1 mm wide. The increase in diameter decreases with construction of the first teleoconch whorl, but increases again on the second teleoconch whorl (Fig. 4H). The spiral keel becomes prominent on the first teleoconch whorl and continues to the aperture of the adult shell, where it generates a significant furrow on the inner side of the outer lip. Apart from this, the holostomous aperture is more or less egg-shaped. While the upper flank of the first teleoconch whorl is almost straight, that of the later whorls is clearly convex (compare POPOVA 1981).

Gross anatomy of *Pyrgula annulata* with notes on *Turricaspia turricula*

The external colouration and anatomy of *Pyrgula annulata* is very similar to that of a hydrobiid. The primary colour of the head-foot is whitish. The upper part of the snout and the cephalic tentacles show black pigmentation. The eyes are situated at basal thickenings of the tentacles. In the living animal, the cephalic tentacles can be extended to a length of approximately 1.2 mm. The left tentacle may differ from the right one by a median lining, which is due to morphological variation. The snout is typical for the Rissooidea and can be extended almost to the same length as the cephalic tentacles. The foot in the crawling animal reaches almost shell length and bears a thin, uncalcified operculum (Figs. 3A–D) which matches the aperture size. Flexibility of the operculum allows the animal to retract into the shell for up to one whorl if necessary.

To the roof of the mantle cavity is attached a whitish, bipectinate gill (of about 25 filaments) alongside which lies a slender, similarly coloured osphradium almost equal in length to the gill. In males the mantle cavity is largely filled by the penis (Fig. 5A), which exhibits a broad, laterally flattened base and a finger-shaped terminal portion. The broad base of the penis is attached near the base of the left tentacle, transversely to the right body half and terminating in the posterior mantle cavity. There are no additional penial appendages. The female genital system is characterized by a sausage-shaped albumen-capsule-gland complex. The bursa copulatrix is sac-like and a seminal receptacle could not be detected (compare RADOMAN 1983).

The gross anatomy and body size of *Turricaspia turricula* (Fig. 5B) is very similar to that of *Pyrgula annulata*. The pig-

mentation of the snout and the cephalic tentacles is weaker in *T. turricula* than in *P. annulata*. There are no obvious differences in shape and general structure of the head-foot. The monopectinate gill consists of about 40 leaflets. The osphradium is slender and almost half as long as the gill. The flattened penis with its broad base and its finger-shaped terminal portion is similar to that of *P. annulata* but there are some bulging outgrowths anteriorly at the base of the narrow end-piece. Moreover, in *T. turricula* the penis base is attached more to the left than in *P. annulata*. Unfortunately, a female specimen of *T. turricula* was not available for examination (but see Discussion). The stomach exhibits a typical hydrobiid morphology and contained detritus, planktic algae, remains of some rhizopodean Protozoa and sponge spicules.

Radula of *Pyrgula annulata*

The radula of *Pyrgula annulata* ($n = 15$) is of the neotaeioglossan type, about 105–115 μm wide (marginalia turned in) and 620–640 μm long, bearing 50–55 rows of teeth (Fig. 3E). Teeth of the anterior rows show significant wear. The general shape of the central (rachidian) teeth is simple (Fig. 3G). A maximum width of about 15–20 μm can be measured across the base. The maximum height of the central teeth ranges between 10–15 μm . The height/width-ratio of teeth of the same radula is variable to some extent. The median attachment-portion projects posteriorly (Fig. 3G), which represents the only notable feature of the basal plate. The cutting edge, which is only slightly narrower than the basal edge and more

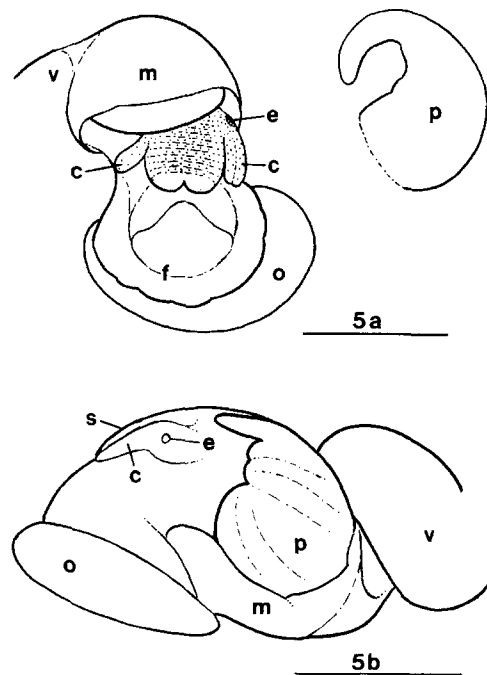


Fig. 5. Gross anatomy of *Pyrgula annulata* (a) and *Turricaspia turricula* (b). Scale lines = 1 mm. **Abbreviations:** c = cephalic tentacle, e = eye, f = foot, m = mantle, o = operculum, p = penis, s = snout, v = visceral mass.

or less rounded laterally, is multicusped with a prominent central denticle accompanied by 5–7 smaller denticles on each side (the latter becoming increasingly smaller towards the outer margin of the tooth). Lateral teeth exhibit a cutting edge very similar to that of the central (rachidian) tooth, but differ in the width of the basal plate which is about 60 μm in the former. The base forms a more or less projecting hump (Figs. 3H-I). Outer and inner marginal teeth are attached by a narrow base and have a length of 70–80 μm (Fig. 3F). Their cutting edges are multicusped and rounded terminally.

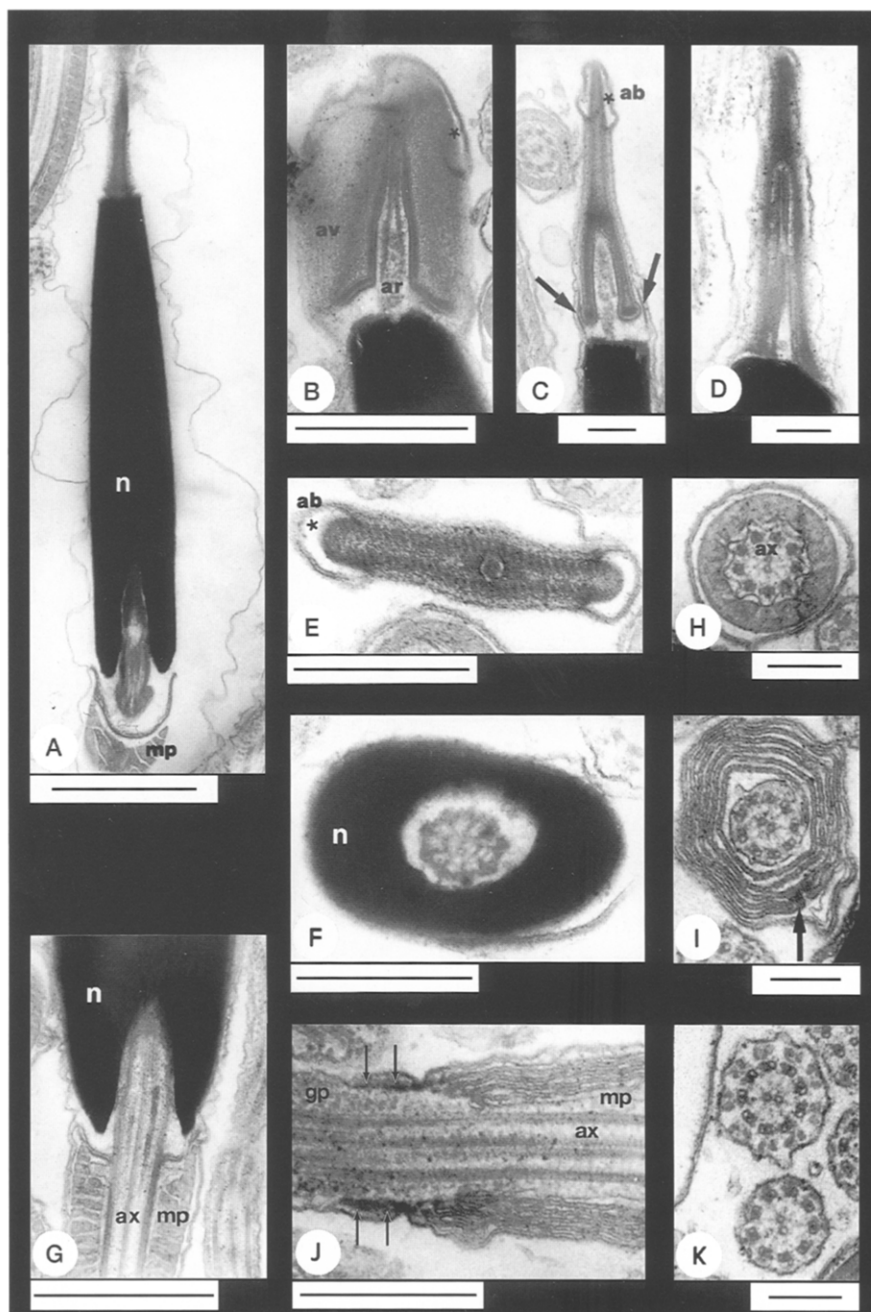
There is no obvious sexual dimorphism in radular characters, but intra-individual and intraspecific variation appear to be considerable.

Spermatozoa of *Pyrgula annulata*

Only euspermatozoa of a single type were observed in the specimens examined (that is, no evidence of paraspermatozoa or euspermatozoal dimorphism were observed – Fig. 6). The following description outlines the fine structure of each euspermatozoan feature, in anterior-posterior sequence.

Acrosomal complex: The acrosomal vesicle is membrane-bound, approximately 1.4–1.5 μm long, strongly compressed laterally (resulting in a spatula-like transverse profile) and approximately 0.95 μm wide basally. The acrosomal vesicle contents are differentiated into a markedly electron-dense outer layer, studded with angularly-inclined, periodi-

Fig. 6. Euspermatozoa of *Pyrgula annulata*: **A:** Longitudinal section through narrow axis of acrosomal complex and nucleus. Scale line = 1 μm . **B:** Longitudinal section through broad axis of acrosomal complex and nucleus - anterior part. Scale line = 1 μm . **C:** Longitudinal section through narrow axis of acrosomal complex and nucleus - anterior part; accessory membranes marked by arrows; apical bleb distinct. Scale line = 0.25 μm . **D:** Longitudinal section through narrow axis of acrosomal complex showing axial rod. Scale line = 0.25 μm . **E:** Transverse section of acrosomal complex. Scale line = 0.5 μm . **F:** Transverse section through base of nucleus with centriolar complex – nucleus slightly compressed. Scale line = 0.5 μm . **G:** Longitudinal section through nucleus-midpiece junction vesicles. Scale line = 1 μm . **H:** Transverse section through midpiece with inner membrane folded around each axonemal doublet. Scale line = 0.25 μm . **I:** Transverse section through membranous sheath at end of midpiece. Scale line = 0.2 μm . **J:** Longitudinal section through membranous sheath of midpiece, annulus (arrow) and beginning of glycogen piece. Note cylindrical, posterior component of annular complex (double arrow). Scale line = 0.5 μm . **K:** Transverse section through glycogen piece with granules distinctly arranged in nine tracts. Scale line = 0.2 μm . **Abbreviations:** ab = apical bleb, ar = axial rod, av = acrosomal vesicle, ax = axoneme, gp = glycogen piece, mp = midpiece, n = nucleus.



cally-spaced plates and a less dense, homogeneous, core region. At the anterior extremity of the acrosome, the acrosomal vesicle membrane expands away from the vesicle contents to form an electron-lucent region, the apical bleb (asterisks in Figs. 6B,C,E). Basally, the acrosomal vesicle is surrounded by a short accessory membrane (arrows in Fig. 6C). A deep but narrow invagination of the vesicle is largely filled by a long axial rod (Figs. 6B,D). The plate between the base of acrosomal vesicle and nuclear apex is centrally perforate.

Nucleus: The nucleus is relatively short (about 4 µm long), solid, highly electron-dense and laterally slightly compressed (Fig. 6A). In transverse section, the base of the nucleus is oval (Fig. 6F), has a maximum diameter of 0.95 µm. This basal region of the nucleus exhibits a short invagination containing an electron-dense centriolar complex and the initial portion of the 9+2 microtubular pattern axoneme (Fig. 6G).

Midpiece: At the junction of nucleus and midpiece, dense membranes contacting the midpiece mitochondria can be detected (Fig. 6G). The midpiece is elongate (length approximately 120 µm) and consists primarily of the 9+2 microtubular pattern axoneme and 7–9 continuous mitochondria which are arranged helically around the axoneme. A single membrane of the mitochondrial sheath directly surrounds the axoneme. This membrane is folded to form a series of longitudinally continuous furrows which are associated with the microtubular doublets (Fig. 6H). The diameter of the posterior midpiece portion is relatively constant and measures about 0.6 µm. In the distal portion of the midpiece the helical mitochondria are replaced by the scroll-like arrangement of double-membranes around the axoneme (Figs. 6I–J). This membranous sheath (terminology of HEALY 1983) is approximately 1.4 µm long and 0.6 µm wide. It appears to be derived from the mitochondrial sheath membranes. Posteriorly at least the outer membranes of the sheath contact the annular complex. Transverse sections reveal that the membranes may fuse at specific points (arrow in Fig. 6I).

Annular complex, glycogen piece and free flagellum: The junction of midpiece and glycogen piece is characterized by a highly electron-dense annular complex (Fig. 6J). The annular complex consists of a highly electron-dense ring (contacting the plasma membrane) and a less-dense cylindrical structure (Fig. 6J). The putative glycogen granules are arranged in nine, longitudinally continuous tracts, each associated with an axonemal doublet (Fig. 6K). Posterior to the glycogen piece the free flagellum (end piece) consists of the axoneme sheathed only by the plasma membrane (Fig. 6K).

Discussion

In the following discussion *Pyrgula annulata* will be compared directly with supposed Caspian pyrgulids, with baicaliids from Lake Baikal and with hydrobiids in general. Where appropriate, comparisons are made with other rissooidean families or genera.

Ecology

In Caspian pyrgulids (RIEDEL, RÖPSTORF & SITNIKOVA, unpubl. data) as well as in hydrobiids (DILLON 2000 and references therein) and baicaliids (KOZHOVA & IZMEST'eva 1998; RIEDEL, RÖPSTORF & SITNIKOVA, unpubl. data) species are known to show analogous aut- and synecologies, which can be summarized as follows: (1) inhabiting oligotrophic or mesotrophic water bodies which become only moderately warmed in summer; (2) living below the wave base; (3) dwelling on and burrowing into soft-substrate; (4) feeding on organic microparticles from the substrate; (5) occurring in large numbers where conditions are suitable. However, potential ecological differences may sometimes generate greater differences within families than between species of different families.

Shell features

More or less turriform, carinated teleoconchs similar to those observed in *Pyrgula annulata*, also occur in the Caspian pyrgulid *Turricaspia dimidiata* (this study - see Fig. 4A), in the hydrobiid *Pyrgulopsis nevadensis* (STEARNS, 1883) or in the baicaliid *Maackia variesculpta* (LINDHOLM, 1909) (SITNIKOVA et al. 2001). In the latter, however, the carina is ornamented by nodules. Teleoconch sizes in *Pyrgula annulata*, *T. dimidiata* and *M. variesculpta* are similar but significantly smaller in *Pyrgulopsis nevadensis* (see HERSHLER & THOMPSON 1987). Protoconchs consisting of about 1.5–1.7 whorls and bearing weak spiral lirae (as in *Pyrgula annulata*) have also been observed in the Caspian pyrgulid *Turricaspia turricula* (Fig. 4B), in the hydrobiid *Pyrgulopsis greggi* (HERSHLER, 1995) and in baicaliids such as *Korotnewia korotnevi* (LINDHOLM, 1909) or *Parabaikalia florii* (W. DYBOWSKI, 1875) (see Fig. 4E; compare SITNIKOVA et al. 2001). Compared with *Pyrgula annulata*, the protoconch apical diameter is usually (but not generally) smaller in hydrobiids (for example see HERSHLER & THOMPSON 1987; PONDER et al. 1989; RIEDEL 1993; HERSHLER 1995) but of comparable size in Caspian pyrgulids and generally larger in baicaliids (see SITNIKOVA et al. 2001). Based upon this evidence, the fossil *Aenigmapyrgus steklovi* is considered to represent a member of the Pyrgulidae.

Anatomy

Gross anatomical features - in particular the head-foot, mantle cavity and visceral mass - do not distinguish *Pyrgula annulata* from other so-called 'pyrgulids' such as *Turricaspia turricula* or from hydrobiids and baicaliids in general (for references see a.o. KOZHOV 1951; PONDER 1988; HERSHLER & THOMPSON 1992; HERSHLER 1995).

Genitalia: the shape of the penis as described here for *Pyrgula annulata* and *Turricaspia turricula* or *Euxinipyrgula milachevitchi* (GOLIKOV & STAROBOGATOV 1966) by SITNIKOVA

& STAROBOGATOV (1999) falls within the morphological range, which also occurs in hydrobiids (for examples see RADOMAN 1983; HERSHLER & THOMPSON 1992) and baicaliids (RADOMAN 1983; RIEDEL, RÖPSTORF & SITNIKOVA, unpubl. data). The base of the penis being attached more to the left than to the right of the neck in *Pyrgula annulata* and *Turricaspia turricula* may appear to be unusual but occurs elsewhere not only in *Euxinipyrgula milachevitchi* (see SITNIKOVA & STAROBOGATOV 1999) but also in some hydrobiids (RADOMAN 1983; RIEDEL, RÖPSTORF & SITNIKOVA, unpubl. data) and some baicaliids (RADOMAN 1983; RIEDEL, RÖPSTORF & SITNIKOVA, unpubl. data). Regarding the female genitalia generalisations can be made (compiled from KOZHOV 1951; RADOMAN 1983; SITNIKOVA 1991; HERSHLER & THOMPSON 1992; HERSHLER 1995; SITNIKOVA & STAROBOGATOV 1998, 1999; RIEDEL, RÖPSTORF & SITNIKOVA, unpubl. data): (1) in pyrgulids and hydrobiids up to 2 true seminal receptacles can be found whereas in baicaliids (except for *Parabaikalia florii*) several to numerous pouches of the coiled oviduct function as seminal receptacles; (2) in pyrgulids and hydrobiids the distal gland of the pallial oviduct is undifferentiated while it is divided into lobes in baicaliids; (3) in contrast to pyrgulids (except for Caspiinae sensu SITNIKOVA & STAROBOGATOV 1998, 1999) and hydrobiids, baicaliids do not exhibit a bursa copulatrix.

Radula

The radula of *Pyrgula annulata* is characterised by its small and simple central tooth (rachidian), which does not bear basal cusps. This feature is listed by RADOMAN (1983) in his diagnoses for Pyrgulidae, Micropyrgulidae and Turricaspiidae. Among the so-called 'pyrgulids' from the Caspian Sea at least *Caspia gmelini* CLESSIN & DYBOWSKI, 1888 (in SITNIKOVA & STAROBOGATOV 1998) exhibits radular teeth typical of hydrobiids (for example see HERSHLER & THOMPSON 1992). This seems to indicate that the Caspiinae (sensu SITNIKOVA & STAROBOGATOV 1998, 1999), which are based on *Caspia* CLESSIN & W. DYBOWSKI, 1886, represent an independent stock from 'true' pyrgulids (see conclusions).

We are aware of only one other rissooidean family bearing rachidians similar to those of *Pyrgula annulata* – the Baicaliidae. From this viewpoint it could be suggested that such a radula type represents a synapomorphy of pyrgulids (excluding *Caspia* spp.) and baicaliids (see Conclusions).

Spermatozoa

Although paraspermatozoa co-occur with euspermatozoa in many groups of caenogastropods (NISHIWAKI 1964; HEALY & JAMIESON 1981; GIUSTI & SELMI 1982; HEALY 1988; HODGSON 1997) the absence of paraspermatozoa in *Pyrgula annulata* appears to be typical of all Rissooidea. Euspermatozoan dimorphism is known in *Bithynia tentaculata* (see KOHNERT 1980) but so far has not been observed in other investigated

species of Bithyniidae (KOHNERT & STORCH 1984; HEALY, unpubl. data). Such dimorphism occurs sporadically in a few other caenogastropod groups (NISHIWAKI & TOCHIMOTO 1969; HEALY 1982) and its significance remains unresolved.

In general the euspermatozoa of rissooideans conform to the type characteristic of most caenogastropods exclusive of the Ampullarioidea, Cyclophoroidea, Cerithioidea and Campaniloidea (these four superfamilies sharing a number of distinctive features, as well as each having certain diagnostic features) (see GIUSTI 1969, 1971; KOHNERT & STORCH 1980, 1984; KOIKE 1985; HEALY 1988, 1996; RÖPSTORF et al., in press). This widespread euspermatozoan type is characterized, among other features, by an apical bleb on the acrosomal vesicle, an accessory sheath surrounding the base of the acrosomal vesicle, 5 or more very elongate mitochondria winding helically around an axoneme and a posterior (tail) region consisting of glycogen deposits arranged around the axoneme.

Within the Rissooidea two groups of families can be distinguished, based on the presence or absence of a most unusual feature - the membranous sheath - at the terminal region of the midpiece. This sheath occurs in the Hydrobiidae (KOHNERT & STORCH 1984; RÖPSTORF et al., in press), Stenothyridae (HEALY 1983), Bithyniidae (KOHNERT 1980; KOHNERT & STORCH 1984), Baicaliidae (RÖPSTORF et al., in press) and also *Pyrgula annulata* (present study) and is known to be absent in the Rissoidae (KOHNERT & STORCH 1984) and Truncatellidae (GIUSTI & MAZZINI 1973). As the sheath has not been observed elsewhere within the Mollusca (or in any other phylum to our knowledge), it has been interpreted by RÖPSTORF et al. (in press) as a synapomorphy for the Hydrobiidae + Stenothyridae + Bithyniidae + Baicaliidae (+ possibly other unstudied rissooidean families). Within this assemblage, *Pyrgula annulata* shows very close eusperm similarities to the Hydrobiidae and Bithyniidae, so close in fact that we cannot identify any obvious feature to differentiate 'pyrgulids' from hydrobiids or bithyniids.

Conclusions

The comparison of *Pyrgula annulata* with other rissooideans provides evidence that this taxon can be differentiated from hydrobiids in general only by means of the radula. Actually hydrobiids such as *Pyrgulopsis* spp. not only exhibit similar shell features to *Pyrgula annulata* (including the embryonic shell), but show considerable anatomical correspondence to *P. annulata* even in the structure of female genitalia, which are usually most important in order to unravel rissooidean systematics (for example see PONDER 1988).

It has been pointed out that the simple central tooth (rachidian) of the radula unites *Pyrgula annulata* with several other rissooidean taxa such as *Micropyrgula stankovici* POLINSKI, 1929 or *Ohridopyrgula macedonica* (BRUSINA, 1896) from lakes of southeast Europe (RADOMAN 1983), *Eu-*

xinipyrgula spp. from the Sea of Azov (SITNIKOVA & STAROBOGATOV 1999), *Turricaspia* spp. from the Caspian Sea (SITNIKOVA & STAROBOGATOV 1998) and baicaliids from Lake Baikal. The simple shape of the central radular tooth can be considered apomorphic due to the fact that all other rissooidean groups exhibit rachidians with basal cusps, and in the stratigraphical context of the evolutionary history. Origin and radiations of Baicaliidae and the 'evolution' of Lake Baikal are more or less linked together. There is some consensus within the literature that the maximum age of Lake Baikal is at least about 25 million years (LOGATCHEV 1993). On the other hand the analysis of nucleotide sequences of the mitochondrial gene cytochrome oxidase subunit 1 indicated that baicaliid radiations took place only about 2 million years ago (ZUBAKOV et al. 1997). More recent calculations range down to a maximum of 6 million years (ZUBAKOV, pers. communication 2000). From this it is at least clear that the modern Baicaliidae represent a comparatively young rissooidean offshoot. Regarding 'pyrgulids', a similar conclusion can be reached. There is no clear evidence for Paleogene or even Cretaceous 'pyrgulids'. Molecular data are not available, but the fossil record indicates that 'pyrgulids' are closely linked to the development of the Neogene Paratethys. From the Tortonian (Upper Miocene) of the northern Aegean *Pyrgula carinata* (GILLET & GEISSERT, 1971) has been documented (RUST 1997), which is strikingly similar to *Turricaspia carinata* (ANDRUSOV 1890) from the Tortonian of the Kertsch peninsular (between Black Sea and Sea of Azov; see NEVESSKAYA et al. 1986). Thus pyrgulids have been clearly proven from Upper Miocene sediments. Questionable 'pyrgulids' such as *Micromelania* have also been described from the Neogene of southeast Europe (see WENZ 1938–44).

Judging from the shell features it is highly probable that *Aenigmapyrgus steklovi* from the Neogene of the Altai Mountains represents a true 'pyrgulid' closely related to *Turricaspia* spp. such as *T. carinata* and *T. dimidiata*. The deposits from the Altai Mountains represent the remains of a long-lived lake (see ZYKIN & KAZANSKY 1996), which could have potentially bridged the huge biogeographical gap between the Caspian Sea or the former eastern Paratethys respectively and Lake Baikal.

Following this argumentation a summarising working hypothesis can be phrased which suggests that 'pyrgulids' represent a Miocene offshoot from an as yet unknown hydrobiid lineage, distinguished by the simplified central radular tooth (lacking basal cusps). Hydrobiids are known already from the Mesozoic (for example see BANDEL & RIEDEL 1994) and cannot be the sistergroup of 'pyrgulids'. In consequence the Hydrobiidae have to be regarded to represent a paraphylum. On the other hand the Baicaliidae probably represent a Pliocene offshoot from the 'Pyrgulidae' which then have to be considered a paraphylum too. The relatively huge protoconchs (SITNIKOVA et al. 2001), differentiated female genitalia (SITNIKOVA 1991) and ultrastructural differences of euspermatozoa

(RÖPSTORF et al., in press) in baicaliids emerge as reliable defining apomorphies for this family.

Regarding the origin of the Baicaliidae an alternative hypothesis can be coined, which takes two things in account: (1) preliminary molecular systematics do not show that pyrgulids and baicaliids are closely related (HAUSDORF & RIEDEL, unpubl. data) - consequently the simplified central radular tooth of pyrgulids and baicaliids must have evolved analogously; (2) several fossil shells from the Cretaceous and the Tertiary of China, Mongolia and Russia were attributed to baicaliids or evolutionary forerunners respectively, particularly by MARTINSON (1959, 1960, 1961), which could indicate that this rissooidean lineage evolved already in the great Mesozoic lakes of Central Asia. This hypothesis, however, cannot yet be falsified, due to the fact that the corresponding fossil shells are not well documented and a modern re-evaluation of the material is necessary.

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