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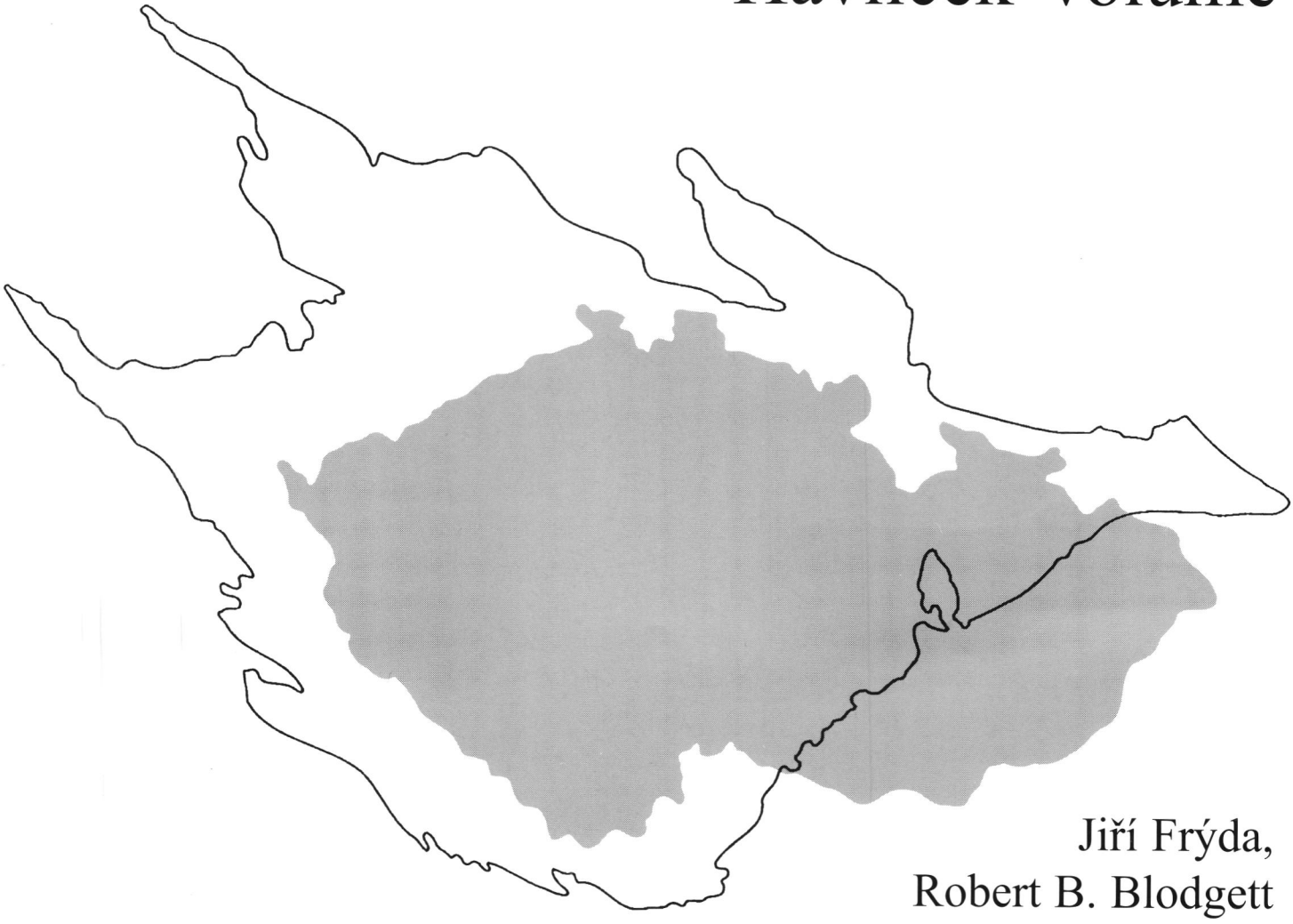

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The Sarganidae (Pyrifusoidea, Latrogastropoda), their taxonomy and paleobiogeography

Čeleď Sarganidae (Pyrifusoidea, Latrogastropoda), její taxonomie a paleobiogeografie

(53 figs)

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The family Sarganidae Stephenson, 1923, represents an extinct group of gastropods of Cretaceous age that contains species with rather characteristic low-spired, subpyriform shells, with anteriorly constricted whorls, large pseudumbilicus and posteriorly notched aperture that anteriorly extends in a narrow siphonal canal. While the teleoconch resembles that of modern Neogastropoda, the almost planispirally-coiled protoconch is like that found among modern Neomesogastropoda. These two represent the Latrogastropoda, as subunit of the gastropod subclass Caenogastropoda which has its origin in the Cretaceous. Two new species, *Sargana chapelvillei* and *S. mississippiensis,* from the Late Campanian Coffee Sand of Mississippi in the USA are described. They closely resemble *Sargana geversi* and two new species, *S. xsosanensis* and *S. kieli,* from the Santonian Umzamba locality in the Eastern Cape Province of South Africa. *Sargana exima* from the Santonian/Campanian of Tamil Nadu in southern India differs from the Gulf-Coast and South African species, but resembles *Praesargana confraga* from the Turonian of California. Also the relation to *Pseudecphora* gen. nov. of the Pseudecphorinae n. subfam., *Morea* of the Moreinae, *Hippocampoides* of the Thalassocynidae, *Schizobasis, Hillites* and *Xsosaites* of the Schizobasinae n. subfam., *Weeksia* and *Lowenstamia* of the Weeksiidae is discussed, all of which resemble *Sargana*. The Sarganidae are seen among the Pyrifusoidea n. superfam. which can neither be considered to belong to the Neomesogastropoda nor the Neogastropoda.

The evolutionary history of the Sarganidae occurred in two geographically very distant regions. Earliest known representatives are from the Turonian of California. They have migrated across the Tethys Ocean to the Gondwanian shelf of the evolving Indian Ocean to develop further species during Santonian time. These migrated to the southern shores of the North American Inland Sea, evolving new species here during Late Campanian/Maastrichtian time. Migration pathway probably was the Southern Atlantic Ocean that provided fitting surface currents as well as cool water stop-over shelf regions, since Sarganidae lived in subtropical environments but not in the tropical water of the Tethys Ocean.

Introduction

Stratigraphical boundaries separating the Jurassic and Cretaceous as well as Cretaceous and Tertiary periods coincide with prominent faunal turnovers and the first appearance data of many new taxa. In contrast, the first appearance data of several modern higher caenogastropod groups with high species diversities began in Mid-Cretaceous time. At this time not only an explosive diversification among angiosperm plants occurred, but during the Aptian/Albian period the Neomesogastropoda and the Neogastropoda (jointly forming the Latrogastropoda Riedel, 2000) made their first appearance, with their ancestral roots still remaining uncertain (see Bandel 1993, 1997, Gründel 1998, 1999, Schröder 1995, Riedel 2000).

Most of the modern neomesogastropod superfamilies, but only few neogastropod superfamilies can be recognized by Campanian time. Several neomesogastropod units have evolved characteristic larval and adult shells (Bandel – Riedel 1994, Bandel 1993, 1999, Riedel 1995, 2000). So there are no difficulties in recognising Campanian members of the sessile Calyptraeoidea Lamarck, 1809 that filtered food from the sea water or collect detritus as they do today. Also the carnivorous Naticoidea Forbes, 1838 were clearly present and drilled holes through the shells of their prey (Taylor et al 1980, 1983). The Cypraeoidea Rafinesque, 1815 had their characteristic highly ornamented larval shell, which is later covered by the teleoconch to form the typical cowrie shell (Groves 1992, Bandel 1993). The species of the Cassoidea Latreille, 1825 and the Laubierinioidea Warén – Bouchet, 1990 developed a characteristic larval shell with an ornamental pattern of rectangles (Riedel 1995). Unlike the listed neomesogastropod groups, the Lamellarioidea Orbigny, 1841, have not been recognized in Cretaceous deposits.

The latrogastropod embryonic shell is significantly larger than that of the cerithiimorphs and littorinimorphs within the Caenogastropoda (Bandel, 1975, 1982, 1993), and usually has a different shape and ornamentation. In the Late Cretaceous, Latrogastropoda diversified rapidly, developing the characteristically large larval shell (Bandel et al. 1997) and also, as alternative to planktotrophic larvae, the extremely yolk-rich embryogenesis (Bandel 1975, 1982).

The core group of Late Cretaceous caenogastropods, having larval shells of the neogastropod shape, includes the genera *Pseudorapa* Holzapfel, 1888, *Pyrifusus* Conrad, 1858, *Bellifusus* Stephenson, 1941, *Cryptorhytis* Meek, 1876, *Pholidotoma* Cossmann, 1896, *Drilluta* Wade, 1916, *Paleopsephaea* Wade, 1926, *Volutoderma* Gabb, 1877, *Hercorhyncus* Conrad, 1868, and *Pyropsis* Conrad, 1860. All of these have species in the Ripley Formation (Maastrichtian) of Mississippi and Tennessee

with the protoconch preserved, and some with protoconchs have also been found in the Coffee Sand (Campanian) of Mississippi. Protoconchs of these genera consist of a large (about 0.5 mm high) conical shell. The initial embryonic shell is fairly large and well differentiated from the remaining protoconch, which usually consists of several whorls of larval shell (Bandel 1993). In contrast to these neogastropod-like Latrogastropoda, the protoconch of *Sargana* is flatly coiled and resembles the Echinospira planktotrophic larval shells of the modern Capulidae or Lamellariidae (Bandel – Riedel 1994). But in contrast to these differences regarding protoconch morphology a total transition in shapes and characters of teleoconch and protoconch can be noted that ranges from *Pyrifusus*-like species to *Sargana*-like ones and even to the planispiral *Weeksia*.

Geographical occurrence of *Sargana* and relation

Sargana occurs not only in the North America where it was first described, but also in South Africa (Eastern Cape Province) on the Indian Ocean and in southern India (Tamil Nadu). However, it does not occur in intermediate areas, such as the richly fossiliferous deposits of the Basin of Tremp in northern Spain, the Ammonite Hills of Egypt's Western Desert of Egypt, or of central Mexico (Kiel, pers. com.), where Cretaceous faunas were more tropical. Rennie (1930) noted the similarity between the Campanian faunas of India and South Africa but did not compare with North American Gulf Coast faunas.

In this paper gastropods from the Santonian to Maastrichtian faunas from Central Europe (Vaals Greensand near Aachen, Campanian), from the Campanian of Southern Europe (Vallcarga Formation near Pobla de Segur, Tremp Basin, Campanian), from the Cenomanian to Maastrichtian of North America (Sohl 1964, Dockery 1993, Stephenson 1941, 1952), the Maastrichtian of Egypt (Ammonite Hills in the Western Desert), the Campanian of Jordan (Amman and Ruseifa Formations, Bandel et al. 1999), the Santonian to Campanian of southeastern India (Trichinopoly Group near Ariyalur in Tamil Nadu, Bandel 2000), the Santonian of Eastern South Africa (Umzamba Formation in Transkei, Eastern Cape Province, Kiel – Bandel 1999), the Campanian of West Africa (Mungo River, north-western Cameroun) Riedel 1932, and the Maastrichtian of South America (Quiriquina Formation in Central Chile, Bandel – Stinnesbeck 2000) were compared, mostly from own experience and own collections. The American fauna provided well preserved protoconchs (Ripley Formation in Mississippi and Tennessee, Late Campanian, Early Maastrichtian). Here the faunas of Ripley Formation in the SE-USA and those of Umzamba Formation in South Africa, as well as the fauna of California (Saul 1996) reveal an astounding similarity of species that lived in the temperate, subtropical shallow seas of both the northern and southern hemisphere, but at different times. On the other hand, they differ from contemporaneous equatorial species that lived in the shallow, tropical Tethys Sea at the same time (northern Spain, Ammonite Hills in Egypt, Jordan). They were also not present in the subtropical to more temperate climate of Europe and SW South America (Vaals and Quiriquina). Regarding climatic conditions at Late Cretaceous times one has to take into consideration that the poles were not covered by ice and the temperature of the world oceans was probably quite a bit warmer than is the case today.

The living environment of the different localities are comparable. The fauna from the Vaals Greensand (Santonian-Campanian), the Ripley Formation (Campanian-Maastrichtian), the Trichinopoly Group (Santonian-Campanian), the Umzamba beds (Santonian-Campanian) and the Quiriquina Formation (Maastrichtian) was a quartz sand or muddy sand bottom in shallow, near shore, marine waters. In the case of the Ammonite Hill fauna (Maastrichtian) the bottom substrate was a mix of quartz sand and carbonate. In Pobla de Segur (Puimanyons Olisthostrome, Campanian) a pebble-beach fauna was repeatedly slumped down a slope into the basin and was mixed with deeper water fauna that lived in more fine grained sediment downslope. Quiriquina and Umzamba also hold species that lived on the rocky cliffs present within the shore.

Other Late Cretaceous faunas studied include estuarine faunas in sediments of coal swamps with weak marine influence (Ajka Coal Formation in central Hungary), a small river delta (Isona Formation in the Tremp Basin, Northern Spain), and of a sandy coast with brackish lagoons sheltered by a beach bar (Brandenberg Gosau, Northern Alps, Tirol). All these environments are similar and represent tropical, coastal fazies of the former Tethys Ocean near its northern shores (Bandel – Riedel 1994, Kowalke – Bandel 1996). Faunal differences in these environments are related to variations in salinity and substrate and the geological age (Santonian to Maastrichtian). These estuarine environments also differ from those in carbonate lagoons found associated with rudist reefs (Mustafa – Bandel 1992, Bandel – Mustafa 1994).

Systematic paleontology

Superfamily P y r i f u s o i d e a superfam. nov.

D i a g n o s i s: Solid, medium-sized to large shells (1–10 cm high) which are usually ornamented by spiral and collabral ribs. The aperture is usually provided with a siphonal canal and a posterior notch or canal next to the suture on the posterior part of the outer lip. This notch gives rise to a subsutural ribbon. The protoconch usually consists of several smooth whorls which may be trochispirally to planispirally coiled. Its embryonic portion consists of almost one whorl, is smooth and measures more than 0.15 mm in diameter. The larval part is also usually smooth and not provided with a sinusigeral projection of the outer lip, which is simple.

Difference: The shell of the Muricoidea Rafinesque, 1825 (= Muricina Riedel 2000) differs by having an ornamented embryonic shell of the protoconch in case of the ontogeny with planktotrophic veliger and usually also ornament present on the larval shell which commonly ends with a sinusigera projection of the outer lip. The teleoconch in Muricoidea and Buccinoidea Rafinesque, 1815 is mostly without the posterior notch of the aperture and the subsutural ribbon created by it.

Family Sarganidae Stephenson, 1923

Description: The low-spired, subpyriform shell has anteriorly constricted whorls with a prominent umbilicus. The aperture is posteriorly notched and anteriorly drawn out to form a narrow, curved, siphonal canal. The pyrifusoid posterior notch is connected to a narrow apical canal, which creates a scalenoid subsutural collar. The ornament consists of axial and spiral elements commonly of equal width and often producing a granular to tubercular pattern. The protoconch is lowly helicoidally to almost planispirally coiled and consists of two to few whorls.
Relations and differences: The flat-topped Sarganidae are represented by *Sargana* with short siphon and rounded tuberculate whorls. Some species of *Praesargana* as presented by Saul (1996) can not be distinguishes from species of *Sargana*, regarding the teleoconch shape and ornament and should better be transferred to *Sargana*. Stephenson (1923, p. 77) erected the family Sarganidae as separate unit of the Muricoidea differing from the other members of this taxon by the columellar fold and the flattened spire. Sohl (1964) accepted the placement with the muricids, but suggested that members of the genera *Actinotrophon* Dall, 1902, *Ecphora* Conrad, 1843, and *Rapana* Schumacher, 1817 are similar to *Sargana* and that, therefore, the family Sarganidae is superfluous. *Sargana,* in his opinion, should be placed in the subfamily Rapaninae of the Muricidae. But the differences in protoconch shape between the Cretaceous *Sargana* and members of the modern relation of *Rapana*, as have been figured by Kool (1993) and of muricid larval shells in general (Bandel et al. 1997) invalidate this opinion and validates the suggestion to place *Sargana* in its own family.

Saul (1996) placed Sarganinae in the Tudiclidae, which family is interpreted to hold Tudiclinae Cossmann, 1901, and the Pyropsinae Stephenson, 1941 in addition. Of these the Tudiclinae are based on a living representative about which very little is known (Saul 1996). *Tudicla spiralis* (Linné, 1767) lives in the Indian Ocean, but differs from *Sargana* by its mode of ontogeny, that includes a lecithotrophic development, and thus the formation of a large sized protoconch with swollen one and a half, rounded whorls. This species may represent a modern relative to the Sarganidae that developed non-planktrotrophic young. But it may just as well be quite unrelated and of somewhat convergent shell shape, which is a very common feature found among the different groups of the Latrogastropoda.

The morphology of the protoconch is a serious obstacle for the placement of *Sargana* with the muricids and most other groups of the Neogastropoda with known protoconch. Muricid larval shells are elevated and usually of the characteristic sinusigera type (Kool 1993, Bandel 1982, 1993, Bandel et al. 1997) which is quite different from that of *Sargana*. And even if embryogenesis is without planktotrophic larva, the protoconch of muricids would not be like that of *Sargana* but would have more elevated shape (Bandel 1975).

Sargana as defined originally by Stephenson (1923) is quite well developed in the Late Turonian of California (Saul 1996). The shape of the protoconch as far as preserved in these early species is very similar to that of some members of the Pyrifusoidea such as *Morea* and *Pyropsis*. In size these protoconchs are rather large (Sohl 1964, Bandel 1993) and they are smooth, rarely granulated in the embryonic whorl. In case of *Morea* and *Sargana* the protoconch shape is low-helicoidal to almost planispiral, closely resembling that of *Weeksia* (Bandel 1988, 1991).

Subfamily Sarganinae Stephenson, 1923

The definition of the family Sarganidae applies. The low spired subpyriform shell has anteriorly constricted whorls with a hollow spindle. The aperture is posteriorly notched and anteriorly drawn out to a narrow curved siphonal canal. There is a subsutural collar that appears on the first whorls of the teleoconch. The ornament consists of axial and spiral elements commonly of equal width and often producing a granular to tubercular pattern. The protoconch is lowly to almost planispirally coiled and consists of one to few whorls. The characteristic genus is *Sargana.*
Remarks: Of the Moreinae the genus *Schizobasis* with similar shell body as found in *Sargana* has a siphon that is twisted to the left (Figs 51, 52), and *Praesargana* has a transitional shell to the Pyropsinae on one side and to *Morea* of the the Moreinae (Figs 42–44) on the other side.

Genus *Sargana* Stephenson, 1923

Generic description: The low-spired subpyriform shell has a vertically corrugated umbilicus and consists of up to four whorls of the teleoconch. The spire is depressed, and the aperture is subcircular with a narrow anterior canal and thickened lips. A posterior notch is formed by a narrow canal which creates a subsutural collar. The ornament of the adult shell consists of strong spiral ribs separated by wide rounded furrows. The revolving ribs are crossed by vertical ribs or growth increments at more or less variable intervals forming nodes or spines at intersection. The protoconch is smooth, lowly helicoidally or planispirally coiled and consists of well-round-

nament, thus, has three widely-spaced apical spiral ribs of which the lower one lies at the periphery and four more narrowly spaced ribs are found on the base. These revolving ribs are crossed by more or less strong collabral increments that form a low lobe in the anterior portion and are straight in the posterior portion of the whorl.
Difference: *S. kieli* differs from *Sargana xsosaensis* by its more rounded apex and whorl sides, and its less strongly developed collabral ornamental elements. The siphon is more sinuous, and the umbilicus less wide. *Sargana geversi* also has a straighter siphon, and its spiral ribs are more nodular than those of *S. kieli*. The narrow umbilicus differs from that of the American species from Ripley Formation. Closest among these is *S. mississippiensis* which also has a strongly twisting siphon and spiral ornament dominating over axial elements. The width height relation, the number of whorls and detail is ornament differ between both species. *Praesargana kennedyi* Saul, 1996 from the Turonian of California has a similar ornament to that of *Sargana kieli,* but is higher than the later. *S. kieli* is similar to *S. mississippiensis*, but is higher. Otherwise the three species, *P. kennedyi*, *S. kieli*, and *S. mississippiensis* resemble each other in ornament.

***Sargana mississippiensis* sp. nov.**
Pl. II, Figs 24–26

Derivatio nominis: Named for the state of Mississippi where the type was collected.
Holotype: The illustrated specimen represents the holotype that is housed in the Dockery collection in the Geological Survey of Mississippi in Jackson.
Locus typicus and stratum typicum: The specimen are from the Late Campanian Coffee Sand of Friendship in northern Mississippi.

Diagnosis: The low-spired shell is wider than high. Its deep umbilicus is surrounded by a moderately corrugated ridge. The spire is depressed and lowly convex with a strong broad subsutural ridge and a narrow median rib on the flattened apical whorl flank. Three keel-like spiral ribs form the ornament of the whorl sides, with the upper one forming a sharp peripheral edge. The aperture is subcircular with a narrow anterior canal that is strongly inclined to the left and curved. The protoconch consists of three well-rounded whorls with almost planispiral coiling.
Description: The low-spired subpyriform shell is wider (about 1.8 cm) than high (about 1.3 cm), has a medium sized umbilicus that is surrounded by a narrow and acute ridge with spines and inclination away from the apertural plane. The teleoconch consists of about 2.5 whorls. The spire is depressed, and the apical shell is low and rounded and almost flat. The aperture is subcircular with a narrow anterior canal that is twisted to the left. The outer and inner lips are thickened with a posterior notch developed between them, which creates a low subsutural ridge with growth increments forming a sinus within it. The apical flank has two more spiral ribs of which the second is the larger. The whorl flank is ornamented with three strong keel-like ribs, the upper of which forms the periphery, and the central of which forms the greatest shell width. The ornament, thus, has three widely spaced spiral ribs that may have one additional smaller rib on the apical flank with finer ribs between them on the side and the base. The revolving ribs are crossed by more or less strong collabral increments that may be fine or scale-like.
Difference: The shell of *Sargana mississippiensis* is smaller and has fewer whorls than found in all the other here described species of *Sargana*. Its ornament resembles that of *Sargana kieli*, which has a similar siphon, but is higher and has a narrower umbilicus.

Genus *Praesargana* Saul and Popenoe, 1993

Generic description: The low spired shell consists of a few whorls of which the last envelops the previous one nearly completely. Ornament consists of several spiral ribs of large tubercles separated from each other by deep grooves. The aperture is roundish with a posterior notch of the outer lip. The inner lip is thick with a sharp fold at the basis of the columella and at the beginning of the short deep siphonal canal, which is bent to the left. The columella is open and bounded by a roughened fasciole. The genotype is *Trophon condoni* White, 1889 from the Californian Chico Group, Turonian (Saul – Popenoe 1993, Figs 27–37).
Difference: *Praesargana* lacks the deep spiral sulcus at the base of the body whorls of *Sargana*. It has finer nodular rather than spinose sculpture. The umbilicus is smaller and shallower, and the siphonal canal is more open. The low spire distinguishes it from *Buccinopsis,* and the rough margin of the umbilicus differs from the smooth margin present in *Morea* which usually also has a higher spire.
Remarks: *Praesargana* has a teleoconch shape that is intermediate between *Sargana* and *Morea* or *Buccinopsis* (Stephenson 1941, Pl. 61, Figs 1–9, Sohl 1964, Pl. 20, Figs 1–26, Pl. 22, Figs 1–7). In the typical *Praesargana* the siphonal canal is not as narrow as in *Sargana*, but not as wide as in *Morea* or *Buccinopsis*. The species *Praesargana argentea* and *P. confraga* as described by Saul (1996) actually belong into the definition of the genus *Sargana* and not in that of the genus *Praesargana* as originally proposed by Saul – Popenoe (1993). This demonstrates on one side the closeness of both genera and on the other side that both occurred and evolved side by side from the Late Turonian to the Campanian-Maastrichtian. *Praesargana* is, thus, not only present in Turonian deposits of the Pacific slope as suggested by Saul – Popenoe (1993) and Saul (1996), but has migrated to the northern shores of the Tethys Ocean by Campanian time. It is not known whether its evolutionary history included a similar complex migration history as is here suggested in case of *Sargana*.

***Praesargana tupeloensis* sp. nov.**
Pl. II, Figs 34–38

Derivatio nominis: This *Praesargana* is named according to its occurrence near the city of Tupelo, Mississippi.
Holotypus: The specimen illustrated in Figs 36–38 represents the holotype that is housed in the collection of Dockery in the Geological Survey of Mississippi, Jackson.
Type locality and stratum typicum: Late Campanian Coffee Sand of Ripley Formation in Friendship (Chapelville), northern Mississippi.

Diagnosis: The generic diagnosis applies to this species. The shell is a little higher than wide. The rounded whorls of which the last one covers most of the others have an ornament of eight spiral ribs on the body whorl. The subsutural ribbon is wide and becomes more distinctive on late whorls of the teleoconch. The inner lip of the aperture is concave and ends with a strong and inclined corner forming a ridge at the begin of the columellar lip. The straight, short siphon is slightly inclined to the left. The umbilicus is surrounded by abandoned siphonal canals.
Description: The low spired teleoconch consists of a bit more than four whorls; the protoconch is not preserved. The last whorl envelops the previous whorls nearly completely and the spire is low and rounded. The shell of the holotype is 2.4 cm high and 2.1 mm wide with well rounded flanks. Ornament consists of eight spiral cords and a raised and rounded subsutural ribbon. The spiral elements are crossed by collabral ribs forming a regular pattern of rounded nodes. The aperture is rounded with a posterior notch on the outer lip that gives rise to the subsutural ribbon and its ornament of forward curved growth increments extending onto the former whorl and forming an undulate suture. The inner lip is thick with a sharp fold at the basis of the columella and at the beginning of the short deep siphonal canal that is bent to the left. The columella is open and bounded by a roughened fasciole displaying the former ends of siphonal canals.
Difference: *Praesargana condoni* from the Turonian Chico Formation of California is similar in ornament, but has stronger shoulders and narrower base. *Praesargana kennedyi* Saul, 1996 from the late Turonian Californian Ladd Formation (Saul 1996, Figs 14–16, 21–23) closely resembles *P. tupeloensis* in shape, but its ornament is not nodular. *Morea rotunda* Sohl, 1964 from Ripley Formation in Mississippi is similar in size and shape, but has a more narrow umbilicus with smooth margin and more spiral ribs (Sohl 1964, Pl. 20, Figs 11, 12).
Remarks: Garvie (1991) suggested to place *Sargana* with the Trichotropidae, but Garvie (1992) noted similarities with the muricids. The first placement he based on the shape of the protoconch which resembles somewhat that of the trichotropids, and the second on the shape of the aperture of the adult shell which differs from the trichotropids by having a posterior notch, as found in some muricids. Garvie (1992) also suggested the cancellariids which was challenged by Saul (1996) who suggested that actually the cancellariid protoconch is provided with more whorls than are present in that of the Sarganidae. But this is not really the case and there exist some similarities of the protoconchs of trichotropids, cancellariids and sarganids.

Saul (1996) noted the difference of the protoconch of Sarganidae to that of modern muricids as for example those described by Kool (1993). She also noted the similarity with protoconchs as found in *Pyropsis* Conrad, 1860, and *Napulus* Stephenson, 1941 as described by Sohl (1964). But her conclusion that Sarganidae and the Pyropsinae in general represent Muricoidea is based on the assumption offered by Ponder – Warén (1988) that the Sarganidae have to be included into this group of caenogastropods. But this is putting to much significance on this classification scheme which was assembled from literature and is probably largely based on the interpretations offered by Sohl (1964). First undoubted muricid species are present in the Paleocene, and here they are provided with a protoconch that resembles that of modern muricids (Bandel 1993, Riedel 2000).

The Sarganidae described by Saul (1996) from the Late Turonian of California represent the oldest known species of this group. Here it is evident that *Praesargana argentea* closely resembles *Sargana xsosaensis* from Umzamba Formation in South Africa, but its spire is more stair-like, and the whorl sides are more flattened on their upper part. Features of the aperture in both species are very similar. *Praesargana kennedyi* from California is higher, but otherwise very similar to *Sargana kieli* from Umzamba Formation, which in turn closely resembles *Sargana mississippiensis*. This later species is the youngest of three species that form the group of flat topped *Sargana* with ornament of spiral ribs dominating. *S. mississippiensis* comes from the Ripley Formation of the SE-USA. *Praesargana confraga* from California is similar to *Sargana eximia* from Santonian-Campanian Trichinopoly Group of SE-India. When the three species from the Santonian of South Africa are compared to species from the Late Campanian to Early Maastrichtian Ripley Formation it is evident that *Sargana mississippiensis* closely resembles *Sargana kieli*, *Sargana stantoni* is similar to *Sargana geversi*, and *Sargana chapelvillei* resembles *Sargana xsosaensis*.

Subfamily Pseudecphorinae subfam. nov.

Diagnosis: The subpyriform shell has anteriorly constricted whorls with a hollow spindle. The aperture is posteriorly indistinctly notched without subsutural band forming. It is anteriorly drawn out to a weakly curving siphonal canal. The concave inner lip ends with a strong plica at the onset of the siphonal canal. The umbilicus is surrounded by a ridge formed of abandoned siphonal canals. Ornament consists of few strong spiral ribs and weak growth lines. The protoconch is lowly coiled with rounded smooth whorls and almost 1 mm in diameter. The characteristic genus is *Pseudecphora*.

Differences: From *Sargana* and Sarganinae distinguishes the higher spire, the ornament being composed only of spiral ribs, and the absence of a subsutural ribbon. Similar is the shape of the protoconch and of the umbilicus. *Pseudecphora* is distinguished from *Lowenstamia* and *Weeksia* of the Weeksiidae by a lowly coiled protoconch, no fine spiral liration of the teleoconch, and by the presence of a siphonal canal. *Hippocampoides* belonging to the Thalassoscynidae is distinguished by a flattened apex including the protoconch and more spinous surrounding of the umbilicus.

Genus *Pseudecphora* gen. nov.
Pl. II, Figs 39–41

Diagnosis: The small (about 10 mm high) shell has a large pseudumbilicus surrounded by a high fasciole, and it is of pyriform shape. Four to five whorls increase markedly in size and the spire is low and acute, but flattened in the location of the protoconch. The ornament consists of regular spiral ridges on the body whorl. The aperture is subcircular and forms a short narrow slightly curved siphonal canal at its anterior end. There is a short but distinct posterior notch at the margin of the outer lip. The protoconch is large and planispirally coiled. The type species is *Ecphora proquadricostata* Wade, 1917 from Coon Creek in Tennessee.
Etymology: Named as combination of *Ecphora* and pseudo, since it looks like *Ecphora,* but does not belong to this genus.

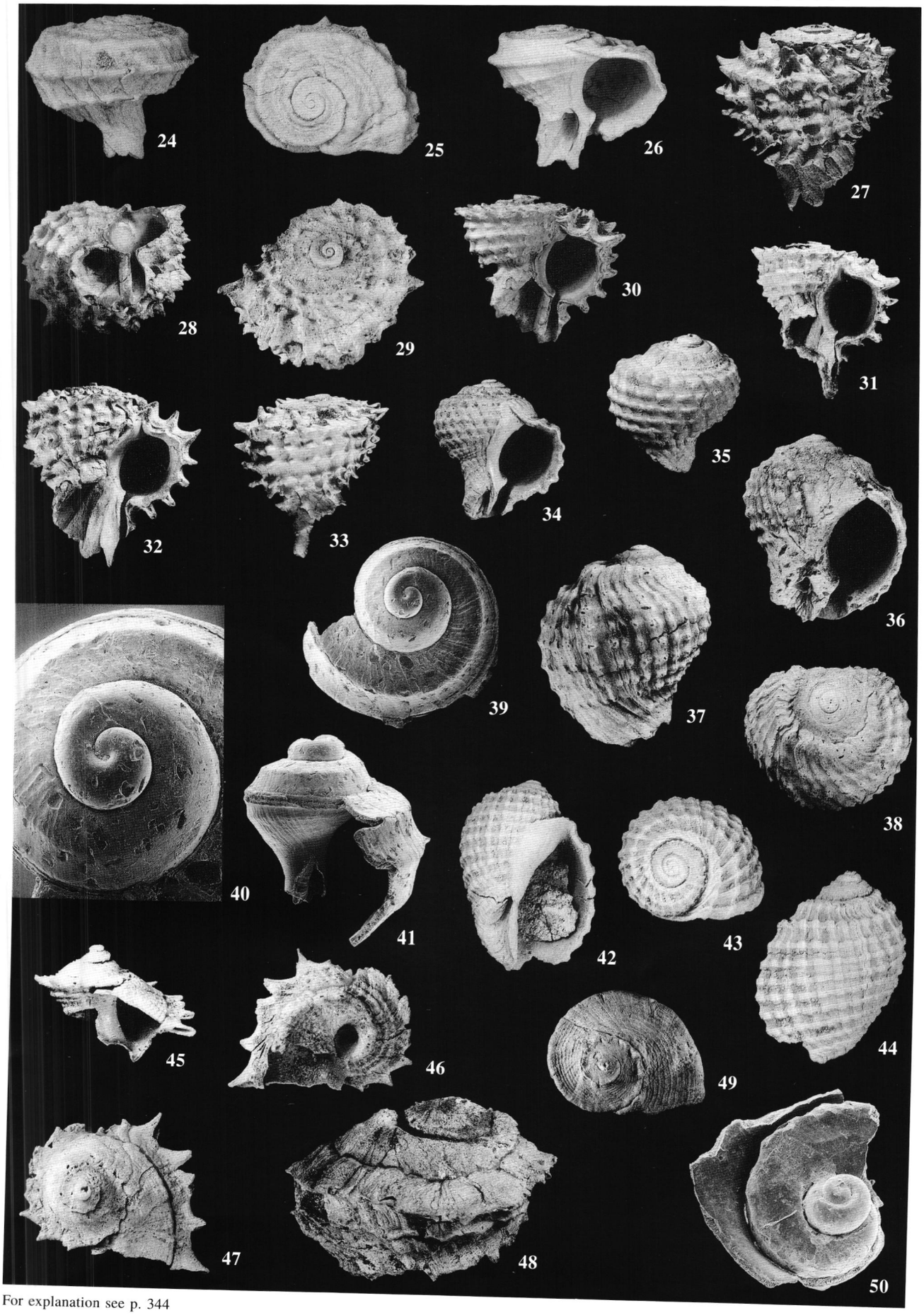
***Pseudecphora proquadricostata* (Conrad, 1843)**

Description: The shell is up to 11 mm high, rarely up to 12 mm high, and 9 mm wide, rarely up to 10 mm wide. Its large pseudumbilicus is surrounded by a prominent keel (fasciole) which in some cases clearly reflects the row of former siphonal canals. Four regular spiral ridges are present on the body whorl of which the uppermost is the subsutural collar. The aperture is subcircular and connected to a short, slightly curved narrow siphonal canal with parallel margins. There is a shallow, but well developed posterior groove that gives rise to a narrow subsutural ridge with prominent growth increments. The inner lip is concave and in its columellar portion free, forming the margin of the pseudumbilicus. According to Sohl (1964, Pl. 19, Figs 1, 5), the fully grown adult shell may reach 12 mm in height and 10 mm in width. Sohl had no protoconch well preserved, but in the specimen from Coffee Sand in Friendship, Mississippi it is well preserved (Figs 39–41). The protoconch lies lowly coiled almost planispiral on the shell apex and consists of two rounded whorls. Its end is clearly indicated by the onset of the teleoconch, which is marked with spiral ridges. The embryonic portion measures about 0.4 mm in width and the fully grown larval shell is a little more than 1 mm wide. The aperture of the protoconch is simply rounded.
Difference: The teleoconch of *Pseudecphora proquadricostata* is dissimilar to that of *Sargana* since its spire is higher and it lacks axial ornament (Wade 1917, Pl. 18,

Explanation of plate

Plate II Fig. 24 – *Sargana mississippiensis* with the holotype from the Late Campanian Coffee Sand of Friendship (Chapelville) in northern Mississippi. Figs 25 and 26 are of the same individual; Fig. 25 – *Sargana mississippiensis* with the holotype with the apical side of 17 mm in width; Fig. 26 – *Sargana mississippiensis* with the holotype in apertural view with 13 mm high shell; Fig. 27 – *Sargana chappelvillei* with the holotype (same as in Fig. 32) seen from behind; Fig. 28 – *Sargana chappelvillei* with umbilical view, same shell as in Fig. 30; Fig. 29 – *Sargana chappelvillei* with apical view of the same individual as in Fig. 31. Width 17 mm; Fig. 30 – *Sargana chappelvillei* with 15 mm high shell from from the Late Campanian of Friendship in Mississippi; Fig. 31 – *Sargana chappelvillei* with 19 mm high shell from the Late Campanian of Friendship in Mississippi; Fig. 32 – *Sargana chappelvillei* with apertural view of the holotype (the same as Fig. 27) from the Late Campanian Coffee Sand of Friendship in northern Mississippi. The shell is 22 mm high; Fig. 33 – *Sargana chappelvillei* of the same individual as 31 with view from behind; Fig. 34 – *Praesargana tupeloensis* with juvenile shell of 12 mm in height from the Late Campanian Coffee Sand of Chapelville, Mississippi; Fig. 35 – *Praesargana tupeloensis* of Fig. 34 seen from behind; Fig. 36 – *Praesargana tupeloensis* with the holotype measuring 22 mm in height from the Late Campanian Coffee Sand of Chapelville in northern Mississippi. Figs. 37 and 38 represent the same individual; Fig. 37 – *Praesargana tupeloensis* with the holotype seen from behind; Fig. 38 – *Praesargana tupeloensis* with the holotype in apical view with 21 mm wide shell; Fig. 39 – *Pseudecphora quadricostata* in apical view with smooth protoconch and juvenile teleoconch of the same individual as in Figs 40, 41. Coffee Sand, Friendship, Mississippi; Fig. 40 – *Pseudecphora quadricostata* in apical view enlarged with smooth protoconch of about 1, 2 mm in diameter and two whorls of the same individual as in Figs 40, 41; Fig. 41 – *Pseudecphora quadricostata* in apertural view with about 2 mm high juvenile shell of the same individual as in Figs 40, 41; Fig. 42 – *Morea rotunda* in apertural view with a 25 mm high shell from the Late Campanian Coffee Sand of Chappelville, Mississippi. Figures 43 and 44 represent the same specimen; Fig. 43 – *Morea rotunda* in apical view; Fig. 44 – *Morea rotunda* in lateral view; Fig. 45 – *Lowenstamia funiculus* with 15 mm wide juvenile shell in apical view with relicts of the erect protoconch and the spiny keel of the teleoconch. Same individual as in Figs. 46, 47; Fig. 46 – *Lowenstamia funiculus* in umbilical view with siphon positioned in the end of the umbilical ridge from Late Campanian Coffee Sand, Chapelville, Mississippi; Fig. 47 – *Lowenstamia funiculus* in apical view with the same individual as in Figs. 45 and 46; Fig. 48 – *Lowenstamia funiculus* with 36 mm wide shell of fully grown specimen seen from the side from Late Campanian Coffee Sand, Chapelville, Mississippi; Fig. 49 – *Lowenstamia lirata* with 19 mm wide shell seen in apical view has a simple peripheral edge. Early Maastrichtian Ripley Formation from Union County Lake, Mississippi; Fig. 50 – *Weeksia amplificata* with about 0.8 mm high larval shell that is well set off from the juvenile teleoconch. Coon Creek, Ripley Formation.

K. Bandel – D. T. Dockery III: The Sarganidae (Pyrifusoidea, Latrogastropoda), their taxonomy and paleobiogeography (Pl. II)



For explanation see p. 344

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References

Akers, R. E. – Akers, T. J. (1997): Texas Cretaceous gastropods. – Texas Paleontological Series. Houston, 6: 1–340.

Bandel, K. (1975): Embryonalgehäuse karibischer Meso-und Neogastropoden (Mollusca). – Abh. Akad. Wiss. Lit., math.-naturwiss. Wiesbaden, Kl. 1975, 1: 1–133.

– (1982): Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. – Fazies, Erlangen, 7:1–198.

– (1988): Repräsentieren die Euomphaloidea eine natürliche Einheit der Gastropoden? – Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg, Hamburg, 67: 1–33.

– (1991): Ontogenetic changes reflected in the morphology of the molluscan shell. – *In:* Schmidt-Kittler, N. – Vogel, K. (Eds) Constructional Morphology and Evolution, Springer Verl. Berlin, 211–230.

– (1992): Evolution der Gastropoden aus biologischer und paläontologischer Sicht. – Veröff. des Übersee-Museums, Naturwiss. Bremen, 11: 17–25.

– (1993): Caenogastropoda during Mesozoic times. – Scripta Geologica, Leiden, Spec. Issue, 2: 7–56.

– (1997): Higher classification and pattern of evolution of the Gastropoda. A synthesis of biological and paleontological data. – Courier Forschungsinstitut Senckenberg, Frankfurt, 201: 57–81.

– (1999): On the origin of the carnivorous gastropod group Naticoidea (Mollusca) in the Cretaceous with description of some convergent but unrelatred groups. – Greifswalder Geowissenschaftliche Beiträge, Greifswald, 6: 143–175.

– (2000): Some gastropods from the Trichinopoly Group, Tamil Nadu, India and their relation to those from the Americal Gulf Coast. – Memoir Geological Society of India, Bangalore, (1999), 46: 65-III.

Bandel, K. – Frýda, J. (1998): Position of Euomphalidae in the system of the Gastropoda. – Senckenbergiana lethaea, Frankfurt, 78: 103–131.

Bandel, K. – Hain, S. – Riedel, F. – Tiemann, H. (1993): Limacosphaera, an unusual mesogastropod (Lamellariidae) larva of the Weddell Sea (Antarctica). – The Nautilus, 107(1): 1–8.

Bandel, K. – Kiel, S. (in prep.): Santonian gastropods from the South African Umzamba Formation.

Bandel, K. – Mustafa, H. (1994): Constructional morphology of some Upper Cretaceous rudists of the Ajlun (Jordan). – Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg, Hamburg, 77: 603–635.

Bandel, K. – Riedel, F. (1994): Classification of recent and fossil Calyptraeoidea with a discussion on neomesogastropod phylogeny. – Berliner geowissenschaftliche Abhandlungen E, Berlin, 13: 329–367.

Bandel, K. – Riedel, F. – Tiemann, H. (1994): A special adaptation to planktonic life in larvae of the Cassoidea (= Tonnoidea) (Gastropoda). – Marine Biology, 118: 101–108.

Bandel, K. – Riedel, F. – Weikert, H. (1997): Planctonic Gastropod Larvae from the Red Sea: A Synopsis. – Ophelia, Helsingör, 47(3): 151–202.

Bandel, K. – Shinaq, R. – Nazzal, J. (1999) Palaeoecological and diagenetical significance of a silicified soft bottom fauna of Campanian age (Quatrana Unit, Jordan). – Mitteilungen des Geologisch-Paläontologischen Instituts, Universität Hamburg, Hamburg, 83: 201–218.

Bandel, K. – Stinnesbeck, W. (2000): Gastropods of the Quriquina Formation (Maastrichtian) in Central Chile: Paleobiogeographic relationships and the description of a few new taxa. – Zentralblatt für Geologie und Paläontologie, Stuttgart, 1, 1999 (7/8): 757–788.

Beu, A. G. – Maxwell, P. A. (1990): Caenozoic Mollusca of New Zealand. – New Zealand Geological Survey Paleontological Bulletin, Lower Hutt, 58: 1–518.

Dockery, D. T. III (1993): The streptoneuran gastropods, exclusive of the Stenoglossa, of northeastern Mississippi. – Bulletin of Mississippi Department of Environmental Quality Office of Geology (Jackson), 129: 1–191.

Garvie, C. L. (1991): Two new species of Muricinae from the Cretaceous and Paleocene of the Gulf Coastal Plain, with comments on the genus *Odontopolys* Gabb, 1860. – Tulane Studies in Geology and Paleontology, 24: 87–92.

Garvie (1992): A second Cretaceous muricid from the Gulf Coastal Plain. – Tulane Studies in Geology and Paleontology, 25: 187–190.

Groves, L. T. (1992): California Cowries (Cypraeacea); past and present, with notes on recent tropical eastern Pacific species. – The Festivus, 24: 101–107.

Gründel, J. (1998): Archaeo- und Caenogastropoda aus dem Dogger Deutschlands und Nordpolens. – Stuttgarter Beiträge Naturkunde, Stuttgart, Ser. B, 260: 1–39, 9 Taf.

– (1999): Gastropoden aus dem höheren Lias von Grimmen, Vorpommern (Deutschland). – Archiv Geschiebekunde, Hamburg, Bd. 2, Heft 9: 629–672, 14 Taf., 1 Tab.

Kase, T. (1990): Late Cretaceous gastropods from the Izumi Group of Southwest Japan. – Journal of Paleontology, 64: 563–578.

Kiel, S. – Bandel, K. (1999): The Pugnellidae, a new stromboidean family (Gastropoda) from the Upper Cretaceous. – Paläontologische Zeitschrift, Stuttgart, 73: 47–58.

Kool, S. P. (1993): Phylogenetic analysis of the Rapaninae (Neogastropoda Muricidae). – Malacologia, 35: 155–259.

Mustafa, H. – Bandel, K. (1992): Gastropods from lagoonal limestones in the Upper Cretaceous of Jordan. – Neues Jahrbuch Geologie und Paläontologie, Abhandlungen, Stuttgart, 185: 349–376.

Rennie, J. V. L. (1930): New Lamellibranchia and Gastropoda from the Upper Cretaceous of Pondoland. – Annals of the South African Museum, Cape Town, 28: 161–257, pls 16–31.

Ponder, W. F. – Warén, A. (1988): Classification of the Caenogastropoda and Heterostropha – A list of the family group and higher category names. – *In:* Ponder, W. F. (Ed.) Prosobranch Phylogeny. Proceedings of a Symposium held at the 9th International Malacological Congress, Edinburgh, Scotland, Malacological Review, Supplement, 4: 88–128.

Popenoe, W. P. – Saul, L. R. (1987) Evolution and classification of the Late Cretaceous–Early Tertiary gastropod Perissitys. – Contributions to Science, Nr. 380, Natural History Museum of Los Angeles County, Los Angeles, 1–37.

Popenoe, W. P. – Saul, L. R. – Susuki, T. (1987): Gyrodiform gastropods from the Pacific Coast Cretaceous and Paleocene. – Journal of Paleontology, 61: 70–100.

Riedel, F. (1994): Recognition of the superfamily Ficoidea Meek, 1864 and definition of the Thalassocynidae fam. nov. (Gastropoda). – Zool. Jb. System, 121: 457–474.

– (1995): An outline of cassoidean phylogeny (Gastropoda). – Contributions to Tertiary and Quarternary Geology, 32: 97–132.

– (2000): Ursprung und Evolution der "höheren" Caenogastropoda. – Berliner Geowissenschaftliche Abhandlungen (F), 32: 1–240.

– (1932): Die Oberkreide vom Mungofluß in Kamerun und ihre Fauna. – Beiträge zur geologischen Erforschung der deutschen Schutzgebiete, Heft, 16: 1–154.

Saul, L. R. (1988): Latest Cretaceous and early Tertiary Tudiclidae and Melongenidae (Gastropoda) from the Pacific slope of North America. – Journal of Paleontology, 62: 880–889.

– (1996): Three new Turonian muricacean Gastropoda from the Santa Ana Mountains, Southern California. – The Veliger, 39: 125–135.

Saul, L. R. – Popenoe, W. P. (1993): Additions to the Pacific Slope Turonian Gastropoda. – The Veliger, 36: 351–388, 138 Figs.

Schröder, M. (1995): Frühontogenetische Schalen jurassischer und unterkretazischer Gastropoden aus Norddeutschland und Polen. – Paläontographica, (Abt. A), 238: 1–95.

Sohl, N. F. (1960): Archaeogastropoda, Mesogastropoda and Stratigraphy of the Ripley Owl Creek, and Prairie Bluff Formation. – United States Geological Survey, Washington, Professional Paper 331A: 1–151.
– (1964): Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owls Creek, and Prairie Bluff Formations. – United States Geological Survey, Washington, Professional Paper 331B: 153–344.
– (1964): Gastropods from the Coffee Sand (Upper Cretaceous) of Mississippi. – United States Geological Survey, Washington, Professional Paper 331C: 345–396.
Stephenson, L. W. (1923): The Cretaceous Formations of North Carolina. Part I. Invertebrate fossils of the Upper Cretaceous Formations. – North Carolina Geological and Economic Survey, Washington, 5: 1–604, 102 pls, 6 Figs.
– (1941): The larger invertebrate fossils of the Navarro group of Texas (exclusive of corals and crustaceans and exclusive of the fauna of the Escondido formation). – The University of Texas Publications, Austin, Texas, 4101: 1–641.
– (1952): Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. – United States Geological Survey, Washington, Professional Paper, 242: 226 pp.
Stoliczka, F. (1867): Cretaceous fauna of southern India. Volume 2, The Gastropoda, pt. 1–4. – India Geological Survey, Memoirs, Palaeontologia Indica, series V:1–204, pls 1–16.
Taylor, J. D. – Morris, N. J. – Taylor, C. N. (1980): Food specialization and the evolution of predatory prosobranch gastropods. – Palaeontology, 23: 375–409.
Taylor J. D. – Cleevely, R. J. – Morris, N. J. (1983): Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. – Palaeontology, 26: 521–553.
Wade, B. (1916): New genera and species of Gastropoda from the Upper Cretaceous (of McNairy Co., Tenn.). – Acad. Natural Sciences, Philadelphia, 68: 455–471.
– (1917): New and little-known Gastropoda from the Upper Cretaceous of Tennessee. – Acad. Natural Sciences, Philadelphia, 69: 280–304.
– (1926): The fauna of the Ripley Formation on Coon Creek, Tennessee. – United States, Geological Survey, Professional Paper, 137: 1–272, Washington.
Wenz, W. (1939): Gastropoda, Teil I. – *In:* Schindewolf, O. H. (Ed.) Handbuch der Paläozoologie, Bd. 6: 1–1639.

Čeleď Sarganidae (Pyrifusoidea, Latrogastropoda), její taxonomie a paleobiogeografie

Čeleď Sarganidae Stephenson, 1923 zahrnuje vyhynulou skupinu křídových gastropodů. Druhy patřící do této čeledě mají typicky nízce kuželovité, subpyriformní ulity, anteriorně zúžené závity, velkou pseudopíštěl a ústí posteriorně nesoucí anální zářez a anteriorně úzký sifonální kanál. Zatímco teleoconcha připomíná moderní neogastropody, téměř planispirálně vinutá protokoncha připomíná protokonchy přítomné u moderních neomesogastropodů. Tyto dva znaky definují Latrogastropody jako skupinu podtřídy Caenogastropoda, která vznikla v křídovém období. Dva nové druhy, *Sargana chapelvillei* a *S. mississippiensis* jsou popsány ze svrchního kampanu jednotky Cogge Sand v Mississippi, USA. Oba velmi připomínají druh *Sargana geversi* a dva nové druhy *S. xsosanensis* a *S. kieli* za santonské lokality Umzamba ve východokapské provincii jižní Afriky. *Sargana exima* ze santonu a campanu Tamil Nadu v jižní Indii se odlišuje od druhů v perském zálivu a jihoafrických druhů, avšak připomíná druh *Praesargana confraga* z turonu Kaliformie. Rovněž je diskutován vztah rodů *Pseudecphora* gen. nov. z podčeledi Pseudecphorinae subfam. nov., *Morea* z Moreinae, *Hippocampoides* z Thalassocynidae, *Schizobasis, Hillites* a *Natalites* z Schizobasinae subfam. nov., *Weeksia* a *Lowenstamia* z Weeksiidae, neboť všechny tyto rody připomínají rod *Sargana*. Čeleď Sarganidae patří do Pyrifusoidea superfam. nov., která nepatří ani do Neomesogastropoda ani mezi Neogastropoda.

Evoluční historie Sarganidae zahrnuje dvě velmi vzdálené oblasti. Nejstarší známí zástupci pochází z turonu Kalifornie. Tyto druhy migrovaly přes Tethydu na gondwanské šelfy vznikajícího Indického oceánu, kde vznikly další druhy v průběhu santonu. Ty dále migrovaly k jižním pobřežím vnitřního moře severoamerického kontinentu, za vzniku nových druhů v pozdním kampanu a maastrichtu. Vhodnou migrační cestou byly pravděpodobně povrchové proudy jižního Atlantického oceánu, zatímco chladné vody zahraňovaly osídlení šelfových oblastí. Čeleď Sarganidae osídlovala jen subtropické oblasti neboť chybí v tropických vodách oceánu Tethys.