

Succession and Speciation of the Pelecypod *Aucella*

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Succession and Speciation of the Pelecypod *Aucella*

By RALPH W. IMLAY

SHORTER CONTRIBUTIONS TO GENERAL GEOLOGY

GEOLOGICAL SURVEY PROFESSIONAL PAPER 314-G

*A study of the utility of the pelecypod
Aucella for mapping rock units in the
Pacific coast region and in Alaska*



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SUCCESSION AND SPECIATION OF THE PELECYPOD *AUCELLA*

BY RALPH W. IMLAY

ABSTRACT

The pelecypod *Aucella*, of latest Jurassic and earliest Cretaceous age, has been subdivided into more than a hundred species on the basis of minor differences without allowing for biological variation, or for variation due to crowding that is normal for an attached gregarious pelecypod. As a result, in any large collection from a single locality, specimens can be selected that fit the definitions of a number of species and yet these so-called species are connected by many specimens showing transitional characteristics. Such an association appears, therefore, to represent a single variable population. If the species of *Aucella* are defined making allowance for variation, the number of species is greatly reduced, but the specific concepts can be grasped readily by geologists and used for mapping purposes. Seven zones based on species of *Aucella* can now be recognized easily in the field in North America, as has been demonstrated by geologists of the U. S. Geological Survey.

INTRODUCTION

Until a few years ago the pelecypod *Aucella* was considered by paleontologists of the U. S. Geological Survey to be of very little stratigraphic value in the study of the Mesozoic. Its presence denoted mainly that the beds in which it occurred were not older than the late Oxfordian stage of the Jurassic or younger than the Hauterivian stage of the Cretaceous. Aucellas from the west coast or Alaska that were small and elongate and had slender, highly incurved beaks were generally compared to, or referred to, *A. piochii* (Gabb) and were assigned questionably to the latest Jurassic Portlandian stage. Aucellas that were medium to fairly large, rounded in outline, and very robust were generally identified as, or compared with, *A. crassa* Pavlow or *A. keyserlingi* Lahusen and assigned a probable Early Cretaceous age. Aucellas that were medium to large, elongate, highly convex, and had a constriction ventral to a swollen umbonal part of the shell were generally identified as *A. crassicollis* Keyserling and assigned an Early Cretaceous age.

One reason for doubting the stratigraphic usefulness of the species of *Aucella* was that in any large collection from a single locality a number of species of *Aucella* could generally be recognized by selecting specimens that fitted the definitions of various species and by disregarding other specimens that had slightly different characteristics. Such diversity of species seemed

unreasonable. As a result not only the validity of the species of *Aucella* as defined was questioned, but, also, the age assignments made for those species.

Such uncertainties concerning the stratigraphic value of Aucellas might have continued indefinitely except for persistent requests for aid from many geologists of the Geological Survey who have been mapping *Aucella*-bearing beds in Alaska and in the west coast States. In both areas the need arose to trace the boundary between the Jurassic and Cretaceous systems, to help identify certain formations by means of fossils in areas of complex structures, to help subdivide sequences involving thousands of feet of strata, to correlate those subdivisions over considerable distances, and to interpret the stratigraphic succession in terms of geologic history as revealed by faunal changes. In both areas Aucellas were the only fossils sufficiently abundant and widespread for purposes of tracing systematic and formational boundaries. Evidently a stratigraphic evaluation of *Aucella* was necessary in order to solve certain geological problems.

Before undertaking such an evaluation, the writer first read many papers dealing with *Aucella*. Two of them were found to be of particular importance. One was a fairly short but well documented and illustrated discussion by Pompeckj (1901) on the characteristics, origin, distribution, and biological relationships of *Aucella*. The other was a comprehensive discussion by Pavlow (1907) in which he summarized everything that had been published previously concerning Aucellas, redescribed and reillustrated all known species, and described many new species. Many of the older species were divided into a number of new species. Reassignments of species were made with great positiveness on the basis of illustrations only. His descriptions were detailed and clearly written; characteristics that might be used to differentiate similar appearing species were discussed fully; and the stratigraphic ranges of the various species were presented adequately. Pavlow's treatment of his subject was masterly and thorough.

Most publications on *Aucella* published since 1907 have dealt with the Aucellas of particular areas. In

general, European paleontologists dealing with Eurasian *Aucellas* have coined few new species and have tended to reduce the number of recognized species. In contrast American paleontologists since 1907 have accepted as valid all the species described by Pavlow and have added many more.

The name *Aucella* was ruled invalid in favor of *Buchia* in 1957 by the International Commission on Zoological Nomenclature (Opinion 492). This decision was received too late to make modifications herein.

DEFINITION OF THE GENUS AUCELLA

The genus *Aucella*, as discussed by Pompeckj (1901, p. 325-332) and Pavlow (1907, p. 8-11), has an obliquely elongated, inequivalved shell. Its beaks are inclined forward and are more or less twisted forward. The beak of the left valve is more prominent than the beak of the right valve and rises above and generally over the right valve. On the right valve, the anterior ear is short and triangular in shape. The posterior ear is a little longer and either merges evenly into the body of the shell or is separated from the main body of the shell by a hollow groove. The byssal notch is long and narrow. The surface of the shell is covered with concentric ribs, or radial striae, or both. The cardinal plate is short, straight, or nearly straight, and mostly posterior to the beak. Its posterior part is occupied by a long, triangular ligamental groove and its anterior part by a notch. Teeth are absent.

ORIGIN AND ECOLOGY OF AUCELLA

Concerning the origin of *Aucella*, Pompeckj (1901, p. 333-351) pointed out that the earliest species, in beds of Oxfordian age, were very similar to associated pelecypods that he referred to the genus *Pseudomonotis*, but which are now called *Meleagrinnella* (equals *Echinotis* Marwick as discussed by Cox, 1940, p. 90, 91). He considered that *Aucella* developed from *Pseudomonotis* by shortening of the ears and cardinal area, by the beaks becoming inclined forward, by the beak of the left valve becoming more prominent, by the development of a distinct articulating groove on the hinge of the left valve, and by concentric ribbing becoming more prominent than radial ribbing.

The origin of *Aucella* from *Meleagrinnella* (equals Jurassic species of *Pseudomonotis*) as suggested by Pompeckj is in harmony with the inference that both genera preferred the same kind of hard substratum on which to attach themselves. *Meleagrinnella* before the appearance of *Aucella*, lived in abundance on the surfaces of sediments that gave rise to thin beds of limestone, sandy limestone, sandstone, and conglomeratic sandstone. In the western interior region it is com-

monly associated with *Ostrea* in sandy beds and with *Camptonectes*, or rarely with *Gryphaea*, in limestone beds. In southwestern and south-central Alaska in the Middle Jurassic (Bajocian) beds it is associated with such pelecypods as *Trigonia*, *Inoceramus*, *Gervillia*, *Modiolus*, *Pleuromya*, *Ostrea*, *Astarte*, and various genera of pectens (Martin, 1926, p. 146-148). In overlying sandy beds of late Oxfordian and Kimmeridgian ages it is associated with *Aucella*, *Pleuromya*, *Astarte*, *Trigonia*, and various pectens (Martin, 1926, p. 177, 178, 214-217), but *Aucella* occurs in much greater numbers than all the other genera. The resemblance of *Meleagrinnella* to *Aucella*, its occurrence in similar kinds of rocks, its scarcity after the appearance of *Aucella*, and its disappearance early in the Early Cretaceous suggests that both genera lived under similar environmental conditions and that *Meleagrinnella* was crowded out by *Aucella*.

Aucella thrived apparently on hard bottoms in shallow, much agitated waters. Pompeckj (1901, p. 332) attributed to agitation the smooth surface on the anterior side of the umbone of many left valves. Such an environment is indicated by the abundance of *Aucella* on hard surfaces of attachment as discussed above, and its scarcity in thick units of siltstone except for widely separated, thin, coquinoïd layers. It is indicated, according to the writer's observations, by the failure of *Aucella* and *Inoceramus* to occur together in the same bed. In fact in Alaska they have never been found associated in the same formation. Considering that species of *Inoceramus* are noted for being facies breakers and are found in most kinds of sediments except those that are conglomeratic, it appears that *Aucella* either lived in shallower waters than *Inoceramus* or that wherever it lived *Inoceramus* could not obtain a foothold. These possibilities are not mutually exclusive.

It has, also, been observed that *Aucellas* may become uncommon or disappear along the strike of certain beds even though lithologic characteristics have not changed. Such a relationship may be explained by an increase in depth of the sea bottom, by an increase in rate of sedimentation, or by lack of a hard substratum. Of course, the presence of only a few specimens of *Aucella* in a thick unit might be explained by submarine slumping and does not prove that the unit was deposited in shallow water.

SPECIATION IN AUCELLA

RANGE OF VARIATION WITHIN AUCELLAN SPECIES

With the various publications by Pompeckj, Pavlow and other paleontologists as background information, the writer attempted to identify the species of *Aucella*

present in the Geological Survey collections from Alaska, California, and Oregon. At first many names were used. Then it was realized that most specimens could be placed easily in a few distinctive species, and that most of the remaining specimens were either deformed, immature, or poorly preserved or were connected with one of the species by specimens having transitional characteristics.

Fortunately it was possible to test these ideas concerning species of *Aucella* in the field where hundreds of specimens could be examined at many localities and at many stratigraphic levels. As a result the writer became convinced that Stanton's (1895, p. 42-47 [1896]) idea that only a few species of Aucellas were present in the west-coast Mesozoic rocks was more nearly correct than Pavlow's idea that many species were present. It became apparent that neither Pavlow (1907) nor Anderson (1938, 1945) took into account the variations in shape, size, and ornamentation that occurred in a single *Aucella* population under different degrees of crowding. When allowance was made for such variations, it was found that the species were greatly reduced in number, but that they could be defined in such a manner as to be easily recognized by field geologists and used for mapping purposes. Such has been demonstrated in both Alaska and Oregon.

Most of the specimens of *Aucella* from North America that have been described can be accommodated in the few species listed on table 1.

AUCELLA CONCENTRICA (SOWERBY)

Aucella concentrica (Sowerby) (see pl. 16, figs. 1-7) includes the specimens referred to *A. bronni* (Roullier), *A. erringtoni* (Gabb) in Meek (1865, p. 479-480, pl. 1, fig. 2), *A. elongata* Hyatt, and *A. aviculaeformis* Hyatt (Martin, 1926, p. 177, 216; Hyatt, 1894, p. 430-434; Pavlow, 1907, p. 14, 82; Crickmay, 1933, p. 53-56; Imlay, 1955, p. 83). A subspecies, *A. concentrica leguminosa* Stoliczka (Holdhaus, 1913, p. 405-408, pl. 97, figs. 5a-d), has been recorded from the west side of Vancouver Island in the lower part of the range of *A. concentrica* (Sowerby) (Jeletsky, 1950, p. 27-29). It has also been found on the west side of Katmai Bay (pl. 16, figs. 8-10) on the Alaskan Peninsula (USGS Mes. locs. 3124 and 3127) associated with *A. concentrica*. This subspecies differs from the typical species by being much more elongated posteriorly and by the umbones on both valves being considerably inflated. Its stratigraphic position on Vancouver Island suggests that its range is late Oxfordian.

AUCELLA SPITIENSIS HOLDHAUS

Aucella spitiensis Holdhaus (pl. 16, figs. 11-17) has been recorded from northern Alaska in association with *A. concentrica* and the ammonite *Amoeboceras* (Imlay, 1955, p. 84, pl. 9, figs. 1-10). This association shows that *A. spitiensis* existed in late Oxfordian or early Kimmeridgian time. It has been obtained in talus collections (USGS Mes. locs. 3124 and 3127) from the Alaskan Peninsula. Another record of *A. spitiensis*, or of a closely similar species, is from the west side of Vancouver Island in the upper part of the range of *A. concentrica* (Sowerby) (Jeletsky, 1950, p. 28, 29), above beds containing *A. concentrica leguminosa* Stoliczka. Jeletsky (1950, p. 31, 32) suggests that the beds containing *A. spitiensis* are of early Kimmeridgian age.

AUCELLA RUGOSA (FISCHER) AND A. MOSQUENSIS (VON BUCH)

Aucella rugosa (Fischer) (pl. 16, figs. 18, 19, 22-25) and *A. mosquensis* (von Buch) (pl. 16, figs. 20, 21) are widespread in Alaska in beds that the writer considers to be of middle Kimmeridgian to early Portlandian age (Imlay, 1955, p. 74, 75, 85). *A. mosquensis* may range a little higher than *A. rugosa*, however, into beds of middle Portlandian age. In Mexico it has been reported with the ammonites *Kossmatia* and *Durangites* (Burckhardt, 1912, p. 206, 221, 236). In California a few specimens similar to *A. mosquensis* have been found in the lower and middle parts of the Knoxville formation (Anderson, 1945, p. 940, 966). These specimens are possibly an aberrant variety of *A. piochii* (Gabb), but they have stouter umbones and shorter, less incurved beaks than is typical of that species. Their possible identity with *A. mosquensis* needs to be confirmed, however, by further collecting in the lower part of the Knoxville formation.

One consideration suggesting caution in identifying *Aucella mosquensis* in the Knoxville formation is its constant association with *Aucella rugosa* (Fischer) in Alaska. Of the two species, *A. rugosa* is much more abundant. In contrast not a single specimen of *A. rugosa* has been recorded from the west coast of the United States. Its absence, however, is in harmony with the absence of ammonites of middle Kimmeridgian to early Portlandian age in that area and is part of the evidence for dating the duration of the Nevadan orogeny of southwestern Oregon and northern California.

AUCELLA PIOCHII (GABB)

Aucella piochii (Gabb) (1864, p. 187, pl. 25, fig. 173) (see pl. 17, figs. 7-10, 12-29) was redescribed by

TABLE 1.—Characteristic

Species	Relative size for genus	Shape of valve			Beak of left valve
		Cross section	Left valve	Right valve	
<i>Aucella concentrica</i> (Sowerby)-----	Medium to large.	Nearly equivalved, compressed.	Gently convex on umbones, flattened posteriorly, elongated obliquely.	Slightly less convex than left valve.	Small, low, curved inward slightly over beak of right valve.
<i>Aucella spitiensis</i> Holdhaus-----	Medium....	Inequivalved, compressed.	Weak to gently convex, elongated obliquely.	Nearly flat to gently convex.	Short, stout, gently incurved over beak of right valve.
<i>Aucella rugosa</i> (Fischer)-----	...do.....	Highly inequivalved, moderately convex.	Moderately convex, elongated posteriorly.	Gently convex to nearly flat.	Moderately long and incurved.
<i>Aucella mosquensis</i> (von Buch)-----	...do.....	...do.....	Strongly convex, elongated posteriorly.	Gently convex.....	Long, much incurved, slightly twisted forward.
<i>Aucella piochii</i> (Gabb)-----	Small.....	Inequivalved, moderately convex.	...do.....	...do.....	Long, slender, much incurved, slightly twisted forward.
<i>Aucella fischeriana</i> (d'Orbigny)-----	Medium....	...do.....	Moderately convex, elongated posteriorly.	...do.....	Narrow, not very prominent, gently incurved.
<i>Aucella subokensis</i> Pavlow-----	Fairly large.	Inequivalved, fairly stout.	Moderately convex, considerably elongated, trigonal in outline.	Moderately convex.....	Fairly stout, curved over beak of right valve.
<i>Aucella okensis</i> Pavlow-----	Large.....	Inequivalved, stout.....	Strongly convex, moderately elongated, ovate in outline.	...do.....	Stout, curved over beak of right valve.
<i>Aucella volgensis</i> Lahusen.....	...do.....	Inequivalved, fairly stout.	Strongly convex, elongated posteriorly.	...do.....	Stout, moderately incurved, slightly twisted forward.
<i>Aucella sublaevis</i> Keyserling-----	Small.....	Slightly inequivalved, plump.	Strongly convex, ventral margin truncated.	Strongly convex, ventral margin truncated.	Small, pointed, projecting.
<i>Aucella crassicolis</i> Keyserling-----	Medium to large.	Moderately inequivalved, very stout.	Strongly convex, elongated in adult.	Strongly convex, elongated in adult.	Elongated, strongly incurved.

Stanton (1895, p. 42-44 [1896]) and restricted to Aucellas whose left valves have a slender, obliquely ovate shape, a prominent, narrow umbo, a strongly incurved beak, and fairly regular weak concentric ribs and undulations. He noted that a few specimens have faint radiating striae. The species as defined by Stanton was subdivided into the following species by Pavlow (1907, p. 82, 83) on the basis of Stanton's publication and of fossils that Stanton sent to the University of Moscow:

- Aucella gabbi* Pavlow (1907, p. 54; Gabb, 1864, p. 187, pl. 25, fig. 173; Stanton, 1895, pl. 4, figs. 2, 3, 5 [1896]).
russiensis Pavlow (1907, p. 50, 83; White, 1888, pl. 3, figs. 10, 11 [1889]).
stantoni Pavlow (1907, p. 48; Stanton, 1895, pl. 4, figs. 6, 7 [1896]).
uncitoides Pavlow (1907, p. 61, 83; Stanton, 1895, pl. 4, fig. 14 [1896]).
andersoni Pavlow (1907, p. 57, pl. 4, fig. 7; Stanton, 1895, pl. 4, fig. 8 [1896]).
subinflata Pavlow (1907, p. 67, pl. 6, fig. 4a-c).
tenuicollis Pavlow (1907, p. 49, pl. 3, fig. 6).
hyatti Pavlow (1907, p. 49, pl. 3, figs. 10a, b).

In addition, one specimen figured by Stanton (1895, pl. 4, fig. 14 [1896]) as *Aucella piochii* var. *ovata* was placed by Pavlow (1907, p. 61, 83) in a new species, *A. uncitoides* Pavlow. The writer considers the specimen in question to be merely an usually large specimen of *A. piochii* (see pl. 17, figs. 12, 29) that lived under conditions favoring its growth.

All these species were accepted by Anderson (1945, p. 964-973), and the following were added.

- Aucella gracilis* Pavlow of Anderson (1945, p. 967, pl. 3, fig. 22a-c).
attenuata Anderson (1945, p. 970, pl. 12, fig. 4a-c).
elderensis Anderson (1945, p. 967, pl. 4, figs. 1-4).
knovillensis Anderson (1945, p. 966, pl. 3, figs. 12-14, pl. 4, fig. 6).
 aff. *A. bononiensis* Pavlow (Anderson, 1945, p. 967, pl. 4, fig. 11a-d).
 cf. *A. bononiensis* Pavlow (Anderson, 1945, p. 968, pl. 6, fig. 5).
terebratuloides Lahusen in Anderson (1945, pl. 13, figs. 7a, b).
russiensis Pavlow in Anderson (1945, p. 968, pl. 3, fig. 21).

Thus an assemblage of Aucellas from the Knoxville formation of Jurassic age that Stanton considered a single species was subsequently subdivided into 15 species. Apparently Stanton had an entirely different concept of a species than either Pavlow or Anderson. This difference in the writer's opinion reflects differences in training, in amount of fieldwork, and in stratigraphic application. Stanton was a practical geologist concerned with the stratigraphic usefulness of fossils. He spent several months in the field each year during most of his active life. He made superb fossil collections. His field notes dealing with stratigraphy are thorough and are still very useful. He recognized differences among the specimens of *Aucella* that are common in the Jurassic Knoxville formation, but as-

North American species of Aucella

Concentric markings		Radial markings		Ranges		
Ribs	Undulations and constrictions	Ribs	Striae	Northern Eurasia	Alaska	Oregon and California
Sharp, regular, fairly low.	Weak undulations on some large specimens.	None.....	Fine, dense, continuous across concentric ribs.	Late Oxfordian to middle Kimmeridgian.	Late Oxfordian to middle Kimmeridgian.	Late Oxfordian? to early Kimmeridgian.
Irregular in strength and spacing.	Irregular, conspicuous.....	do.....	Weak, scattered, mostly on umbones.	Late Oxfordian to Kimmeridgian.	Late Oxfordian to early Kimmeridgian.	Not identified.
High, narrow, widely and regularly spaced.	Uncommon.....	do.....	Very fine, dense.	Late Kimmeridgian to early Portlandian.	Middle Kimmeridgian to early Portlandian.	Do.
Low, variable in strength, irregularly spaced.	Common, irregularly spaced, conspicuous.	do.....	Fairly fine, scattered, not evident on some specimens.	do.....	Middle Kimmeridgian to early(?) Portlandian.	Not definitely identified.
do.....	Fairly common, irregular, weak.	Uncommon, weak, scattered.	None.....	Portlandian (mainly middle and late).	Portlandian.....	Middle to late Portlandian.
Sharp, low, widely spaced, some shells nearly smooth.	None.....	None.....	do.....	Middle to late Portlandian (most common in late Portlandian).	Not identified.....	Middle? to late Portlandian.
Sharp, fairly high, moderately spaced.	do.....	do.....	do.....	Late Jurassic? (Riasanites Rjasanensis zone) and early Berriasian.	Berriasian.....	Not identified.
Sharp, high, very widely spaced, becoming coarse in adult.	do.....	do.....	do.....	Early Berriasian.....	do.....	Do.
Fine to coarse, fairly regular.	Fairly common, irregular, generally weak.	Uncommon.....	do.....	Late Portlandian, Berriasian, and early Valanginian.	Not identified.....	Do.
Commonly weak, become faint near ventral margin.	A constriction occurs on several of the largest specimens.	None.....	Very fine, closely spaced.	Middle to late Valanginian Hauterivian?	Probably early Valanginian.	Do.
Highly variable, weak to strong, regular to irregular in spacing.	Irregular, weak to strong, present on medium to large specimens.	do.....	None.....	Valanginian (also, possibly late Berriasian).	Valanginian.....	Middle to late Valanginian.

cribed the differences to normal variation within a species, to environmental factors, or to accidents of preservation. In contrast, Pavlow and Anderson considered the differences worthy of specific distinctions and described them in great detail. As with many other paleontologists of their time, they made no allowance for biological or ecological factors in their definitions of species.

Concerning *Aucella piochii* (Gabb), the writer considers that Stanton's concept (1895, p. 42-43 [1896]) of the species is correct. In any large collection from a single locality (see pl. 17, figs. 12-29) in the Knoxville formation specimens can be selected that will fit the concepts of many of the species of *Aucella* described by Pavlow and Anderson, but many other specimens will not quite fit and yet they appear to be part of the same population as the described species. Whenever minute fragmentation of species results in the listing of many species of a single genus from a single locality the validity of the species may be suspect.

An extreme example of such fragmentation is afforded by Anderson (1945, p. 942, 971), who lists 11 species of *Aucella* from 1 locality (California Acad. Sci. loc. 28037) near the top of the Knoxville formation. These species are reported to have been obtained from a thickness of 400 feet. Such a thickness in some parts of the world might represent considerable time, but within the 12,000 to 16,000 feet of the Knoxville

formation, dated as middle to late Portlandian on the basis of ammonites, the 400 feet represents a minute part of Jurassic time. All the aucellan specimens except one from the locality in question may easily be assigned in the writer's opinion to two species, namely *Aucella piochii* (Gabb) and *A. fischeriana* (d'Orbigny). The exception is *A. occidentalis* Anderson (1945, p. 971, pl. 12, fig. 2a-c), which resembles *A. volgensis* Lahusen and will be discussed later.

AUCELLA FISCHERIANA (d'ORBIGNY)

Aucella fischeriana (d'Orbigny) (pl. 17, figs. 1-6, 11) is employed herein for Aucellas from California and Oregon that have been described under the following names:

- Aucella piochii* var. *ovata* Stanton (1895, p. 43, 44, pl. 4, figs. 11-13 [1896]).
- terebratuloides* Lahusen in Pavlow (1907, p. 60, 83; Stanton, 1895, pl. 4, figs. 11-13 [1896]).
- sollasi* Pavlow (1907, p. 39; Stanton, 1895, pl. 4, figs. 4 [1896]).
- fischeriana* (d'Orbigny) in Anderson (1945, p. 970, pl. 12, figs. 1, 5).
- trigonoides* Lahusen in Anderson (1945, p. 971, pl. 13, figs. 4a-c).
- sollasi* Pavlow in Anderson (1945, p. 965, pl. 3, figs. 8-11; pl. 2, figs. 9, 10).

The Aucellas from the west coast listed under the above names were considered by Stanton (1895, p. 43

[1896]) to be merely a variety (subspecies of modern usage) of *Aucella piochii* and to differ from the typical variety "by its larger size, more broadly triangular form, greater convexity, and coarser more remote concentric undulations. The posterior ear is scarcely at all developed in either valve, and the beak of the right valve is much more prominent and pointed so that the hinge line is short and angular."

Most of the specimens in the Geological Survey collections that are labeled by Stanton as *Aucella piochii* var. *ovata* greatly resemble *A. trigonoides* Lahusen (1888, p. 36, 37, pl. 2, figs. 21-24; Pavlow, 1907, p. 55, pl. 4, figs. 23-25), as noted by Stanton (1895, p. 43 [1896]), but likewise resemble *A. fischeriana* (d'Orbigny) (1845, p. 472, pl. 46, figs. 8-10; Lahusen, 1888, p. 37, pl. 2, figs. 14-20; Pavlow, 1907, p. 58, pl. 4, figs. 15-19). Lahusen (1888, p. 37) distinguishes *A. fischeriana* (d'Orbigny) from *A. trigonoides* Lahusen by its finer ribbing, more swollen right valve, and more elongate, less trigonal-shaped shell. The writer, after examining the various illustrations of these species and several specimens of each species from Russia identified by A. P. Pavlow in 1892, doubts very much whether *A. trigonoides* is more than a variant of *A. fischeriana*. Regardless of possible synonymy, most of the specimens in question from California show characteristics that are typical of *A. fischeriana*. Furthermore, the name *A. fischeriana* (d'Orbigny) has the advantage over *A. trigonoides* Lahusen of being one of the oldest used for an *Aucella*; both Pavlow and Anderson have published excellent illustrations of the species, and both authors mention that the species is very common near the top of the Jurassic.

Interestingly, Pavlow (1907, p. 55, 58) notes that some specimens of *Aucella trigonoides* Lahusen greatly resemble *A. gabbi* Pavlow (1907, p. 54), but that other specimens are more triangular, more elongate, and have shorter beaks. As *A. gabbi* is a synonym of *A. piochii* (Gabb), Stanton's (1895, p. 43 [1896]) comparison of his *A. piochii* var. *ovata* with *A. trigonoides* is quite apt. Similarly the writer has noted that in beds containing both *A. piochii* (Gabb) and *A. fischeriana* (d'Orbigny), there are many small specimens that could belong to *A. piochii* or could be immature specimens of *A. fischeriana*. Such an association suggests that *A. fischeriana* is closely related to *A. piochii*.

Aucella fischeriana (d'Orbigny) is probably represented in the lower and middle parts of the Knoxville formation by the specimens that Pavlow (1907, p. 39; Stanton, 1895, pl. 4, fig. 4 [1896]) and Anderson (1945, p. 965, pl. 2, figs. 9, 10, pl. 3, figs. 8-11) referred to *A. sollasi* Pavlow. It is common, however, only in the upper part of the formation. It is associated with *A.*

piochii (Gabb) throughout its range and becomes more common than that species at the top of its range.

AUCELLA OKENSIS PAVLOW

Aucella okensis Pavlow (1907, p. 40, pl. 1, figs. 10a-c, 11a-c) (see pl. 18, figs. 15-19) is one of the most easily recognized species of *Aucella* because of its large size and very coarse, widely spaced ribbing. In some respects it resembles certain species of *Inoceramus*. It has considerable stratigraphic value, too, because it occurs at the very base of the Cretaceous. In North America it has been identified in northern Alaska, in the Upper Yukon region in east-central Alaska, in the Harrison Lake area of British Columbia (Crickmay, 1930, p. 40-42), and in the west side of Vancouver Island (Jeletsky, 1950, p. 42, 43). One specimen illustrated by Pavlow (1907, pl. 1, figs. 10a-c) is reported to be from California. This report may be an error because the collections of the U. S. Geological Survey do not contain any representative of the species from the west-coast States. Anderson (1945, p. 940, 942) mentioned the species as occurring in the uppermost part of the Knoxville formation but did not publish any illustration. It is probable that he had in mind some variant of *A. fischeriana* (d'Orbigny).

AUCELLA SUBOKENSIS PAVLOW

Aucella subokensis Pavlow (1907, p. 41, 42, pl. 1, figs. 17a-c) (see pl. 18, figs. 9, 10) is associated with *A. okensis* in the basal Cretaceous beds in Alaska and northern Eurasia. It resembles *A. okensis* Pavlow considerably, but is distinguished by its smaller size, more elongate, trigonal outline, smaller beaks, and finer, more closely spaced ribs. Its characteristics are somewhat intermediate between *A. okensis* and *A. fischeriana* (d'Orbigny). From the latter it is distinguished by being larger, stouter, and less elongate, and by having coarser, sparser ribbing. Somewhat less comparable is *A. volgensis* Lahusen (1888, p. 38, pl. 3, figs. 1-16), which is more elongate posteriorly, has more elongate umbones, and bears weaker, less regular, closer spaced ribs.

AUCELLA VOLGENSIS LAHUSEN

Aucella volgensis Lahusen (pl. 18, figs. 7, 8, 12-14) has features intermediate between those of *A. subokensis* Pavlow and *A. crassicolis* Keyserling. Comparisons with *A. subokensis* have been made under the discussion of that species. It differs from *A. crassicolis* by being larger, higher, more obliquely elongated, and less inflated, by the beak on the left valve being much less incurved, and by the right valve being much less convex. When specimens showing both valves are

compared in lateral view the differences are striking. *A. crassicolis* is much more inflated and more nearly equivalved.

The range of *Aucella volgensis* according to Lahusen (1888, p. 26, 38, 39) in his original description is from the Late Jurassic zone of *Craspedites nodiger* Eichwald into the earliest Cretaceous zone of *Subcraspedites spasskensis*. Its range according to Pavlow (1907, p. 27, chart opposite p. 84) is through the lowest three zones of the Cretaceous as high as the base of the zone of *Polyptychites keyserlingi*, and it is most abundant in the lowest zone of *Subcraspedites spasskensis*. In spite of the different ranges assigned by these authors, their published illustrations show that they were discussing the same species. Confirmation of this is afforded by three specimens identified by Pavlow and sent by him to the U. S. National Museum in 1892.

Aucella volgensis Lahusen has not been definitely identified in North America. This seems rather strange considering that it is well characterized, has a long range, and is fairly common in northern Eurasia. The specimens from northern Alaska that the writer assigns to *A. subokensis* and *A. crassicolis* were examined carefully to see if any of them might more properly be assigned to *A. volgensis*. Jeletsky (1950, p. 41) mentions the presence of some Aucellas similar to *A. volgensis* Lahusen in beds of Early Cretaceous age on the west side of Vancouver Island. In California, an *Aucella* found in the basal sandy beds of the Cretaceous was identified by Anderson (1945, p. 972, pl. 10, fig. 1) as *Aucella* aff. *A. volgensis* Lahusen, but he notes that his specimen does not conform to the published figures of the species.

Possibly *Aucella volgensis* is represented in the highest Jurassic beds in California by the specimens that were named *A. occidentalis* Anderson (1945, p. 971, 972, pl. 12, figs. 2a-c). This species is represented by 3 specimens found only at 1 locality that furnished many specimens of *A. fischeriana* (d'Orbigny) and *A. piochii* (Gabb). It differs from the associated *A. fischeriana* (d'Orbigny) by being considerably more convex, by its left valve having a much stouter umbo and a less strongly incurved beak, by its right valve being more inflated, and by its ribbing being more irregular in strength and spacing. It differs from *A. crassicolis* Keyserling in the overlying Cretaceous beds by having a much less convex right valve. Its chances of being derived from the Cretaceous beds because of some accident of stream erosion, or mishandling, seems unlikely because three specimens were found. It is possibly a representative of *A. volgensis* Lahusen, but

its identification with that species or any other species cannot be made until a sufficient number of specimens are found to show its range in variation.

AUCELLA SUBLAEVIS KEYSERLING

Aucella sublaevis Keyserling (pl. 18, figs. 1-6, 11) is characterized by being small and plump, by the right valve being only slightly smaller and less convex than the left, by the ventral margins of the two valves bending abruptly toward each other, and by the shell bearing numerous fine radial striae. In Alaska it occupies a stratigraphic position directly above *A. okensis* Pavlow and *A. subokensis* Pavlow and directly below *A. crassicolis* Keyserling. It has not been found in Cretaceous beds in the west-coast States. In northern Russia and Spitzbergen *A. sublaevis* is reported in beds of middle to late Valanginian age (Pavlow, 1907, p. 64; Sokolov and Bodylevsky, 1931, p. 118) and is associated at the top of its range with *A. crassicolis* Keyserling. Some specimens from Hauterivian beds in northern Germany have been assigned to *A. sublaevis* Keyserling (Sokolov and Bodylevsky, 1931, p. 45, 118; Wollemann, 1900, pl. 2, figs. 8, 9; Pavlow, 1907, p. 63, 79), but they have a much less convex right valve.

AUCELLA CRASSICOLLIS KEYSERLING

Aucella crassicolis Keyserling (pl. 19, figs. 1-24) is employed herein for Aucellas from Alaska and the United States that have been described under the following names:

- Aucella piochii* (Gabb) in part (1869, pl. 32, figs. 92, 92a, b).
- concentrica* Fischer in White (1884, p. 13, 14, pl. 6, figs. 2-12; 1888, p. 231, pl. 4, figs. 3-5, 11-17, 21 [1889]).
- crassicolis* Keyserling (Stanton, 1895, p. 45-47, pl. 5, figs. 1-4, 7-13, pl. 6, figs. 1-5 [1896]).
- crassicolis* Keyserling (Pavlow, 1907, pl. 5, figs. 8, 10, 11, pl. 6, figs. 3-5).
- crassa* Pavlow (1907, p. 69; White, 1888, pl. 4, figs. 16, 17 [1889]; White, 1884, pl. 6, figs. 9, 10; Stanton, 1895, pl. 5, figs. 1-6, 9, pl. 6, figs. 1, 2 [1896]; Stewart, 1930, p. 112, pl. 2, fig. 4).
- keyserlingi* Lahusen in Pavlow (1907, p. 62; Stanton, 1895, pl. 5, figs. 12, 13 [1896]).
- terebratuloides* var. *regularis* Pavlow (1907, p. 60, 83, pl. 5, fig. 7).
- terebratuloides* Lahusen in Pavlow (1907, p. 60, 81; White, 1884, pl. 6, figs. 2-5).
- piriformis* Lahusen in Pavlow (1907, p. 63, 81; White, 1884, pl. 6, figs. 6, 7; Anderson, 1938, pl. 8, figs. 3, 4).
- solida* Lahusen in Pavlow (1907, p. 64, 81; White, 1884, pl. 6, fig. 8; 1888, pl. 4, fig. 21 [1889]; Anderson, 1938, p. 105, pl. 10, figs. 3, 4).
- inflata* Toula in Pavlow (1907, p. 68, 81; White, 1884, pl. 6, fig. 11; Anderson, 1938, p. 104, pl. 8, figs. 5, 6).
- uncitoides* Pavlow (1907, p. 83; Stanton, 1895, pl. 6, fig. 5 [1896]).

The Aucellas described by C. A. White in 1884 were obtained from a single locality in the Port Moller area near the southwest end of the Alaskan Peninsula. White (1884, p. 14) considered that the fossils showed such perfect gradation of form that all belonged without doubt to one variable species. He published many figures simply to show the amount of variation possible within a single species. To the writer his conclusions are sound. Yet Pavlow (1907, p. 81) assigned the specimens figured by White to five species.

Among the specimens from California described by T. W. Stanton as *Aucella crassicolis* Keyserling, Pavlow (1907, p. 62, 69) recognized four species. In a California collection of Aucellas at the University of Moscow, Pavlow (1907, p. 83) recognized a variety of still another species. However, he referred most of the specimens to *A. crassa* Pavlow and *A. crassicolis* Keyserling. Most of the Aucellas from the Cretaceous of California discussed by Pavlow were considered by Stewart (1930, p. 112, 113) to belong to one species which he called *A. crassa* Pavlow rather than *A. crassicolis* Keyserling because he did not know the relationships of the American Aucellas with the Eurasian Aucellas and preferred, therefore, to use a local name.

The writer agrees with Stanton (1895, p. 46 [1896]) and Stewart (1930, p. 108, 112, 113) that the robust Aucellas in the Early Cretaceous Paskenta formation (equals upper part of Knoxville formation of Stanton, 1895, p. 11-13 [1896]) belong to a single highly variable species and that the variants to which Pavlow has attached so many names are connected by many specimens showing transitional characteristics. The variation in coarseness of ribbing is probably mostly biologic, but is no greater than in other species of *Aucella* as defined by Pavlow. The variations in shape, in curvature of the beak, or in the strength of constrictions are probably related to crowding on the sea bottom, to changes in the environment during growth, or to deformation after burial. The shape of any particular species of *Aucella* is not apt to be any more stable than that of other gregarious pelecypods, such as *Ostrea* or *Gryphea*, and considerable allowance must be made, therefore, in the definition of species of such pelecypods. If any of the named variants had stratigraphic significance, the name might properly be retained as a subspecies, but such has not yet been proven.

Among the variants of *Aucella crassicolis* Keyserling to which Pavlow gave specific names, the most common has been called *A. crassa* Pavlow (pl. 19, figs. 10, 11, 13, 16, 18-20, 23, 24). This variant is highly convex in cross section; its left valve is fairly round in outline and has a strongly incurved beak; its shell bears pronounced, widely spaced concentric ribs and generally

weak constrictions, but may be weakly ribbed. The next common variant represented is the one to which the name *A. crassicolis* was originally applied (pl. 19, figs. 3-6, 9, 17, 22). This variant differs from *A. crassa* by being more elongate, by having at least one pronounced constriction that separates a swollen umbonal area from the rest of the shell, and by its ribbing varying from fine to coarse on different specimens. However, the umbonal part of the shell is identical in appearance with small specimens of *A. crassa*, and the greater elongation of *A. crassicolis* than of *A. crassa* appears to be related to the development of one or more constrictions that modified the normal growth of the shell.

The other variants of *Aucella crassicolis* are not common in the basal Cretaceous beds in California and Oregon but can be selected in large collections of Aucellas. The variant called *A. solida* Lahusen (pl. 19, fig. 12, 21) differs from the typical variant *A. crassicolis* by being less elongate, by lacking a constricted umbo, and by its surface being nearly smooth, or marked by a few wide concentric constrictions. The variant *A. inflata* Toulas is as convex as *A. crassa*, but differs in being less regularly rounded, a little more elongate posteriorly, and generally has slightly finer ribbing. The variant that Pavlow (1907, p. 83; Stanton, 1895, pl. 6, fig. 5 [1896]) referred to *A. uncitoides* Pavlow is slightly more elongate than the associated variant called *A. crassa*. A comparable specimen is shown on plate 19, fig. 14.

Another possible variant is *Aucella keyserlingi* Lahusen (1888, p. 40, 41; Pavlow, 1907, p. 62, 63) (see pl. 19, figs. 1, 2, 7, 8, 15), which differs from *A. crassa* by being much less convex and slightly more elongate, by having rather closely and regularly spaced thin concentric ribs, and by the presence rarely of radial ribs. *A. keyserlingi* appears to be a distinct, well-characterized species in Eurasia. In collections from California and Oregon, however, specimens that fit the descriptions of *A. keyserlingi* fairly well are associated with others that are transitional to *A. crassa* and *A. crassicolis*.

Evidently in California and Oregon the robust Aucellas of middle to late Valanginian age all represent one variable species. This conclusion does not mean that all the robust Aucellas of the same age in Eurasia belong to one species. There may be local species in Eurasia that never existed in North America and the names of some Eurasian species may have been misapplied in North America.

AUCELLAN SPECIES OF QUESTIONABLE VALIDITY

In addition to the 10 aucellan species from North America whose validity seems well established, there

may be several others whose validity can be determined only by additional fieldwork. These include the species identified by Anderson (1938, p. 106, pl. 8, figs. 8, 9) with *Aucella lahusei* Pavlow (1907, p. 51, pl. 3, figs. 16-23), which species occurs in Russia in the latest Jurassic and the earliest zone of the Cretaceous. Anderson's specimens have more elongate umbones and more strongly incurved beaks than *A. lahusei*, but otherwise his comparison is quite apt. He notes, however, that his specimens are from the basal beds of the California Cretaceous and are younger than *A. lahusei*. Interestingly the specimen shown by Anderson on his plate 8, figure 8, is remarkably similar to one of the specimens figured by Stanton (1895, pl. 4, fig. 14 [1896]) that Pavlow (1907, p. 61, 83) placed in a new species, *A. uncitoides*. Also, Anderson's specimen on his plate 8, figure 9, is nearly identical with a specimen figured by Stanton (1895, pl. 4, figs. 11-13 [1896]) that Pavlow (1907, p. 60, 83) placed in *A. terebratuloides* Lahusen. The writer, as discussed previously, considers the last mentioned specimen as an immature representative of *A. fischeriana* d'Orbigny and the other specimen illustrated by Stanton on his plate 4, figure 14, as an adult of *A. piochii* Gabb. The discovery of these species in the basal beds of the Paskenta formation, overlying beds where they normally occur, suggests that they may have been derived by erosion of the Jurassic Knoxville formation.

Another *Aucella* was referred by Anderson (1945, p. 968, pl. 6, figs. 7a-c) to *A. krotovi* Pavlow (1907, p. 32, pl. 2, figs. 31, 32) on the basis of specimens from Quinto Creek, Stanislaus County, Calif. The species occurs in Russia in the latest Jurassic. Anderson's specimen of *Aucella* was considered by him to be of Late Jurassic age because of its association with certain ammonites and with *Aucella stantoni* Pavlow (Anderson, 1945, p. 969, 983, 984). The ammonites probably belong to the genera *Lytoceras* and *Phylloceras* and, as such, have little age value. However, *A. stantoni* is a synonym of *A. piochii* (Gabb) in the writer's opinion and is indicative of a middle to late Portlandian age. This identification is confirmed by the presence of *A. piochii* (Gabb) from Quinto Creek in the collections at Stanford University.

Aucella krotovi Pavlow of Anderson differs from any other known species in the Jurassic Knoxville formation by the beak on its left valve being only weakly incurved and by the umbonal part of the right valve being nearly as prominent as the corresponding part of the left valve. In most characteristics it resembles *A. krotovi* Pavlow from Russia, but differs by having a relatively larger, more convex right valve.

A small, elongate *Aucella* from the Cretaceous Paskenta formation was recorded by Anderson (1938, p. 106, pl. 29, figs. 7-9) under the name *A. nuciformis* Pavlow (1907, p. 52, pl. 3, figs. 27a-c, 28a-c), which species occurs in Russia in the Berriasian. The specimen illustrated by Anderson on his plate 29, figures 8, 9, is a left valve that resembles the left valve of *A. nuciformis* as figured by Pavlow, but could be an immature specimen of *A. crassicolis* (Keyserling). The other specimen illustrated by Anderson on his plate 29, figure 7, is characterized by its right valve being nearly as convex as the left valve and by having swollen umbones that are marked ventrally by a constriction. This specimen appears to be a variant of *A. crassicolis* that is slightly more elongate than average for the species. The identification of such Aucellas can be made more easily in the field than in the laboratory because many more specimens are available to show the possible variations within aucellan populations.

Still other aucellan species may be present in Cretaceous beds near McCarthy Creek in Tehama County, Calif., above the 1,200 to 1,500 feet, or more, of sandy beds that contain an abundance of *A. crassicolis* Keyserling. According to Anderson (1932, p. 322; 1938, p. 46), these sandy beds are overlain by a sequence consisting mostly of shale that has furnished a few specimens of *Aucella*. In particular he records *Aucella* as much as 1,200 feet above the highest occurrence of Valanginian ammonites near the base of the shale sequence. This record is interesting because these shale beds were considered by Stanton (1895, p. 17, 18 [1896]) to belong in the lower part of the Horsetown formation. The question arises whether the *Aucella* recorded by Anderson actually belongs to that genus, or to the similar appearing genus *Aucellina* of late Aptian to Cenomanian age, or even to an immature *Inoceramus*.

Stratigraphically the presence of *Aucella* on McCarthy Creek as much as 1,200 feet above the top of the sandy beds containing *Aucella crassicolis* Keyserling seems improbable, considering that Stanton (1895, p. 18 [1896]) found the late Hauterivian ammonite "*Neocraspedites*" *aguila* Anderson (USGS Mes. locs. 1092, 2267) nearby in Tehama County only 400 to 500 feet above the beds containing *Aucella crassicolis* Keyserling. The age of this ammonite is determined in the Ono area, Shasta County, by its position only a few hundred feet above beds containing the middle Hauterivian ammonite *Simbirskites* (Anderson, 1938, p. 47, 111, 122, 147, 154, 208) and many hundreds of feet below beds containing the early Barremian ammonite *Pulchellia* (Anderson, 1938, p. 65, 197). The age of "*N*" *aguila* Anderson is younger, therefore, than

the reported occurrence of *Aucella* in beds of early Hauterivian age in England (Woods, 1905, p. 71) and of middle Hauterivian age in northern Germany (Wollemann, 1900, p. 56-59; Pavlow, 1907, p. 79) and central Russia (Sokolov and Bodylevsky, 1931, p. 118; Chetyrkina and Shugin, 1937, p. 25).

These occurrences of *Aucella* in beds of Hauterivian age have not been well substantiated. Aucellas are easily reworked into younger beds, in a manner similar to Gryphaeas and Belemnites. The occurrence in the early Hauterivian Claxby Ironstone in England is particularly suspect because Spath (1924, p. 81, 82) reports that some of the ammonites are derived from the underlying formations of Valanginian and Berriasian age. Except for these possible occurrences, *Aucella* disappeared abruptly at the end of Valanginian time and, therefore, the higher occurrences of *Aucella* on McCarthy Creek reported by Anderson are probably misidentifications.

It is possible that the specimens in question from McCarthy Creek belong to the genus *Aucellina*, which is closely similar to *Aucella* in shape and ornamentation. It differs from *Aucella* mainly by lacking an articulating groove in the hinge area of the left valve, by the right valve having a long, low, flat anterior ear, instead of a short triangular ear, and by the presence of a comblike row of small teeth on both edges of the byssal notch (Pompeckj, 1901, p. 365, 366; Pavlow, 1907, p. 85). These features that distinguish the two genera are commonly not preserved or exposed and generally have to be exposed by laborious picking and grinding methods. The genus *Aucellina* has been recognized in Albian beds in the western interior of Canada (McLearn, 1945, pl. 5, fig. 3, 1948), in Alaska (Imlay and Reeside, 1954, p. 229, 240), and in the Mitchell area of central Oregon. It is probably represented in California in beds of Late Aptian and Albian age by specimens that Anderson (1938, p. 65, 107) refers to *Aucella*, but the hinge characters of those specimens should be examined to decide their generic assignment.

It is possible, also, that the specimens recorded as *Aucella* by Anderson from 1,200 feet above sandy beds containing Valanginian ammonites are actually immature specimens of *Inoceramus ovatooides* Anderson (1938, p. 100, pl. 6, fig. 2). The immature specimens of this species, which were named *I. colonicus* Anderson (1938, p. 100, pl. 4, figs. 10-12, pl. 5, fig. 1), are similar in shape to *Aucella piochii* (Gabb). Their identification with *Inoceramus* rather than *Aucella* ordinarily should be easily made because their shell has an inner nacreous layer and an outer prismatic layer. Very small specimens lacking the prismatic layer might

easily be mistaken for *Aucella*, however, as even T. W. Stanton was confused. In his notebook, dated September 3, 1900, he mentions finding a "*Crioceras* and a small *Aucella*?" (USGS Mes. loc. 2269), about three-quarters of a mile southeast of the building at the Wilcox Ranch and from 400 to 500 feet above the sandy beds containing *Aucella crassicolis* Keyserling. The specimen of "*Crioceras*," herein identified with *Hoplcrioceras remondi* (Gabb), appeared to Stanton to be at about the same level as USGS Mes. locs. 1092 and 2267, from which he obtained an ammonite now identified as "*Neocraspedites*" *aguila* Anderson. Stanton had collected the same ammonites near Ono, Shasta County, and had not found *Aucella* with them. He was much puzzled, therefore, to find an *Aucella*-like pelecypod associated with these ammonites elsewhere. The pelecypod that puzzled Stanton is about 11 millimeters in length, has a thin nacreous layer, and is indeed similar in shape to immature Aucellas. Its nacreous layer and its shape can be matched, however, with immature specimens of *Inoceramus ovatooides* Anderson in the Geological Survey collections.

STRATIGRAPHIC DISTRIBUTION OF AUCELLA

The stratigraphic distribution of the common species of *Aucella* in the Western States and Alaska is shown on figure 36. Seven zones based on species of *Aucella* are clearly defined. In addition the zone of *Aucella concentrica* may be divisible locally into two subzones by the presence of *A. concentrica leguminosa* Stoliczka in the lower part of the zone and *A. spitiensis* Holdhaus in the upper part. Such a division still has to be proved finally by fieldwork. Also, the overlap of the range of *A. concentrica* with that of *A. rugosa* (Fischer) and the associated *A. mosquensis* (von Buch) has proved useful stratigraphically in Alaska. In the Lower Cretaceous rocks there may be another zone between the zones of *A. okensis* Pavlow and *A. sublaevis* Keyserling that should be represented by *A. volgensis* Lahusen. This seems probable considering the ranges reported for those species in Eurasia, the fact that *A. volgensis* appears to be well characterized, and the reported occurrence of an *Aucella* similar to *A. volgensis* from the west side of Vancouver Island (Jeletsky, 1950, p. 41).

The usefulness of these seven zones for mapping purposes is evident, but it could be greatly increased by careful studies of the population variation and stratigraphic succession of *Aucella*. Most of such work must be done in the field rather than the laboratory because of the greater ease in examining great numbers of Aucellas at many places and many levels.

EUROPEAN STAGES	CHARACTERISTIC AUCELLAS AND AMMONITES IN OREGON AND CALIFORNIA	CHARACTERISTIC AUCELLAS AND AMMONITES IN ALASKA	NORTHERN ALASKA	SOUTHWESTERN OREGON	CALIFORNIA
LOWER CRETACEOUS (IN PART)	Hauterivian	<i>Hertleinites aguila</i>	No fossil evidence	Sandstone and sandy siltstone, dark-greenish-gray, massive to medium-bedded. Limestone concretions	Siltstone and shale, dark-gray
		<i>Simbirskites broadi</i>			
VALANGINIAN	Aucella crassicolis	<i>Simbirskites aff. S. elatus</i>	Oxpikruak formation	Siltstone, sandy, gray. Many thin beds of dark-greenish-gray sandstone. Few limestone lenses	Paskenta formation of Anderson ?
		<i>Wellisia packardii</i>			
BERTIASIAN	No fossil evidence	<i>Wellisia oregonensis</i>	Tigtlukpuk formation and upper part of Kingak formation	Siltstone, medium-to dark-gray. Pebble and limestone lenses in lower part	Knoxville formation (present only in Coast Ranges)
		<i>Olcostephanus n. sp.</i>			
PURBECKIAN	Aucella fischeriana	<i>Homolomites mutabilis</i> and <i>Sarasimella angulata</i>	No fossil evidence	Folding, erosion, and regional metamorphism	Mariposa slate (present only in Sierra Nevada)
		<i>Kilianella crassiplicata</i> and <i>Thurmanniceras californicum</i> ?			
PORTLANDIAN	Aucella piochii	No fossil evidence	Aucella sublaevis	Myrtle formation (type area)	Logtown Ridge formation
		<i>Substereoceras stantoni</i> , <i>Protacanthodiscus crossi</i> , and <i>Proniceras</i> (not zoned)			
KIMMERIDGIAN	No fossil evidence	<i>Aucella piochii</i>	No fossil evidence	Rogue formation	Rogue formation
		<i>Kossmatia dilleri</i> and <i>Durangites</i>			
UPPER JURASSIC (IN PART)	Aucella concentrica	<i>Aucella rigosa</i> and <i>Aucella mosquensis</i>	Aucella okenensis and <i>A. subokensis</i>	Galice formation	Mariposa slate (present only in Sierra Nevada)
		<i>Aucella concentrica</i> and <i>A. spitiensis</i>			
OXFORDIAN	<i>Amoeboceras (Amoebites) dubium</i>	<i>Amoeboceras (Prionodoceras) spiniferum</i>	<i>Cardioceras distans</i> <i>Cardioceras martini</i>	?	?

Figure 36.—Stratigraphic distribution of *Aucella* in the Western States and Alaska.

CONCLUSIONS

In summation, *Aucella* has been divided into so many species on the basis of minute differences of shape, size, and ornamentation that in many large collections the so-called species appear to grade into each other and to represent a single population. Most authors dealing with *Aucella* have not considered that an attached gregarious pelecypod is apt to exhibit considerable variation owing to crowding or to slightly different ecological conditions from place to place. Some of the species that have been described have been based on immature or deformed specimens. If species of *Aucella* are defined, making allowance for both biological and environmental factors, their numbers are greatly reduced, but the specific concepts can be grasped and applied readily by field geologists for mapping purposes as has been done in recent years in Alaska and in the west-coast States.

DESCRIPTIONS OF MENTIONED U. S. GEOLOGICAL SURVEY MESOZOIC LOCALITIES

997. Half a mile northwest of Snellings Ranch, near Paskenta, Tehama County, Calif. J. S. Diller and James Storrs, 1893.
1010. One-fourth mile northwest of Shelton Ranch buildings, in upper part of sandy beds containing abundant *Aucellas*, Tehama County, Calif. J. S. Diller and James Storrs, 1893.
1091. Half a mile east of Wilcox Ranch buildings, in upper part of sandy beds containing abundant *Aucellas*, Tehama County, Calif. J. S. Diller, T. W. Stanton, and James Storrs, 1893.
1092. One-half to three-fourths of a mile northeast of Wilcox Ranch buildings, in lower 200 feet of shale beds directly overlying the sandy beds containing *Aucella crassicolis* Keyserling, Tehama County, Calif. J. S. Diller, T. W. Stanton, and James Storrs, 1893.
1225. Knoxville formation at Buck Hill near Cache Creek, 5 miles northeast of Palmer Ranch, Lake County, Calif. T. W. Stanton, 1894.
2267. One-half to three-fourths of a mile northeast of Wilcox Ranch buildings, about 400 to 500 feet above the top of the sandy beds containing *Aucella crassicolis* Keyserling, Tehama County, Calif. T. W. Stanton, 1900.
2269. About three-fourths of a mile southeast of Wilcox Ranch buildings, from 400 to 500 feet above the top of the sandy beds containing *Aucella crassicolis* Keyserling, Tehama County, Calif. T. W. Stanton, 1900.
2275. Knoxville formation, 5 miles west of Lowry's Ranch in gulch south of North Fork of Elder Creek, Tehama County, Calif. T. W. Stanton, 1900.
2285. Knoxville formation, Stony Creek at Stulls Hole, about 5 miles west of Fruto, Glenn County, Calif. T. W. Stanton, 1900.
2287. Conglomeratic sandstone, 450 feet thick, overlying shale beds containing *Aucella piochii* (Gabb), in Stony Creek about 5 miles west of Fruto, Glenn County Calif. T. W. Stanton, 1900.
3124. Naknek formation, west side of Katmai Bay, 2½ miles southwest of village of Katmai, Alaskan Peninsula, Alaska. G. C. Martin, 1904.
3127. Naknek formation, from talus half a mile north of USGS Mes. loc. 3124 and at about same stratigraphic position. G. C. Martin, 1904.
10248. Naknek formation, about 500 feet above sea level on Bear Mountain, Katmai Bay, Alaskan Peninsula, Alaska. C. N. Fenner, 1919.
11360. Naknek formation, Fossil Creek, north of Lake Becharof, southwest Alaska. Dr. Laymore, 1922.
20343. Swift formation, sandy shale above thick sandstone ledge in upper part of lower member, on north side of Great Northern Railway about one-quarter of a mile east of Autumn Creek at south side of Glacier Park, Mont. Wm. Cobban and R. W. Imlay, 1946.
21028. Kingak shale, Canning River, 2½ miles south of Black Island, lat 69°30'45" N., long 146°18'45" W., northern Alaska. George Gryc, 1947.
22127. Tiglukpuk formation, large cutbank on southwest side of Kukpowruk River, lat 68°42'30" N., long 163°14' W., northern Alaska. E. G. Sable, 1949.
22472. Okpikruak formation, north bank of Seagull Creek, Nimiuktuk Valley, DeLong Mountains, lat 68°19'50" N., long 159°59' W., northern Alaska. M. C. and A. N. Lachenbruch, 1950.
22514. Okpikruak formation, northeast of Ekakevik Mountain, lat 68°36' N., long 156°57' W., northern Alaska. B. H. Kent, 1950.
22724. Okpikruak formation, ridge one-fourth of a mile west of lakes at base of Thunder Mountain, lat 68°40'30" N., long 160°20'50" W., northern Alaska. R. H. Morris, 1951.
22736. Okpikruak formation, east bank of Nuka River, lat 68°40'30" N., long 160°03' W., northern Alaska. R. H. Morris, 1951.
22757. Okpikruak formation, Kemik Creek, lat 69°26' N., long 147°10' W., northern Alaska. Samuel Keller, 1951.
22762. Okpikruak formation, Kashivi Creek, lat 69°12' N., long 147°44' W., northern Alaska. Samuel Keller, 1951.
22768. Kingak shale, from 500 to 800 feet above local base at Lupine River, lat 68°52' N., long 148°22' W., northern Alaska. Samuel Keller, 1951.
22769. Kingak shale, about 300 feet above local base at Lupine River, lat 68°52' N., long 148°22' W., northern Alaska. Samuel Keller, 1951.
22780. Okpikruak formation, hills three-fourths of a mile east of east-central fork of Driftwood Creek, lat 68°38'05" N., long 160°29'20" W., northern Alaska. E. G. Sable, 1951.
22790. Okpikruak formation, north bank of Nuka River, lat 68°42'10" N., long 159°56'50" W., northern Alaska. E. G. Sable, 1951.
23554. Okpikruak formation, north bank of Nuka River, lat 68°40'45" N., long 160°02'45" W., northern Alaska. E. G. Sable, 1951.
23560. Okpikruak formation, north bank of Nuka River, lat 68°41'30" N., long 159°59' W., northern Alaska. E. G. Sable, 1951.

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<i>erringtoni</i> , <i>Aucella</i>	157		

PLATES 16-19

PLATE 16

[Figures natural size unless otherwise indicated]

FIGURES 1-7. *Aucella concentrica* (J. de C. Sowerby) (p. 157).

1-3. Two left valves and one right valve of plesiotypes, USNM 129046, from USGS Mes. loc. 20343, at south edge of Glacier Park, Mont.

4, 5. Left and right valves of plesiotype, USNM 108749, from USGS Mes. loc. 10248 near Katmai Bay, southwest Alaska.

6, 7. Right and left valves of plesiotype, USNM 129047, from USGS Mes. loc. 10248, near Katmai Bay, southwest Alaska.

8-10. *Aucella concentrica leguminosa* Stoliczka (p. 157). Dorsal and lateral views of plesiotype, USNM 129048, from USGS Mes. loc. 3124, near Katmai Bay, southwest Alaska.

11-17. *Aucella spitiensis* Holdhaus (p. 157).

11-13. Left valve, dorsal view, and right valve of plesiotype, USNM 129050, from USGS Mes. loc. 3127, near Katmai Bay, southwest Alaska.

14, 15. Left and right valves of plesiotype, USNM 129049, from USGS Mes. loc. 3124, near Katmai Bay, southwest Alaska.

16, 17. Right valves of plesiotypes, USNM 108746 c, d, from USGS Mes. loc. 21028, northern Alaska.

18, 19, 22-25. *Aucella rugosa* (Fischer) (p. 157).

18, 19, 23-24. Left valves of plesiotypes, USNM 108741, from USGS Mes. loc. 22768, northern Alaska.

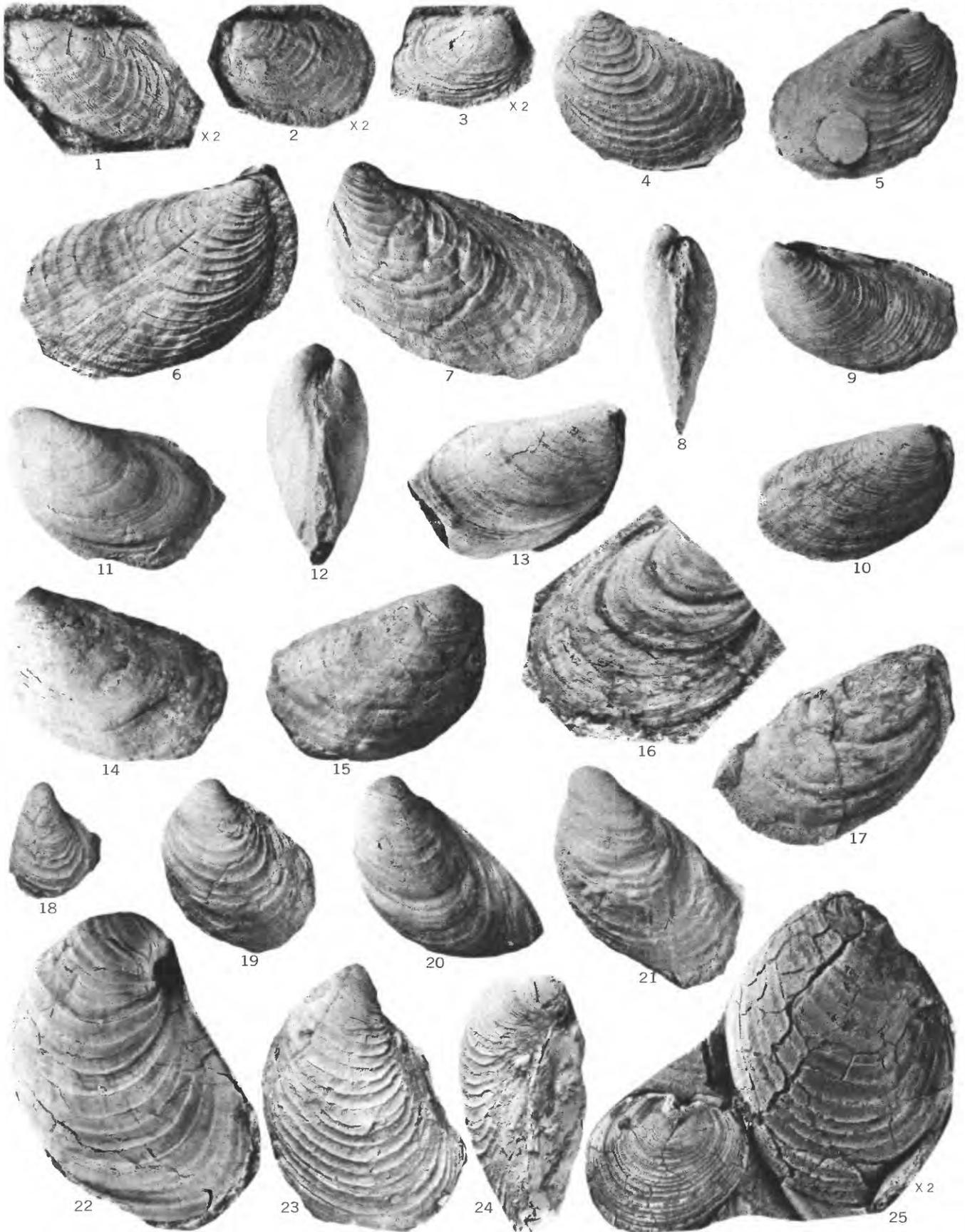
Fig. 24 is a ventrodorsal view showing greater convexity of the left valve.

22. Left valve of plesiotype, USNM 129051, from USGS Mes. loc. 11360, southwest Alaska.

25. Small right valve and larger left valve of plesiotype, USNM 108740, from USGS Mes. loc. 22127, northern Alaska. Specimens are enlarged two times to show radial markings.

20, 21. *Aucella mosquensis* (von Buch) (p. 157).

Left valves of plesiotypes, USNM 108748, from USGS Mes. loc. 22769, northern Alaska.



JURASSIC AUCELLAS



JURASSIC AUCELLAS

PLATE 17

[All figures natural size]

FIGURES 1-6, 11. *Aucella fischeriana* (d'Orbigny) (p. 159).

1, 5. Left valves of plesiotypes, Calif. Acad. Sci. 8679 and 8677, from CAS loc. 28037 on Watson Creek, 6 miles north of Winslow bridge, Glenn County, Calif.

2-4. Left valve, posterior dorsal view, and right valve of plesiotype, USNM 22221, from Khorochowo, near Moscow, Russia.

6, 11. Lateral and dorsal views of left valve of plesiotype, USNM 129054, from USGS Mes. loc. 2285, Glenn County, Calif.

7-10, 12-29. *Aucella piochii* (Gabb) (p. 157).

7-9. Dorsal view, left and right valves of plesiotype, USNM 23032, from USGS Mes. loc. 1084, Tehama County, Calif. This specimen was illustrated by Stanton (1896, pl. 4, figs. 6, 7) and was assigned by Pavlow (1907, p. 48) to a new species, *A. stantoni* Pavlow.

10. Left valve of plaster replica of holotype in University of California type collections, from Colusa County, Calif.

12-20. Left valves from a single locality showing variations in shape, size, and ornamentation. Plesiotypes, USNM 129052, from USGS Mes. loc. 1225, Lake County, Calif.

21-29. Left valves from a single locality showing variations in shape, size, and ornamentation. Plesiotypes, USNM 129053, from USGS Mes. loc. 2275, Tehama County, Calif.

PLATE 18

[Figures natural size unless otherwise indicated]

FIGURES 1-6, 11. *Aucella sublaevis* Keyserling (p. 161).

1-3. Right valve, anterior view, and left valve of an average specimen. Plesiotype 128680, USGS Mes. loc. 22736, northern Alaska.

4, 11. Left valve ($\times 1$ and $\times 2$) of a specimen in which radial striation is conspicuous. Plesiotype, USNM 128681, from USGS Mes. loc. 23554, northern Alaska.

5, 6. Left valve and anterior view of a large specimen. Plesiotype, USNM 128680, from USGS Mes. loc. 22736, northern Alaska.

7, 8, 12-14. *Aucella volgensis* Lahusen (p. 160).

7, 8. Left valve and anterior view of plesiotype, USNM 22223, from Kachpour, Russia.

12-14. Anterior view, right valve and left valve of plesiotype, USNM 22223b from Kachpour, Russia.

9, 10. *Aucella subokensis* Pavlow (p. 160).

Anterior view and left valve of plesiotype, USNM 128677, from USGS Mes. loc. 22762, northern Alaska.

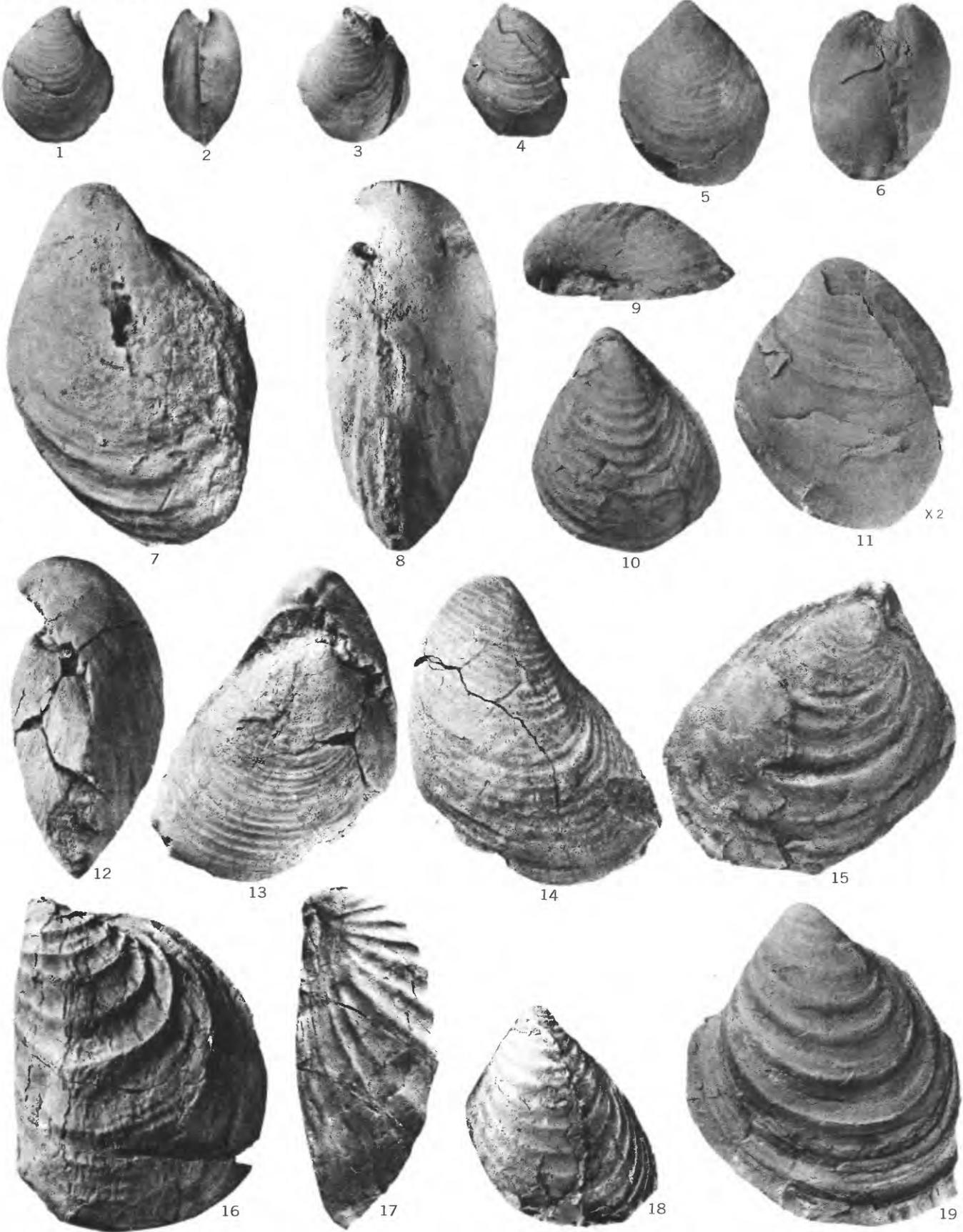
15-19. *Aucella okensis* Pavlow (p. 160).

15. Right valve of plesiotype, USNM 128675, from USGS Mes. loc. 22790, northern Alaska.

16, 17. Left valve and anterior view of plesiotype, USNM 128672, from USGS Mes. loc. 22472, northern Alaska.

18. Rubber cast of external mold of left valve. Plesiotype, USNM 128673, from USGS Mes. loc. 22724, northern Alaska.

19. Left valve of plesiotype, USNM 128674, from USGS Mes. loc. 22757, northern Alaska.



CRETACEOUS AUCELLAS

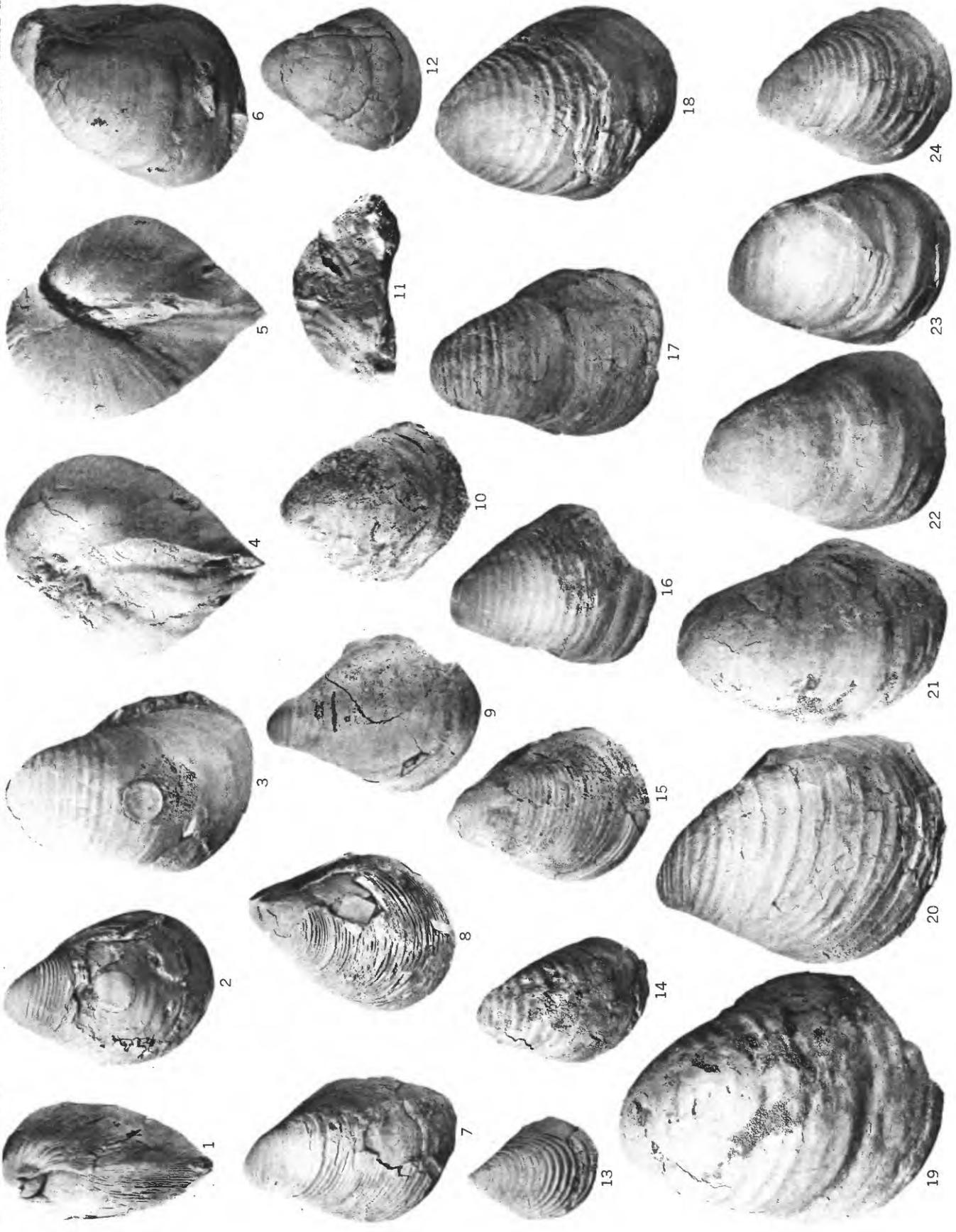


PLATE 19

[All figures natural size]

FIGURES 1-24. *Aucella crassicolis* Keyserling (p. 161).

- 1, 2, 8. Anterior view, left valve, and right valve of plesiotype, USNM 23038, from USGS Mes. loc. 1091, Tehama County, Calif. This specimen was figured by Stanton (1896, pl. 5, figs. 12, 13) and assigned by Pavlow (1907, p. 62) to *A. keyserlingi* Lahusen.
- 3-6. Left valve, anterior view, posterior view, and right valve of a single individual. Plesiotype, USNM 23252, from USGS Mes. loc. 1010, Tehama County, Calif.
7. Left valve showing fine, concentric ribbing similar to specimen shown in figs. 1, 2, 8. Plesiotype, USNM 129057, from USGS Mes. loc. 1091, Tehama County, Calif.
9. Left valve showing constricted umbone. Plesiotype, USNM 128686, from USGS Mes. loc. 22780, northern Alaska.
- 10, 11. Left valve and anterior view of plesiotype, USNM 128683, from USGS Mes. loc. 22514. Similar plump specimens are commonly referred to *A. crassa* Pavlow.
12. Left valve marked by broad undulations. Plesiotype, USNM 128687, from USGS Mes. loc. 23560, northern Alaska. Similar plump, smooth specimens are commonly referred to *A. solida* Lahusen.
- 13-18. Left valves from a single locality to show variation in shape and ornamentation. Plesiotypes, USNM 129055, from USGS Mes. loc. 997, Tehama County, Calif.
- 19-24. Left valves from a single locality to show variation in shape and ornamentation. Plesiotypes, USNM 129056, from USGS Mes. loc. 2287, Glenn County, Calif.