Systematics and Distributions of Pyrgulifera Meek[1])

By John T. C. Yen

Professor of Geology on the faculty of Arts and Science of the Villanova University

(With 26 figures on plate 2)

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The present work comprises studies in the morphology, habitat conditions, geological and geographical distributions, and speciation of the genus *Pyrgulifera* Meek. The genus was described in 1877 to accommodate a characteristic species of gastropod from the Bear River formation of the Cenomanian age. The type section of the Bear River is exposed in the southwestern part of Wyoming. Meek's nomination of the genus soon arrested the attention of European paleontologists who recognized the morphological features of Meek's genus to be well fitted to a number of their species of gastropeds which had been hitherto arbitrarily assigned to such genera as *Melania, Tanalia, Paludomous, Melanopsis,* and other marine and freshwater genera of gastropods. These species were accordingly transferred to *Pyrgulifera,* and their generic identification thus became established.

When my previous research projects over the western interior area were in progress, I had opportunities of examining all the North American species of *Pyrgulifera* both in the field as well as in the museum collections. During my recent trip to Europe in 1955 and 1956, I was able to examine all the interesting collections available in Austria, Germany and France. The findings from both sides of the Atlantic Ocean constitute the present work. It represents a first effort in the current century to study this characteristic genus, the species of which demonstrated clearly their biostratigraphic importance in the Upper Cretaceous times.

In completing this work, I am reminded of the pleasant and cordial friends abroad who have rendered all possible assistance to the work. In addition to many others to be mentioned elsewhere, I would like to express here my heartfelt thanks to the Museum of Natural History in Vienna. His effort in making available collections of material and some scattering literature for my benefits is a classic example of friendly cooperation in scientific research.

I also want to express my thanks to Professor Jean Rogers of Muséum national d'Histoire naturelle in Paris, as I am much indebted for his assistance in searching some of the literature cited in this work which were recently published in the Balkan States and the distributions of which seem to be rather limited. Monsieur Rogers is the Director of Center d'Études et de documentation paleontologiques in Paris, an organization which is attempting to keep world wide records of the paleontological works, so that they may become available for references to those who are interested. It is obviously clear to all geologists and paleontologists that such a center is exceedingly useful, practical and time-saving, and that it deserves an international support for the maintenance and progress of this organization.

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Review of Literature

Meek (1860) described *humerosa* as a species of *Melania* from a shale bed exposed in "Sulphur Creek, near Bear River, Wyoming, directly on the Union Pacific Railroad, where it occurs in the upheaved beds in great numbers, along with numerous fresh-water and perhaps some brackish water shells, belonging to the horizon of the latest Cretaceous or oldest Tertiary." On account of the subsequent changes in time, some part of the above quotation needs modification, though, "Sulphur Creek" remains to be one of the classic localities of the Bear River formation. Meek in 1872 transferred his species to *Pyrgulifera*, a new genus he proposed without a description. He supplied the description in one of his later works (1877).

White (1895) offered a lengthy discussion on various species of *Pyrgulifera* including a geographical and time distribution of the genus. He also described *P. stantoni* from a "later bed exposed in north of the type-locality of the Bear River". In the same year, he also described *P. meeki* from "an Upper Cretaceous bed in north of Fairbury, Nebraska". After having examined the type and other specimens of this form, it seems to be certain that *P. meeki* is not a species of this genus.

From the later part of the preceding century to the late twenties, many records of *P. humerosa* have crept into the geological and paleontological literature. But nearly all of them were repetitious data from the Bear River type-locality in southwestern corner of Wyoming, a few being said to be from the neighboring Idaho and Utah, though this has not been confirmed.

Stephenson (1953) described *P. ornata, P. costata, P. c. tuberata* and *P. c. sublaevis* from the Dexter and the Lewisville Members of the Woodbine formation of Cenomanian age exposed in northeastern part of Texas. His *P. c. sublaevis* does not seem to belong to this genus; other forms may provide interesting material for consideration in a monographic study of this genus.

The present writer (1954), after having done extensive field collecting and studying in the vicinity of Evanston and the general area of Cokeville, in southwestern part of Wyoming, described two additional subspecies, namely, *P. humerosa cokevillensis* and *P. stantoni elongatus* from north of Cokeville. Their enclosing beds represent a presently unnamed formation, which may most probably be of Upper Cenomanian age.

The European species of *Pyrgulifera* were described under various generic names before Meek's publication of his genus. In southern France, Matheron (1842) described *M. lyra* and *M. armata* from the lignite beds in the lower Rhone basin. These species are true *Pyrgulifera*. However, the generic identification of Rolle's *P. gradata* (1858) and Roule's *P. matheroni* (1844) are highly doubtful. *Hantkenia munieri*, which was described by Repelin (1902) from the Gardonian formation of Upper Cenomanian age exposed in southeast of France, may be considered a typical species of *Pyrgulifera*. Recently Fabre-Taxy (1951) recorded both *P. lyra* and *P. matheroni* from the Campanian beds in the lower Rhone basin. Juliette Villatte (1953) also recorded *P. acinosa* Zekeli from the Campanian brackish water beds in Belesta, Ariege, but her species is almost certain not a species of this genus. G. Termier (1954) recorded *P. acinosa* from the Gardonian beds at Dordogne in southeast of France, but it is most probably a species of *P. munieri* (Repelin). Her *P. springer* (Sowerby 1831) does not belong to *Pyrgulifera* at all.

Two species were described by Holzapfel (1887), namely, *P. decheni* and *P. neumayri* as of this genus from the Aachener sands of Upper Cretaceous age. After an examination of the available collections of specimens in Aachen, Germany, which includes some of the Holzapfel's original lots, it is certain that none of his two species is *Pyrgulifera*.

In the peri-Alpine area, several species of *Pyrgulifera* have been described: *P. pichleri* (Hoernes 1857), *P. p. nassaeformis* and *P. spinosa* of Sandberger (1875) from the

coal beds of the Gosau formation near Brandenberg in North Tirol, Austria. A number of species and varieties were also described from the coal seams of the Ajka formation in the western part of Hungary. Among the Hungarian species, *P. glabra* (Hantken 1878), *P. rickeri* (Tausch 1885) and *P. hantkeni* (Oppenheim 1892) are recognized as true species of this genus. Four species and one subspecies are described as new in this work, which were considered by Tausch as the so-called intermediate forms. Others such as *acinosa* Zekeli (1852), *corrosa* Frech (1887), *ajkaensis* Tausch (1885), *riethmülleri* Oppenheim (1892) and *striata* Tausch (1885) do not belong to this genus. These eliminations are fully discussed elsewhere in this paper in relation to their morphological features and systematic positions.

During the past few years, a number of records of *Pyrgulifera* from the Balkan States have been referred to *Pyrgulifera*: Besić (1948) recorded *pichleri* together with an undeterminable form from the upper Senonian beds from Serbia. Pasić (1951) gave *P. pichleri* and *P. louristana* Doubille from the Senonian strata of Gora in Yougoslavia. Judged by the illustrations, these identifications seem to be very doubtful. Pasić (1951) also described *P. hoecki* and *P. decussata* in addition to *P. czjzeki* and an undeterminable form. But all these records of *Pyrgulifera* must be considered as provisional.

Three more species should be mentioned here, namely *P. japonica* Matumoto (1938), *P. praecursor* Sandberger (1875) and *P. stomatopsidum* Stache (1889). *P. japonica* is known only by a single specimen. Judged by Matumoto's description and drawing figures, it is probably a species of *Pyrgulifera*. More collecting of additional specimens may substantiate this record and may prove that the species of *Pyrgulifera* had a world-wide distribution. The other two forms do not seem to belong to this genus.

Morphological Features

The original description of the genus by Meek (1877) is quoted as follows: "Shell subovate, thick, imperforate; spire produced, turrited; volutions angular, shouldered, and nodular above; surface typically with vertical ridges and revolving markings; aperture subovate, faintly sinuous, but not notched or distinctly angular below; outer lip prominent in outline below the middle, retreating at the base, and subsinuous at the termination of the shoulder of the body volution above; peristome continuous; inner lip a little callous below, and thickened all the way up, but without a protuberant callus above, sometimes with a shallow umbilical furrow along its outer margin below."

Meek considered it to be related to *Lithasia* Haldeman, but said it "differs in not having its aperture distinctly angular and notched, or subcanaliculate below, in wanting a protuberance at the top of the inner lip, and in having a more produced, distinctly turrited spire, as well as very different surface marking."

In summarizing the above description and note, we have the characteristic features of the genus: thick shell substance, produced and turrited spire, angular and shouldered whorls, aperture more or less sinuous but not prominently notched, furrowed or closed but not perforated at the umbilicus.

In addition to the above mentioned outstanding features of the adult stage, attention should be directed to those features of the earlier stages which have been hitherto neglected. The neglect has brought it about that several of the non-congeneric forms are questionably assigned to this genus.

The early conchial stage is of fusoid shape, bearing riblets in decussating with the spiral lines, and more or less angulately shouldered. These features in the earlier whorls show that they are distinctly different from those of the corresponding stages in such forms as *acinosa* of Zekeli, *ajkaensis* of Tausch, *corrosa* of Frech, and several others which were referred by some authors to species of *Pyrgulifera*.

In adult individuals, the spire of the shells is produced and turrited. The character of the turrition is important because it is formed by the angular shoulder with its spiny or nodular tubercles and a shelf below the suture, which marks the faint notch on the outer lip margin. Such forms as *ajkaensis* of Tausch, *costata sublaevis* of Stephenson, *matheroni* of Roule, and others do not possess this feature. It is true that the shoulder angulation exhibits considerable amount of variation among different species. The acceleration of such features often produce quite different shape of shells. But the variation is a matter of difference of degree in development, and the shelf, however narrow it may be, is always traceable. Moreover, the coiling of whorls is close and tied to the axis, and there is no perforated umbilicus. In some species such as *P. glabra*, *P. protarmata*, *P. acutispira* and *P. compressa*, the umbilical area is broadly or narrowly furrowed, and such a shallow opening sometimes is partly closed by the columellar margin. The columella is well developed and well defined but it is never broad or spreading.

The sculptures consist of ribs, riblets and riblines, which are usually decussated by variably fine to coarse spiral lines. Their intersections along the shoulder angulations produce various kinds of prominent to obscure tubercles such as those of *P. humerosa*, *P. stantoni*, *P. compressa*, *P. nassaeformis* to *P. protarmata*. The development of such tubercles sometimes highly accelerated into sharply projecting spines as in cases of *P. acutispira* and *P. pichleri*. On the other hand, the tubercles may be reduced to traces as in *P. glabra* and *P. rickeri*. The variation of sculptures in *Pyrgulifera*, whenever they are found to be constant, is demonstrated to have value in specific and subspecific distinction.

Tausch (1886) had considered a number of species of the Ajka formation to be the intermediate gradations of some previously described species such as *P. pichleri*, *P. lyra*, *P. armata*, etc. His decision in this case was obviously under the influence of the great paleontologist Neumayr. However, Tausch apparently overlooked the fact that the classic work of Neumayr on "Paludina" was definitely tied in with the precise stratigraphic data of the Miocene to Pliocene beds in the Balkan States. The demonstration of the conception is clear and convincing. While Tausch's consideration in his species of *Pyrgulifera* was nothing more than lumping them into one group and another, such as taking *P acutispira* to be forms "between *P. pichleri* and *P. lyra*, and between *P. pichleri* and *P. armata*." His material all came from the Ajka formation, and he took them to be gradational between the species which had been described from the beds of Santonian, Campanian and Maastrichtian

ages in Austria and France. Neither morphological features nor stratigraphic background were carefully analysized. His pattern in conception of species is not demonstrative nor practical.

Superficial resemblance in appearance can often be misleading. No better examples than "*Purpurina*" *serrata* Quensdt and *Paramelania damoni* Smith can illustrate their resemblance to species of *Pyrgulifera*. "*Purpurina*" *serrata* was described from the Jurassic Oolitic beds exposed in southwestern part of Germany. *Paramelania damoni* is from the Recent molluscan fauna now existing in Lake Tanganyika of Africa.

Both *Paramelania damoni* Smith and "*Purpurina*" *serrata* Quensdt resemble in general shape of the shell and superficial appearance in sculpture of some species of *Pyrgulifera*. However, the Recent genus of the Lake Tanganyika is readily different by having a well developed posterior notch, a broader and deeper anterior sinus, its peristomal margin thickened outwardly or produced at both anterior and posterior ends, and its riblets appearing to be in form of closely spaced varices with fine and slightly projecting growth lines on surface of their interspaces. Moreover, close comparison between "*Purpurina*" *serrata* and species of *Pyrgulifera* indicates that the Jurassic species bears a more prominent anterior opening which is actually in form of a broad but short siphonal notch, and the surface of the whorls bears finely but distinctly fimbriated sculpture.

The differences in anterior and posterior openings marked on the peristomal margin probably indicate modifications of excretory organs and siphonal processes of the internal part of the animals. The changes expressed in pattern of the sculpture are evidently resulted from the different structures on edge of the mantle, which encloses the internal part of the snails. Such differences in morphological features together with the well known differences in geological ages are sufficient to establish each one of their generic distinction, and consequently, the *damoni* of Smith and the *serrata* of Quensdt can not be considered as being congeneric with species of *Pyrgulifera*. However, it is highly probable that these three genera belong to the same family. Pending further consideration over the divergent opinions, Pleuroceratidae, which is much in the sense of Melaniidae of Thiele, is used for the present.

Habitat Conditions

From an analysis of the pertaining data, it seems to be reasonably assured that we can find possible answers about the habitat conditions of the species of *Pyrgulifera* such as salinity of water, biotic association, geographic background and conditions of entombment.

First of all, let us examine all the existing information relating to the deposits in which species of *Pyrgulifera* were described and recorded. There are three geographical areas: (1) the southwestern Wyoming in the United States, (2) the Lower Rhone Basin in southern France, and (3) the peri-Alpine region in Austria and Hungary.

The first area: the Bear River formation is outcropped at four localities near Evanston, Wyoming, namely, the Sulphur Creek, the Fossil cut, the Shell Hallow and the "new road cut." The first three are classic localities, where C. A. White, T. W. Stanton and others had studied and collected for almost half a century. The fourth one, while it has been known only in recent years, when a new road was built, is by far the best section of the formation. The entire sequence which is exposed along the road cut on the east side of the Bear River Valley consists of some 180 units of limestones, sandstones, shales, mudstones and thin bands of bentonites and other minor units, which aggregate to a total thickness of about 1,500 feet. *Pyrgulifera* is found in limestones and calcareous shales together with *Corbicula*, *Corbula*, *Mesoneritina*, *Pachychiloides* and other genera of smaller sizes. This formation may be considered as one of the most convincing illustrations to indicate the changes in the conditions of deposition repeatedly oscillating from brackish water to freshwater or vice versa. However, the findings of *Pyrgulifera* seem to be frequently in the calcareous shales and occasionally in the limestones, which contain species of mollusks, the existence of which require freshwater or the water of low salinity. Such transitional conditions exist usually in an estuarine area where the lower couse of a river is always affected by tide-flows. Salt water comes upward at high tide and freshwater discharges farther outward at low tide. Such changing environmental conditions are generally not favorable for organic beings to adapt. But, species of different genera in the Cerithiidae are found to occur in both sea water and brackish water, and species of Hydrobiidae are found in both freshwater and brackish water areas.

The present writer (1954) has presented some ecologic and geographic interpretations on the Bear River formation and its partly contemporaneous beds exposed in north of Cokeville, Wyoming. The latter is an unnamed formation of 2,000 to 2,500 feet thickness. Species of *Pyrgulifera* occured in a dark, argillaceous shale in the upper part of the sequence. They are found together with molluscan species of such freshwater genera as *Unio*, *Viviparus*, *Campeloma*, *Lioplacoides*, *Valvata* and *Physa*. Such an assemblage indicates well that the enclosing deposit is of freshwater origin.

The second area: the Gardonian formation in southern France, where *P. munieri* Repelin was found with many individuals, yields similar indication of having alternating brackish water and freshwater conditions in deposition. It seems to be reasonably certain, therefore, that the medium was fresh-water of that the salinity of the water was low. The geographic set-up was probably also estuarine, and could be comparable in many respects to the Bear River formation.

Species of *Pyrgulifera* were also described from the lignit beds at Les Martigues and Rognac in the lower Rhone Basin, France, together with a number of terrestrial and freshwater species of mollusks. Previous authors such as Vasseur (1894), Oppenheim (1895) and more recently Madame

Fabre-Taxy (1951) all agreed that the enclosing deposits are of freshwater origin and termed it as "Fluvio-lacustre." The species contained in Madame Fabre-Taxy's list may represent an admixture of both freshwater and brackish water species, and therefore, the geographic background could still be estuarine with but some woodland and swampy areas in the near vicinity to account for the rich accumulation of the carbonaceous material in the lignite beds.

The third area: Species of *Pyrgulifera* were found abundantly in the Ajka formation exposed in the western part of Hungary, and the Gosau formation in north Tirol of Austria. The Ajka formation consists of freshwater and brackish water (lagoon type) deposits with a maximum thickness to some 80 meters (240 feet), containing species of *Campylostylus*, *Dejanira*, *Melanopsis*, *Auricula*, *Corbicula*, *Corbula*, etc. *Pyrgulifera* occured in the coal seams at different levels in the sequence. These non-marine deposits are overlain by a group of marls, clayey marls and limestones of marine origin, which yield species of *Turritella*, *Astrate*, *Anomia*, *Pecten*, *Gryphaea*, *Trigonia*, *Cardium*, *Lima* and *Hippurites*. The Gosau formation consists of a series of brackish and marine depositions, which produced species of *Inocermus*, *Hippurites*, *Radiolites*, *Nerinea*, *Actaeonella*, *Belemnitella* together with many other kinds of marine invertebrates. Coal seams are located near the upper part of the sequence in which *Pyrgulifera* was found in association with *Nerinea*, *Actaeonella* and *Omphalia*. There is one striking similarity between the Ajka and the Gosau formations: the species of *Pyrgulifera* were found in connection with the coal seams within the formations. We may interpret this as an indication that these beds were brackish or even freshwater depositions.

In elucidating all the presently available facts and their derivative interpretations, the present writer is led to conclude: first, that the species of *Pyrgulifera* existed in freshwater, or fresh-brackish water, the salinity of which was low, say less than five percent. It is probable that these animals had an unusual molecular concentration of their body fluids, which had a higher osmatic pressure than that of the true freshwater forms. The geographic background, where the species of *Pyrgulifera* existed, was probably a coastal plain estuary. Their habitat areas might vary in distance from the coast in different places mentioned above, though they were probably all within the lower course of a river. With the exception of the Gosau formation in Austria, species of *Pyrgulifera* were found in association with freshwater or brackish water species of invertebrates. In the Gosau formation, they were recorded with brackish water and marine invertebrates. But, this cannot be readily taken to suggest that *Pyrgulifera* had marine habitat. These species on the one hand could have actually existed in the brackish water habitat with a higher salinity, say 10 to 15 percent, and there are ample number of examples among the mollusks to indicate that some species of the same genus, say, *Hydrobia*, for example, live in freshwater habitat, while others live in

brackish water. At the same time, these species of *Pyrgulifera* could have been carried by strong descending currents from the inland waters. For their relationship with the other marine forms in the biotic assemblage, let us borrow the term from Wasmund (1926), is the thanatocoensis.

Geological and Geographical Distributions

The distribution of the species of *Pyrgulifera* in time is given in the following order from the Cenomanian stage at the base of Upper Cretaceous progressively to the younger stages:

(1) The Bear River formation which is exposed in southwestern part of Wyoming of the United States is of Cenomanian age. It contains one species, namely, *P. humerosa* (Meek), with abundance of generally well preserved individuals.

(2) The unnamed sequence in north of Cokeville, Wyoming, is partly contemporaneous and partly younger in age than that of the Bear River formation. These beds yield the following species and subspecies of the genus:

Pyrgulifera humerosa cokevillensis Yen,
Pyrgulifera stantoni White,
Pyrgulifera stantoni elongata Yen.

(3) The Woodbine formation is also of Cenomanian age and it is exposed in northeastern part of Texas of the United States. Species of *Pyrgulifera* were found at various members of the formation, and they are numerated below:

Pyrgulifera ornata Stephenson,
Pyrgulifera costata Stephenson,
Pyrgulifera costata tuberata Stephenson.

(4) The Gardonian formation is exposed in south and southeast of France and it is assigned to be of Upper Cenomanian age. One species was described, namely, *P. munieri* (Repelin).

(5) The Ajka formation is exposed in the western part of Hungary, and it contains the following species:

Pyrgulifera acutispira, spec. nov.,
Pyrgulifera compressa, spec. nov.,
Pyrgulifera compressa nodulifera, subspec. nov.,
Pyrgulifera protarmata, spec. nov.,
Pyrgulifera inflata, spec. nov.,
Pyrgulifera glabra (Hantken),
Pyrgulifera rickeri Tausch,
Pyrgulifera hantkeni Oppenheim.

Little new light has been cast on the age problem of the Ajka formation since Tausch (1886) and Oppenheim (1892) considered that the sequence was to be of Turonian to Senonian age. Later authors either were repeating the same confecture or merely avoided the issue by leaving it to be "Obere Kreide". A more critical study of the problem requires additional first hand paleontological and stratigraphical data. On basis of the presently available collections of specimens and literature, the present writer is convinced: First, that the Ajka formation is not contemporaneous with the *Pyrgulitera*-bearing beds of the Gosau formation in Austria. This conviction is supported by the fact that no conspecific forms of *Pyrgulifera* or any other genus has been reported in the two sequences, the localtions of which are separated by such a comparatively short distance. The so-called *P. pichleri* recorded from the Ajka beds is not identical with that species of the Gosau beds as it is pointed out elsewhere in this paper. Secondly, the Ajka formation possibly represents an intermediate stage between the Cenomanian

The Geological Distribution of *Pyrgulifera*

Species	The Bear River formation (Cenomanian)	The Cokeville Sequence (Upper Cenomanian)	The Woodbine formation (Cenomanian)	The Gardonian formation (Upper Cenomanian)	The Ajka formation (Santonian-Coniacian)	The Gosau formation (Campanian-Santonian)	The litnite beds, Les Martigues (Santonian-Campanian)	The lignite beds, Rognac (Maastrichtian)
Pyrgulifera humerosa	×	—	—	—	—	—	—	—
P. h. cokevillensis	—	×	—	—	—	—	—	—
P. stantoni	—	×	—	—	—	—	—	—
P. s. elongata	—	×	—	—	—	—	—	—
P. ornata	—	—	×	—	—	—	—	—
P. costata	—	—	×	—	—	—	—	—
P. c. tuberata	—	—	×	—	—	—	—	—
P. munieri	—	—	—	×	—	—	—	—
P. acutispira	—	—	—	—	×	—	—	—
P. compressa	—	—	—	—	×	—	—	—
P. c. nodulifera	—	—	—	—	×	—	—	—
P. protarmata	—	—	—	—	×	—	—	—
P. inflata	—	—	—	—	×	—	—	—
P. glabra	—	—	—	—	×	—	—	—
P. rickeri	—	—	—	—	×	—	—	—
P. hantkeni	—	—	—	—	×	—	—	—
P. pichleri	—	—	—	—	—	×	—	—
P. p. nassaeformis	—	—	—	—	—	×	—	—
P. spinosa	—	—	—	—	—	×	—	—
P. lyra	—	—	—	—	—	—	×	—
P. armata	—	—	—	—	—	—	—	×

(such as the Bear River and the Gardonian formations) on one side, and the Santonian to Campanian (the Gosau formation and lignite beds in southern France) on the other. It is probably somewhere between the post-Cenomanian and pre-Campanian. stages. And thirdly, the Ajka formation is probably older than the Gosau formation. This view is supported by the discovery that the Ajka beds yield more species of *Pyrgulifera* than the Gosau formation does. They also contain such extinct genera as *Dejanira* and *Strophostoma,* which are not found in the Gosau beds. The geo-historical development of the fauna seems to show that the species of *Pyrgulifera* had a prosperous time and wider range in geographic distribution in the early part of the Upper Cretaceous times. They gradually became either extinct in places or much reduced elsewhere in the later stages. Finally, they seem to be completely extinct throughout the Holarctic regions since the Maastrichtian times. It is reasonable to assume, therefore, that the Ajka formation may be placed somewhere between the Santonian and Coniacian ages. Such a view is well in accordance with the age assignment by Tausch (1886) and Oppenheim (1892).

(6) The Gosau formation has been well studied by several geologists and paleontologists in the preceding century, and more recently by Kerner-Marilaun (1934),

Brinkmann (1935) and Zapfe (1937). Kuhn (1947) has assigned different parts of the formation to different ages: his lower Gosau is Coniacian to lower Santonian; his middle Gosau is upper Santonian to Campanian; and his upper Gosau is Maastrichtian. The marl deposits with coal seams of the brackish water origin are included in his middle Gosau, and are considered to be Santonian to Campanian age. These deposits yield the following species of *Pyrgulifera*:

Pyrgulifera pichleri (Hoernes),
Pyrgulifera pichleri nassaeformis (Sandberger),
Pyrgulifera spinosa (Sandberger).

(7) The lignite beds in less Martigues of the lower Rhone basin, France, produces *Pyrgulifera lyra* (Matheron). According to Fabre-Taxy (1951), the species of *Pyrgulifera* were recorded together with an admixture of species of *Campylostylus, Corbicula, Unio*, etc. These beds were considered by Repelin (1902) as being of the Santonian and by Madame Fabre-Taxy as lower Campanian age.

(8) The lignite beds in Rognac also in the lower Rhone basin yields *P. armata* (Matheron), assigned to be of Danian age by Repelin. This age assignment was possibly meant the top of the Cretaceous. The remains of sauropod dinosaurs were recorded in the red clays of the Rognacian stage still within the cretaceous boundary. If so, this assignment could mean Maastrichtian age, since geologists in recent years are inclined to consider that the Danian sequence may actually represent the basal part of the Cainozoic Paleocene instead of the Mesozoic Cretaceous. While this view has not been generally accepted, it is worth careful consideration.

Descriptive account of species

It should be noted that only those species which are considered to be *Pyrgulifera*, are included in the present account. A number of forms either doubtful in identification or insufficiently known by records which have been referred to elsewhere in this paper, is not repeated here. The type lots of all the new species and subspecies described in this work are preserved in the collections of the Naturhistorisches Museum or the Paleontological Institute of the University, both in Vienna.

Pyrgulifera humerosa (Meek 1860) (Figs. 21, 22)

Melania humerosa, Meek, Proc. Acad. Nat. Sci. Phila., *v.* 12, p. 313, 1860; *Pyrgulifera humerosa*, Yen, U.S. Geol. Survey Prof. Paper 254-B, p. 54, pl. 17, fig. 12, 13, 1954.

This is an extremely common species at various localities of the Bear River formation, and they yield abundance of individuals, especially in the Shell Hallow locality, about 7 miles in north of Evanston, Wyoming, where they occured in a fissile shale bed. These specimens are generally well preserved except their outer lip margins being usually broken off.

Several records from European localities which were assigned to this species are erroneous. Its distribution, as far as the available records indicate, seems to be confined to the Bear River formation only.

Pyrgulifera humerosa cokevillensis Yen (Fig. 24)

Pyrgulifera humerosa cokevillensis, Yen, U. S. Geol. Survey Prof. Paper 254-B, p. 54, pl. 18, fig. 1, 1954.

This subspecies is well characterized by its much smaller size, narrower outline of shell, and bearing finer and closer nodulations on the angular shoulder than those of the forma typica of the species.

The enclosing deposits are located about 2 miles northeast of Cokeville, Wyoming, and some 60 miles in north of the Bear River formation localities. Its occurrence is less abundant in individuals, however, it is by no means uncommon.

Pyrgulifera stantoni White (Figs. 25, 26)

Pyrgulifera stantoni, White, U.S. Geol. Survey Bulletin, 128, p. 57, pl. 9, fig. 1–3, 1895; Yen, U.S. Geol. Survey Prof. Paper 254-B, p. 54, pl. 17, fig. 14, 15, 1954.

The outstanding differences between this species and P. humerosa are its much smaller size, more elongated outline of shell, having spire much greater than the body whorl, and bearing well developed and more closely spaced ribs extending over the upper two-third of the body whorl.

Pyrgulifera stantoni elongata Yen (Fig. 23)

Pyrgulifera stantoni elongata, Yen, U.S. Geol. Survey Prof. Paper 254-B, p. 54, pl. 17, fig. 16; pl. 18, fig. 2.

This subspecies differs from the preceding species by its elongately subfusiform shape and having acutely turrited spire and descending body whorl. The sculpture is much less prominently developed. The apical whorls of most of the species of *Pyrgulifera* are usually not preserved, however, a few specimens of the younger stages of this form show their apical whorls in melanoid appearance.

Pyrgulifera ornata Stephenson

Pyrgulifera ornata, Stephenson, U.S. Geol. Survey Prof. Paper 242, p. 159, pl. 37, fig. 1, 2, 1953.

The Woodbine formation in northeast of Texas.

Pyrgulifera costata Stephenson

Pyrgulifera costata, Stephenson, U. S. Geol. Survey Prof. Paper 242, p. 158, pl. 37, fig. 14, 15, 16, 1953.

The Woodbine formation in northeast of Texas.

Pyrgulifera costata tuberata Stephenson

Pyrgulifera costata tuberata, Stephenson, U. S. Geol. Survey Prof. Paper 242, p. 158, pl. 37, fig. 3, 4, 1953.

The Woodbine formation in northeast of Texas.

Pyrgulifera acutispira, spec. nov. (Figs. 9, 16, 19, 20)

Shell broadly ovate in outline, of thick substance and narrowly furrowed in the umbilical area. The spire is highly turrited and the body whorl is reduced at the base and descending at the aperture. The apical whorls appear melanoid, and the later ones are well angular along the shoulder. The surface of the earlier whorls bears fine decussation of riblines and spiral lines. The nodulations appear gradually along the shoulder, then developing either into nodular tubercles, produced or subdued spines on the penult and body whorls. The aperture is of broadly ovate form, having inner lip margin

thickened but well defined and being sinuous between columellar and basal margins. The holotype measures 23.4 in altitude of shell, 16.0 in width; 11.2 in height of aperture and 8.0 in width.

This species was considered by Tausch as his "between *P. pichleri* and *P. lyra*," and "between *P. pichleri* and *P. armata*."

The species is decidedly different by size and sculpture from *P. pichleri* and *P. nassaeformis*. It has some superficial resemblance of *P. spinosa*, but it is readily distinguished from that species by its more markedly angular shoulder and the surface features on the whorls of the spire.

Pyrgulifera compressa, spec. nov. (Fig. 5)

Shell broadly subfusiform in outline and thick, having an acutely turrited spire. The early whorls are obtusely and later ones more strongly angular along the shoulder. The nodulations are only faintly traceable on the spire whorls, and they become prominent on the body whorl, on which well developed and heavy ribs extend from the suture to the base. The spiral lines appear faintly over the interspaces of the ribs. The aperture is descending, of ovate shape, and the inner lip margin is thickened and well defined, bearing a well developed anterior sinus below. The holotype measures 26.5 in altitude of shell, 16.0 in width; 10.5 in height of aperture and 8.0 in width.

This species was considered by Tausch to be forms "between *P. glabra* and *P. rickeri* to *P. pichleri*." Again the features of its earlier whorls are markedly different from those of *P. pichleri*, and its well developed sculpture separate it from *P. glabra* and *P. rickeri*.

Pyrgulifera compressa nodulifera, subspec. nov. (Figs. 6, 11)

This subspecies is characterized by its broader outline of shell, less pronounced nodulations on the shoulder, less prominent ribs on the body whorl. The nodulations are very obscure on the spire whorls and they are only noticeable along the shoulder of the body whorl. Some of the ribs are partially developed, but the spiral lines are better visible. The aperture is broader and its inner lip margin is thinner. The holotype measures 25.5 in altitude of shell, 18.0 in its width; 13.0 in height of aperture and 10.5 in its width.

Pyrgulifera protarmata, spec. nov. (Fig. 7)

Shell of smaller size than that of the preceding species, of thick substance. The spire has about the same height of the body whorl. The features of the earlier whorls are closely similar to those of the previously mentioned forms. The sculpture of the later whorls is much simpler. The shoulder angulation is well marked by a spiral carina and a couple of well developed spiral lines. The riblines are very obscure. The aperture is subovate in outline, outer lip margin sharp and inner lip margin thickened. The anterior sinus is faint.

The umbilical area is openly furrowed. The holotype measure 18.6 in altitude of shell, its width 13.0; 8.5 in height of aperture and 6.8 in width.

This species is characterized by its simpler scultpure. The tubercles on the shoulder are only faintly traceable along a well developed spiral carina, and a few coarse and distinct spiral lines appear above and below close to the shoulder carination, and also around the umbilical area. Otherwise both the spiral and rib lines are faint although not absent.

Pyrgulifera inflata, spec. nov. (Fig. 8)

Shell broadly ovate in outline, of thick substance, having a turrited spire and inflated body whorl. The spire is about one-fifth shorter than the body whorl. The sculpture of the earlier whorls are closely similar to that of *P. acutispira*, but the last four are increasing gradually in size, bearing two prominent spiral carinae along the shoulder angulation and numerous coarse and fine spiral lines. The two carinae are developed into two spiral series of tubercles on the shoulder of the body whorl, in addition to faintly developed spiral and rib lines which are marked above and below the shoulder angulation. The aperture is broadly ovate in outline, somewhat produced below, outer lip margin sharp and inner lip thickened and defined. The holotype measure 22.3 in altitude of shell, 16.8 in width; 12.5 in height of aperture and 10.0 in width.

This species is characterized by its broadly turrited spire, inflated body whorl, and its two series of tubercles along the shoulder angulation, which do not extend over the surface of the body whorl as that in *P. compressa*.

Pyrgulifera glabra (Hantken) (Figs. 10, 12, 13)

Paludomus pichleri var. *glabra*, Hantken, Die Kohlenflötze und Kohlenbergbau, S. 179, 1878; Tausch, SB. Akad. Wiss. Wien, *v.* 90, S. 64 t. 1, fig. 1, 2, 1885; Abh. Geol. Reichsanst., *v.* 12, S. 5, t. 1, fig. 1, 2, 3, 1886.

This species resembles *P. protarmata* in size and shape of the shell, however, it differs characteristically in pattern of the sculpture on the last couple of whorls. Instead of having a faintly tubercled spiral carina along the shoulder angulation, it bears two well developed and distinct spiral lines along the angulated shoulder and few weaker ones above and below the angulation. The features of the earlier whorls are much similar to those of the other species.

Pyrgulifera rickeri Tausch (Figs. 14, 15)

Pyrgulifera rickeri, Tausch, SB. Akad. Wiss. Wien, *v.* 90, S. 66, t. 2, fig. 6, 6a, 7, 1885.

This species is characterized by its pattern of sculpture on the larger whorls. The shoulder angulation is strongly developed, and the shoulder shelf is moderately wide, well excavated, and prominently marked. The sculpture and the turrition of the earlier whorls are much similar to those of *P. protarmata* and *P. glabra*.

Pyrgulifera hantkeni Oppenheim

Pyrgulifera hantkeni, Oppenheim, Z. Deutsch. Geol. Ges., *v.* 44, S. 745, t. 34, fig. 1, 1a, 1892.

This species is known only by Oppenheim's brief description and illustrations. I have not been able to uncover any specimen of this species in the collections of the Ajka material in Vienna. The species was described from Csingerthal bei Ajka."

Judged by the original record, there seems to be little doubt that it is a species of *Pyrgulifera,* which is probably related to the preceding species. Further study of the type-lot material should be necessary before this record can be definitely established.

Pyrgulifera pichleri (Hoernes) (Figs. 1, 2)

Melanopsis pichleri, Hoernes in: Pichler, Jahrb. k.k. geol. Reichsanst., *v.* 7, S. 735, 1856; *Tanalia pichleri,* Stoliczka, SB. Akad. Wiss. Wien, *v.* 38, S. 487, t. 1, fig. 7, 8, 1860; *Pyrgulifera pichleri,* Tausch, SB. Akad. Wiss. Wien, *v.* 90, S. 62, t. 1, fig. 7, 8, 9, 1885.

This species was first described without figure by the author as *Melanopsis* from the Gosau beds exposed in Brandenberg of north Tirol. It was transferred into *Tanalia* by Stoliczka, who gave five figures to illustrate 4 specimens which were assigned by him to this species. Only his figures 7 and 8 represent this species, while the others (6a, 6b, and 9) belong to *Buccinum acinosum* Zekeli (1852), which is not a species of *Pyrgulifera.*

His ill-proposed combination together with his application of priority law led Stoliczka (1865) to treat *P. pichleri* as a synonym of *B. acinosum* Zekeli. This issue was cleared up by Sandberger (1875), who assigned the species to *Paludomus,* and also separated those forms with stronger and sharply developed tubercles along the shoulder angulation as a variety of this species named as *spinosa.*

This species is characterized by its smaller size than most of the species of the genus, its broadly turrited spire, and bearing prominent ribs on surface of the body whorl together with sharp tubercles along its shoulder angulation. The spiral sculpture is also clear and distinct, but it is in form of coarse lines only.

Pyrgulifera pichleri nassaeformis (Sandberger) (Fig. 4)

Paludomus pichleri var. *nassaeformis,* Sandberger, Die Land- und Süßwasser-Conchyl., S. 76, t. 3, fig. 9, 9a, 1875.

This subspecies or variety differs from its preceding species by its higher spire, much more heavily developed ribs and stronger spiral lines. The interspaces between the ribs are also wider, and the shoulder angulation is less sharply marked.

Pyrgulifera spinosa Sandberger (Fig. 3)

Paludomus pichleri var. *spinosa,* Sandberger, Die Land- und Süßwasser-Conchyl., S. 76, t. 3, fig. 7, 7a, 1875; *Pyrgulifera spinosa,* Oppenheim., Z. Deutsch Geol. Ges., *v.* 42, S. 744, t. 33, fig. 12, 1892.

This species has the features of its earlier whorls more closely similar to those of the preceding two forms, however, it differs from either one by its higher spire (the spire is slightly greater than the body whorl), and its well developed spiny tubercles along the shoulder angulation of the body whorl. The shoulder shelf is moderately wide and more or less concave. The whorl

surface below the shoulder bears only faint spiral lines and growth striae. The aperture is ovate in outline: outer lip margin often broken off, inner lip margin well thickened.

Pyrgulifera lyra (Matheron)

Melanopsis lyra, Matheron, Catalogue méthod., Rep. trav. Soc. Statis. Marseille, *v.* 6, p. 221, pl. 37, fig. 8, 9, 1842; *Pyrgulifera lyra,* Fabre-Taxy, Am. Paleontologie, *v.* 37, p. 112, pl. 2, fig. 7, 1951.

Madame Fabre-Taxy has recently reviewed well the material of this species from the lignite beds in les Martigue and the vicinal regions. Although it was described originally under *Melanopsis,* this and the following species constitute the first known records of *Pyrgulifera.*

The species is characterized by its closely spaced, distinct riblets which extends over nearly the entire body whorl. The fine riblets remind one the strings of an instrument. The shoulder shelf is narrow however it is present, and the fine tubercles along the shoulder angulation are distinct. The features of its earlier whorls together with the more closely spaced riblets and narrower shoulder shelf can readily differentiate this species from some of the Ajka specimens, which had been taken to represent this species by some earlier authors.

Pyrgulifera armata (Matheron)

Melanopsis armata, Matheron, Rep. trav. Soc. Statis. Marseille, *v.* 6, p. 222, pl. 37, fig. 12, 13, 1842; Tausch, SB. Akad. Wiss. Wien, *v.* 90, S. 64, t. 1, Fig. 13, 1885; Fabre-Taxy, Ann. Paleontologie, *v.* 37, p. 112, 1951.

This species is readily distinguished from the preceding one by their distinct differences in sculpture. Such differences are well illustrated by Matheron's original figures, which appear to be faithfully and correctly done, and they are also remarked by Madame Fabre-Taxy.

It is characterized by its highly turrited spire which is greater than the body whorl, sharply angulated shoulder, moderately broad shoulder shelf, and fine but sharp tubercles on the shoulder.

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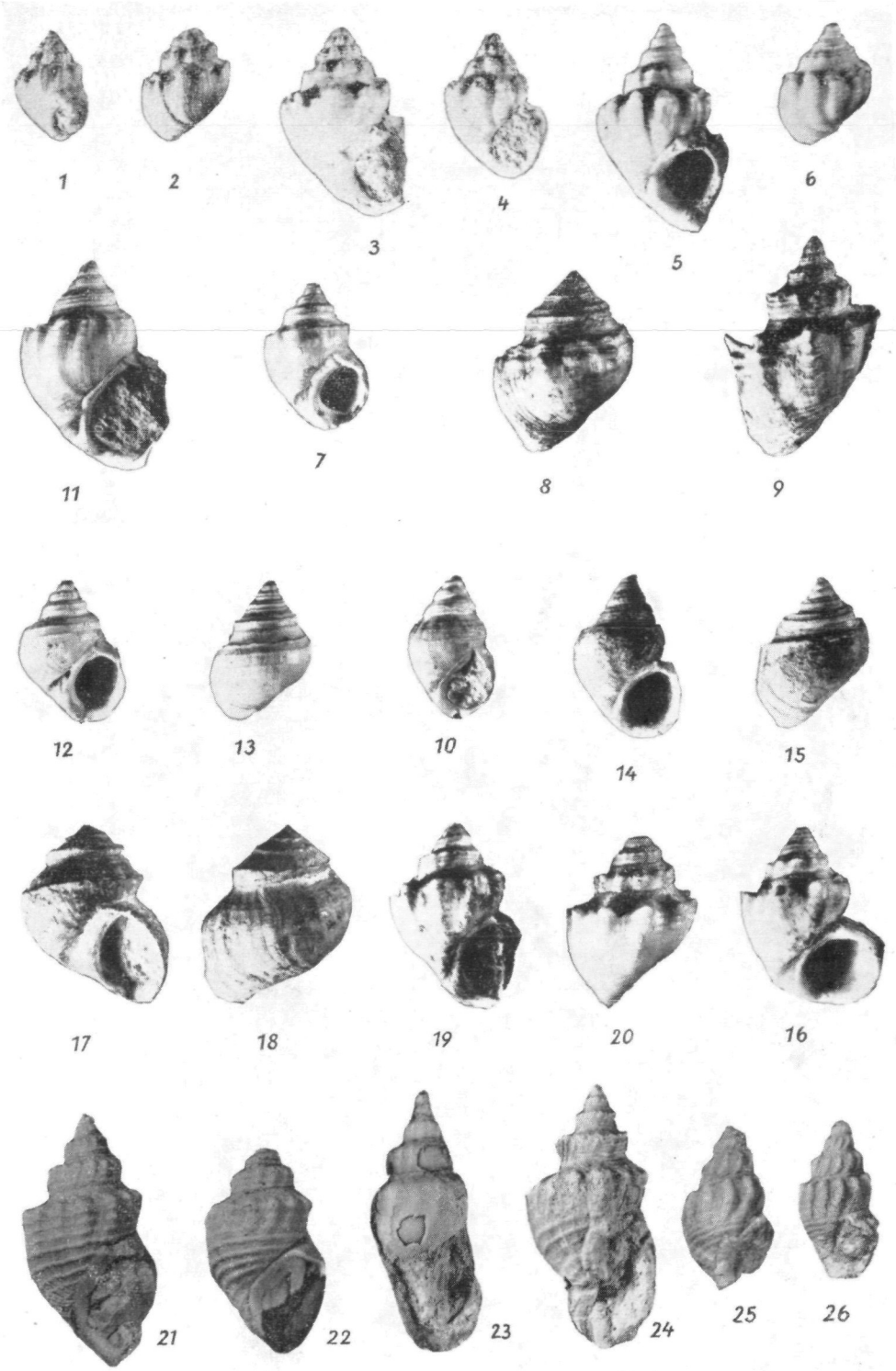

Explanations of plate

Figs. 1, 2. *Pyrgulifera pichleri* (Hoernes) — from the Gosau formation at Brandenberg, North Tirol, Austria. — Fig. 3. *Pyrgulifera spinosa* (Sandberger), same as the preceding species. — Fig. 4. *Pyrgulifera pichleri nassaeformis* (Sandberger), same as the preceding species. — Fig. 5. *Pyrgulifera compressa,* spec. nov., from the Ajka formation at Csingerthal, Ajka, Western Hungary. — Fig. 6, 11. *Pyrgulifera compressa nodulifera,* subspec. nov., same as the preceding species. — Fig. 7. *Pyrgulifera protarmata,* spec. nov., same as the preceding species. — Fig. 8. *Pyrgulifera inflata,* spec. nov., same as the preceding species. — Figs. 9, 16, 19, 20. *Pyrgulifera acutispira,* spec. nov., same as the preceding species. — Figs. 10, 12, 13. *Pyrgulifera glabra* (Hantken), same as the preceding species. — Figs. 14, 15. *Pyrgulifera rickeri* Tausch, same as the preceding species. — Figs. 17, 18. "*Pyrgulifera*" *ajkaensis* Tausch, same as the preceding species; showing the differences in general shape, spire and sculpture from those of true species of *Pyrgulifera.* — Figs. 21, 22. *Pyrgulifera humerosa* (Meek), from the Bear River formation at the shell Hallow Locality, about 7 miles north of Evanston, Wyoming. X 1. — Fig. 23. *Pyrgulifera stantoni elongata* Yen, from the Cokeville beds on north side near the mouth of the Third Creek, Lincoln County, Wyoming. X 2. — Fig. 24. *Pyrgulifera humerosa cokevillensis* Yen, from the Cokeville beds at about 2 miles northeast of Cokeville, Wyoming. X 2. — Figs. 25, 26. *Pyrgulifera stanton* White, same as the preceding subspecies. X 1. — The figures 1 to 20 are slightly enlarged than the natural size of the specimens.