

REVISION OF THE ALATOCONCHIDAE: A REMARKABLE FAMILY OF PERMIAN BIVALVES

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ABSTRACT. Genera and species in the family Alatoconchidae are described and reillustrated, including a major revision of the type genus, and a family concept is established that transfers them from the Megalodontacea to the Ambonychiacea. *Saikraconcha* n. gen., with *S. tunisiensis* n. sp. as type species, and *Dereconcha* n. subgen., with *S. (D.) kamparensis* n. sp. as type species, are described. Two lineages are present in the family, with one including *Shikamaia* and its subgenera *Alatoconcha* and *Tanchintongia*, and the other including *Saikraconcha* and its subgenus *Dereconcha*. Both lineages show similar evolutionary change in form. Alatoconchids are limited in occurrence to the Old World Permian Tethyan province, having a distribution similar to that of the verbeekid fusulinaceans. Rapid evolution of species, and their distinctive form, make them stratigraphically useful in the Tethyan province.

Alatoconchids are the most unusual of late Paleozoic bivalves. They are strongly flattened in a dorsal-ventral direction, producing wide wing-like flanges on each valve. Some species had very large and heavy shells, as much as 1 m in length and 10 kg or more in weight, making them nearly the largest known bivalves. Small shells (mostly juveniles) were byssally attached, but large ones were free-living on a soft sediment surface, and are one of the few groups of recliners to have a vertically aligned plane of commissure.

THE alatoconchid bivalves are a distinctive group that differ from other bivalves in their form and large size, and their unusual life habits. These were the Giant Clams of the Permian. The largest individuals in the family probably reached lengths of 100 cm, and had a thick-walled shell up to 3 cm thick. Their most unusual character is the form of the shell, which has wide, alate, wing-like extensions of the valves formed by an isoclinal fold in the shell wall. This produced a very flattened shell, extended in a plane perpendicular to the plane of commissure. They were epifaunal surface dwellers, adapted to a free-living existence on the sea floor, despite large size and great weight. The wide, alate extensions of the shell acted as outriggers to hold the shell up on soft substrate, and to prevent tipping over during rough-water conditions.

Alatoconchids are the largest of all bivalves of the late Palaeozoic, and the most unusual in form, yet they were first described only fifteen years ago. They have been overlooked because of sporadic occurrence, and because they occur in areas where Permian faunas have been little studied. They were strictly tropical in distribution, and were confined to the Old World Permian Tethyan province, having a geographic distribution similar to that of the verbeekid fusulinaceans. The unusual form and lack of complete shells in early collections combined to make understanding and description of these bivalves especially difficult. With larger collections available for study, and additional occurrences of alatoconchids documented, it is now possible to resolve questions about characters of the hinge and form that were hurdles to understanding these magnificent bivalves. There are significant differences between species in hinge characters as well as in form, suggesting that there was rapid evolutionary change in the family during the Permian.

PREVIOUS WORK

The family Alatoconchidae and its type genus were introduced concurrently with the description of an unusual late Permian species from Afghanistan (Termier *et al.* 1973). Ozaki (1968) had previously introduced a new genus and species on material from Japan that subsequently could be identified as a member of this family, and Runnegar and Gobbett (1975) also introduced a new genus and species

for material from Malaysia that proved to be related to the Afghanistan material. These three reports were all done on fragmentary material, and when they were written the authors were all unaware of the work done by previous workers. Because of this, no comparisons were made between taxa, and the authors came to conflicting interpretations of the taxonomic relationships and basic form of the shells. Soon after Runnegar and Gobbett completed their manuscript, an investigation of late Permian strata in Tunisia (Newell *et al.* 1976) yielded a collection of specimens clearly related to the Afghan and Malaysian taxa, and a much larger Malaysian collection, with many significant specimens not studied by Runnegar and Gobbett, was assembled from the type locality of their genus.

The limited understanding, and conflicting interpretations, of the taxa made a revision of the group highly desirable. For this purpose most of the Malaysian, Afghan, and Tunisian material has been brought together for comparison. Furthermore, Boyd has studied the Malaysian collection deposited by Runnegar and Gobbett in the Sedgwick Museum at Cambridge, and some of these specimens have been rephotographed. The present paper provides an emended and expanded diagnosis of the family Alatoconchidae, reviews the three previously described genera and subgenera assignable to that family, and introduces one new genus and one new subgenus of alatoconchids.

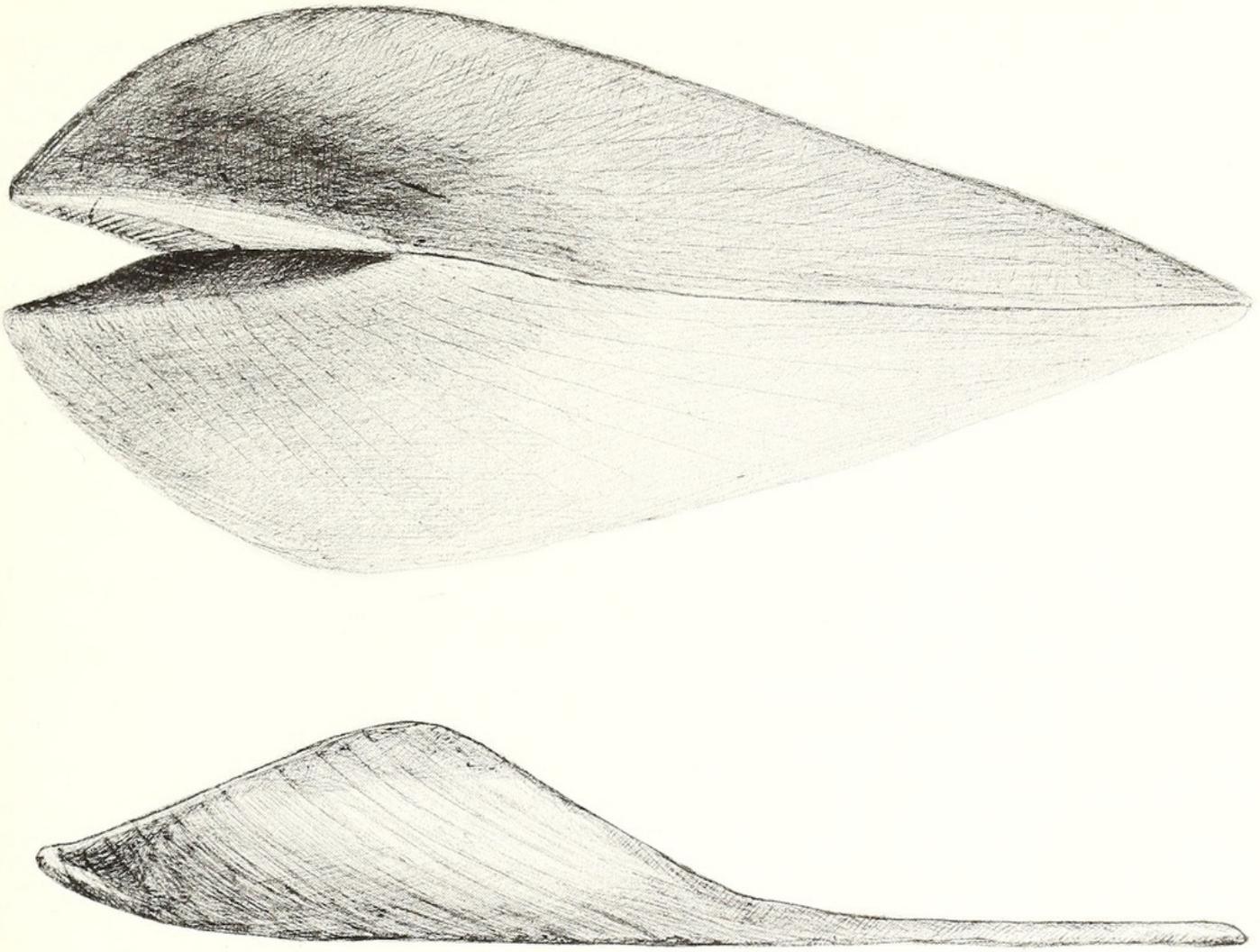
Considering the fragmental nature of the specimens available to previous workers, and the unusual shell form, it is not surprising that contradictory interpretations of morphology and relationships have been generated by different workers. Ozaki (1968) was unable to assign his material even to phylum, and in reconstruction assumed it to have a form like modern fungoid corals. Termier *et al.* (1973) and Runnegar and Gobbett (1975) were able to determine that their fossils were large, unusual bivalves, but arrived at quite different interpretations about hinge and form and consequently placed them in different orders. This diversity of interpretation obscures the fact that once the basic form is known, the fossils can be seen to be related to each other and to belong in one taxonomic group. The unusual form of these shells has led authors to describe them as 'problematical', 'bizarre', and 'aberrant', and their obscure relationships have given them the status of a mystery group among bivalves.

The report by Runnegar and Gobbett (1975), with its many photographs of specimens and suggested reconstruction of the complete shell, stimulated recognition of alatoconchids by other palaeontologists. Earlier reports were reinterpreted in the light of the Runnegar and Gobbett (1975) reconstruction, and alatoconchids were reported from several new localities. These reports have shown them to occur widely throughout the Permian Tethyan biogeographic province. The remaining task is to determine the character of the hinge and interiors, as well as the true form of the complete shell. Enough material is now available for study to resolve some of these problems, to interpret the taxonomic relationships and life habits, and to explain their biogeographic distribution.

FORM

A major difficulty in understanding alatoconchids is in determining the complete form of a single shell. Shells have several flaring edges which extend in more than one plane, and growing edges were fragile compared to older parts of the shell, so shell breakage was common after death of the animal. The H. S. Lee mine locality in Malaysia has yielded enough material to make possible a complete reconstruction of the shell, and specimens of various growth stages are available for study.

The form of *Shikamaia (Tanchintongia) perakensis* serves as a model for understanding the fragmentary material of other species, since comparison of available specimens and illustrations shows homology of the major shell features. The alate, wing-like flanges of the shell result from a major extension of the umbonal carinae in both valves, perpendicular to the plane of commissure, so that part of each valve is drawn out into a fold with nearly parallel sides (text-fig. 1). The shell is compressed in the dorsal-ventral direction, and is elongated in the anterior-posterior direction. The ventral surface of both valves is essentially flat, and forms a large planar surface perpendicular to the plane of commissure. Near the hinge the dorsal surface is extended along the plane of commissure to form a dorsal crest extending perpendicular to the flat ventral surface. Thus the anterior portion of



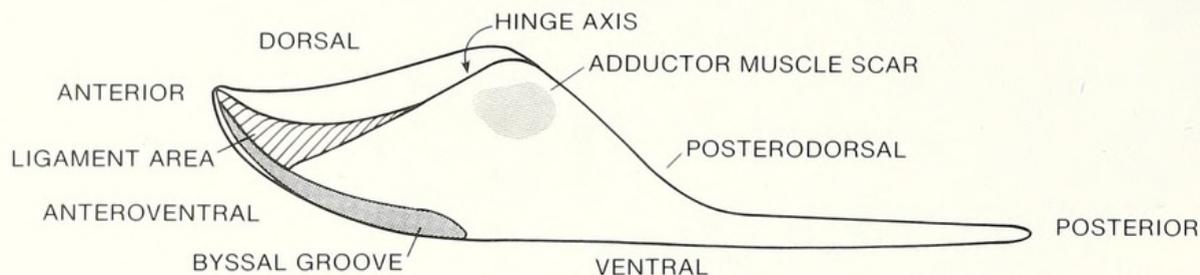
TEXT-FIG. 1. Reconstruction of adult shell form of *Shikamaia (Tanchintongia) perakensis*, showing dorsal and lateral views. Reconstruction of the posterior end differs from that of Runnegar and Gobbett (1975).

each valve has a triangular cross-section, and the articulated valves have a triangular cross-section on the anterior (beak) half of the shell. The posterior half of the shell consists only of the flat flanges ('wings'), and has a very compressed cross-section. The carinae of the shells have an elliptical outline in dorsal-ventral view, not the roughly parallel outline suggested by Runnegar and Gobbett (1975). A feature present only in juvenile growth stages of *S. (T.) perakensis*, but prominent in several other species, is a collar-like extension of the shell margin around the byssal groove. It projects below the flat ventral surface, opposite the dorsal crest, and is a distinctive feature for this group. All species in the family have significant umbonal infilling, and exhibit considerable allometric change during growth.

A major change in alatoconchid shell form occurs through the Permian as a progressive shortening of the shell along the anterior-posterior axis produced a more rounded outline in younger species, at the same time that compression along the dorsal-ventral axis caused an increase in the proportion of the valve forming the wing-like flange. *S. (T.) perakensis* and *Saikraconcha (Dereconcha) kamparensis* n. gen. n. sp., the oldest known alatoconchids, have an elongate form and a large body cavity with a high dorsal crest, while *Shikamaia (Alatoconcha) vampyra* and *Saikraconcha tunisiensis* n. gen. n. sp., the youngest known alatoconchids, have a nearly rounded outline and more flattened form, which is best developed in *S. tunisiensis*. This form is found in the modern bivalves *Corculum* and *Placuna*, both of which are free-living on the surface of medium- to coarse-grained substrates.

SHELL ORIENTATION

The unusual shell form of alatoconchids makes it difficult to apply the standard conventions of determining anterior–posterior axis on either the hinge axis or the oral–anal axis (Cox 1969), since such orientations would have little relevance to life orientation, and the axis would not correspond with major shell features. Therefore, in this study the anterior–posterior axis is designated as the axis including the beak and abapical end of the shell, and the dorsal–ventral axis is almost at right angles to this, and determined as a perpendicular to the large, flat basal surface (text-fig. 2) This convention



TEXT-FIG. 2. Orientation and location of shell features on right valve of *Shikamaia* (*Tanchintongia*) *perakensis*.

of orientation is doubly convenient, since prominent shell features occur on the axes, making description easy, and it corresponds closely with life orientation of the animal. The ligament-bearing portion of the margin is dorsal, and the byssal groove area (indicating position of foot) is ventral or anteroventral. The large adductor muscle scar, resulting from an anisomyarian musculature, indicates the posterior direction, so the beak end is anterior. This convention is similar to that used for myalinids and mytilids, since all these groups have a produced anterior end and a flattened margin where byssal attachment occurs.

LIFE ORIENTATION

The life orientation of alatoconchids can be inferred from the form of the shell, in combination with its massive character. They are believed to have been epifaunal, with the large flat ventral surface oriented parallel to the sediment surface. This is the only stable position for a very heavy shell, and the ventral surface must have been downward for the byssus and byssal groove to be functional. This position is illustrated (shown in cross-section) by Runnegar and Gobbett (1975) and Thiele and Tichy (1980), but is opposite to that inferred by Termier *et al.* (1973) and Kochansky-Devidé (1978). The latter two reports were on material separated from outcrop and lacking field evidence for positioning, whereas the available field data for *Shikamaia* (*Tanchintongia*) *perakensis* and *S. akasakaensis* show the ventral surface downward to be correct. This should apply to all species in the family.

Modern bivalve genera with a very flattened form provide some useful comparisons. Very flattened form is correlated with free-living, epifaunal habits when the shell is nearly circular in outline—such as the Pectinidae, and the genera *Corculum* (Cardiidae) and *Placuna* (Anomiidae). Alatoconchids like *Saikraconcha tunisiensis* have a form quite similar to *Corculum*, which is flattened in an anterior–posterior direction and has large wings in which the shell is folded in such a way that the sides are nearly parallel to each other. Since the hinges of the two groups are fundamentally different, the similar shapes exemplify convergence in form. *Corculum* lies on the substrate with its wings parallel to the sediment surface. Its nearly flat surface (posterior for it) is up (Bartsch 1947; Kawaguti 1950; Vogel 1975), and it is positioned like a typical cardiid bivalve. In *Corculum*, the anterior projection of the shell houses the foot—an organ of positioning, which on occasion does secrete some byssal threads (Kawaguti 1950)—and the flat posterior surface is adapted for transmitting light to culture endosymbiotic zooxanthellae (Kawaguti 1950; Vogel 1975). From this comparison it is apparent that the flat surface of such a shell indicates horizontality, but does not indicate an up or

down direction for the shell. The location of the foot indicates a down direction, and this can be determined by the position of the byssal opening. Using this relationship, *S. tunisiensis* can be confidently oriented, since it has a byssal notch, indicating the location of the foot. The byssal collar was oriented downward, with the wing-like flanges horizontal on the sediment surface. This is the same orientation as for *Shikamaia (Tanchintongia) perakensis*, and supports the idea of ventral-down orientation for all species in the family.

LIFE HABITS

Alatoconchids are inferred to have been epifaunal suspension-feeders, with a reclining habit. The large, wing-like flanges, byssal opening, and very thick, heavy shell indicate an epifaunal habit. Inasmuch as modern epifaunal bivalves are practically all suspension feeders, there is no reason to doubt that this mode of feeding typified the alatoconchids. The heavy, alate, wing-like flanges are functionally adapted for resting on the surface of the substrate, as well as for stabilizing a shell subject to current or wave activity, and are incompatible with an infaunal habit. The byssal opening of smaller specimens indicates either epifaunal attachment or a partially buried endobysate condition, but the latter condition would be impractical for a shell with wide, wing-like flanges. A very thick, massive shell is associated with epifaunal habit in modern families of bivalves (Ostreidae, Isognomonidae, Chamidae, Tridacnidae), and is very rare among infaunal bivalves. Since large alatoconchids do not have a functional byssal opening, byssal attachment of small growth stages changed to a reclining life habit, lying passive and unattached on the surface of the sediment. Stanley (1970, p. 35) notes that a striking feature of reclining forms is their tendency to develop very thick shells, which is certainly true of the alatoconchids.

Most recliners are inequivalved and pleurothetic (resting on one valve), reflecting their evolution from ancestors cemented by one valve, whereas alatoconchids have a non-pleurothetic orientation, with a vertical plane of commissure. This is a result of evolution from byssally attached ancestors, where the byssus emerged from between the valves. Smaller alatoconchids were byssally attached, and only large alatoconchids achieved a completely reclining life habit. For bivalves with a vertically aligned plane of commissure, a true reclining life habit requires large, flat supporting surfaces on both valves. Even so, the rarity of vertically aligned planes of commissure among recliners suggests that this condition is disadvantageous. Such bivalves have a partly buried shell margin along the supporting surface of the shell, which presents a potential problem with sediment fouling. Whenever the shell opens to allow feeding, the bottom margin opens as well, and sediment could be forced up into the interior of the shell. Being passive animals, the reduced foot was probably of little use in performing a cleaning function when sediment did enter the shell. This functional disadvantage could be alleviated by a minimal shell opening, and by uptilting the abapical shell margins.

The flat basal surface probably did not maintain a truly horizontal position, since the heavy, infilled umbones would tend to settle down into the sediment, at the same time rotating the much lighter posterior end up a short distance above the substrate. This orientation would be beneficial, lifting much of the abapical shell margin a bit above the substrate to improve suspension-feeding capabilities, while reducing the problem of sediment fouling along some of the ventral margin, yet not sacrificing the stability afforded by the wide flanges spread across the sediment surface. A rotation of 10° would have the desired effect, and a consistent down-tipped beak is to be expected of such umbo-heavy shells. This suggests that heavy, infilled umbones are functionally useful in alatoconchids, rather than an accidental feature.

ENVIRONMENTAL SETTING

Alatoconchid occurrences have been referred to as reefs (Salopek 1942, referred to the Yugoslav occurrence as an oyster-bank), and the bivalves have been described as reefal in character (Termier *et al.* 1973). Such interpretations for alatoconchids are not warranted by either their morphology or by their mode of occurrence; none have actually been found in reef deposits, although the Tunisian

specimens are from a stratigraphic interval containing bioherms. The large wing-like flange is poorly adapted for a reef-top environment, but is a good adaptation for life on a loose sediment surface. Furthermore, alatoconchid shells have a regular growth form showing no evidence of crowding during life. While a reef habitat can be ruled out, alatoconchids may have occurred in bank settings (following terminology of Heckel 1974), where large numbers of these large shells created baffles that trapped sediment. However, they appear capable of only limited bank development, and certainly not to the stage of a typical oysterbank. The abundance of alatoconchid shells at localities in Yugoslavia, Malaysia, and Japan suggests that these bivalves tended to live in gregarious clusters. This would explain the large number of specimens found at some localities, in contrast to the relatively small number of localities that have yielded alatoconchids. Both the H. S. Lee locality in Malaysia (see Runnegar and Gobbett 1975, pls. 45 and 46) and a previously unreported occurrence in Japan (K. Ozaki, in correspondence) have many bivalved specimens preserved in life position.

Alatoconchids occur in a matrix of fine-grained sediment containing bioclasts in Tunisia, Afghanistan, Malaysia, and Japan. In the Malaysian and Tunisian occurrences, the rock is light-coloured packstone, poorly sorted, with a bimodal mixture of many broken and complete bioclasts (excluding the alatoconchids themselves) in a fine-grained matrix. Diverse molluscs, and common foraminifers, ostracodes, calcareous algae, and echinoderm plates indicate a shallow depositional environment, probably sublittoral, with moderate or intermittent wave/current energy conditions. The conclusion of Runnegar and Gobbett (1975, p. 321) that *Shikamaia* (*Tanchintongia*) *perakensis* lived in a high-energy environment is not supported by the nature of the sediment, which contains much fine-grained material. In the Afghan and Japanese occurrences, the rock is a dark-coloured, silty, lime mudstone, containing bioclasts and some non-carbonate sediment. The fine grain size and dark coloration indicate low-energy depositional conditions.

The available field information suggests that alatoconchids preferred fine-grained sediment substrates. The large size and great weight of the shell require that the substrate have good bearing strength, such as muddy sand or even stiff mud, but alatoconchids have not been found in winnowed sands or in coarser sediments. They appear to have preferred moderate-energy environments, even if capable of surviving in high-energy environments. Associated fossils—calcareous algae, corals, brachiopods, molluscs—indicate shallow or very shallow water conditions.

GEOGRAPHIC DISTRIBUTION

Alatoconchids occur from the Mediterranean region eastward to Japan. They are known from Djebel Tebaga in central Tunisia (Boyd and Newell 1979), the Velebit Mountains in northern Yugoslavia (Kochansky-Devidé 1978), two localities near Mahallat in central western Iran, and one locality near Shahpoor in the north-western corner of Iran (Thiele and Tichy 1980), two localities (Al-e Say Pass and Bulola Peaks) in central Afghanistan (Termier *et al.* 1973), the Kinta Valley in west Malaysia (Runnegar and Gobbett 1975), and two localities in the Akasaka area in central Japan (Ozaki 1968). This distribution coincides closely with the extent of the Tethyan marine province of the Permian, which occupied the palaeoequatorial zone from the present Mediterranean eastward to east Asia. Alatoconchids are known from all major parts of the province except China, and in future collecting they should be found there as well.

Can the distribution of the alatoconchids be expected to extend to the tropical Permian deposits of the American continents? At present they have not been found in the Americas, and it is reasonable to infer that they will not be found there. The high diversity of organisms, widespread occurrences of reefs, and palaeomagnetic data, all indicate that the Permian strata of west Texas and adjoining New Mexico and Mexico were deposited within a tropical climatic belt, yet no alatoconchids have been found there despite the fact that these sequences are among the most intensively studied Permian deposits in the world. This is not due to absence of the appropriate depositional environment, or to paucity of outcrops. The well-exposed strata contain fine- to coarse-grained siliciclastic and carbonate shelf sediments, and small to large reefs with associated back-reef and basinal fore-reef environments.

Alatoconchids appear to have been excluded from the Americas during the Permian much as modern Indo-Pacific province species are excluded from the Americas today (Emerson 1978).

Since the alatoconchids have a distribution coincident with the Tethyan province as presently known (Yancey 1979), they themselves help define the province, and are an excellent indicator because they are large and easily recognized, even in a fragmentary condition. With this addition, there are three groups of large invertebrates, taxonomically distinct at the family level, which help define the Permian Tethyan province: the bivalve family Alatoconchidae, the fusulinacean family Verbeekinidae (see Gobbett 1967; Ross 1967), and the coral family Waagenophyllidae (see Minato and Kato 1965; Rowett 1972).

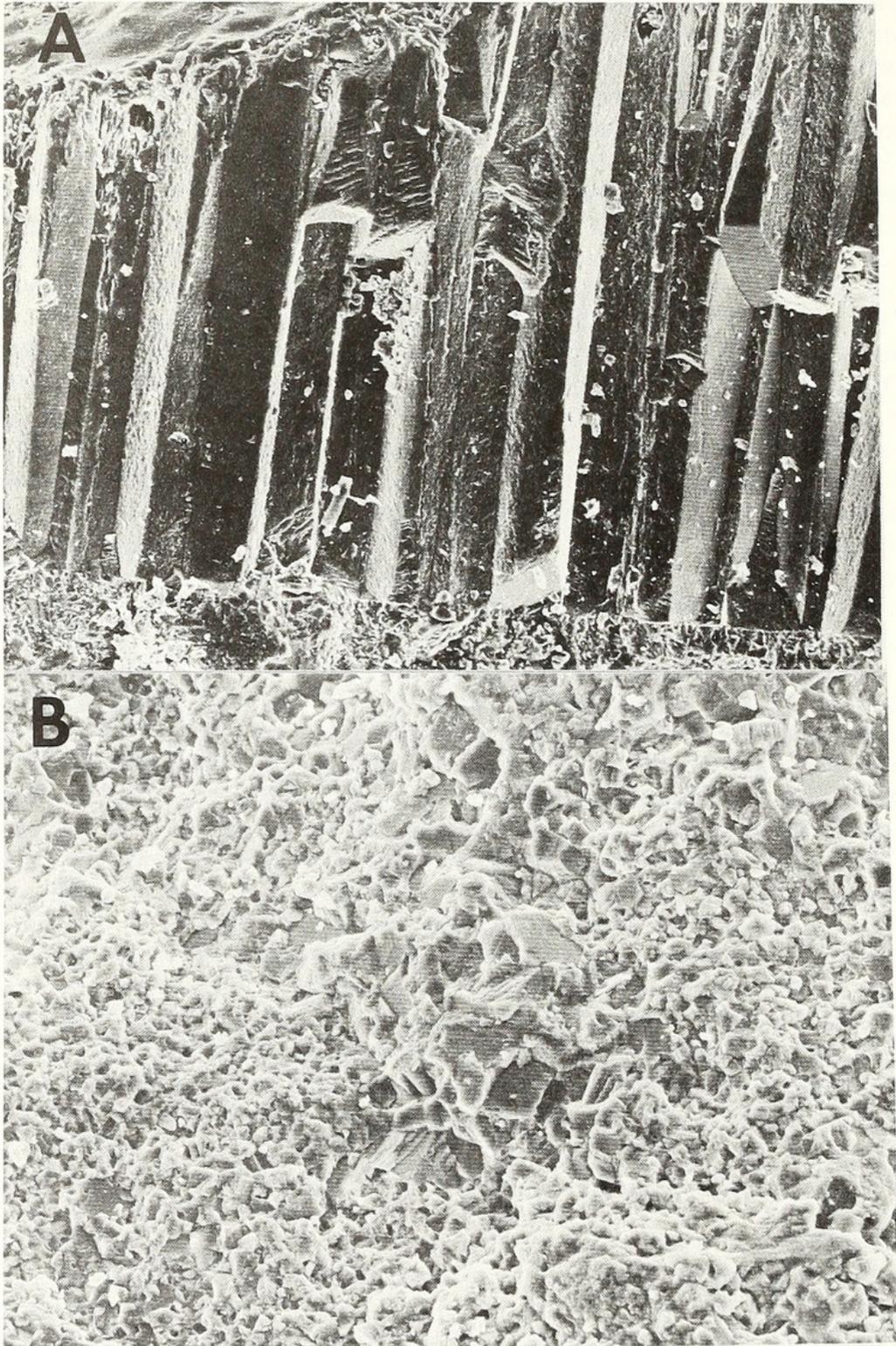
AGE DISTRIBUTION

Alatoconchids are known from an interval including about half of the Permian System. This interval includes the *Pseudofusulina*, *Parafusulina*, and *Neoschwagerina* assemblage zones of the generalized Japanese standard (see Toriyama *et al.* 1974; Minato *et al.* 1978), which corresponds to the Leonardian and Guadalupian series of the Texas succession (see Ross and Nassichuk 1970). No consistent set of stage or zone names has been established for the Tethyan province, so alatoconchid occurrences are referred to in terms of local fusulinid zones where possible. The oldest known alatoconchids, *Shikamaia (Tanchintongia) perakensis* and *Saikraconcha (Dereconcha) kamparensis*, are from Malaysian strata of the *Pseudofusulina ambigua* Zone, which Ingavat *et al.* (1980) correlate with the lower part of the Artinskian Stage, and Runnegar and Gobbett (1975) correlate with the lower part of the Leonardian Series. Unidentified alatoconchids of similar age are known from Iran (Thiele and Tichy 1980). *Shikamaia akasakaensis* is reported to occur in the *Parafusulina* Zone of the Akasaka Limestone (Ozaki 1968), suggesting a younger age than the Malaysian or Iranian beds. However, the age determination for the Akasaka alatoconchids is based on fusulinids from loose limestone blocks not directly associated with the bivalves, and possibly derived from other horizons.

The youngest occurrences are from Tunisia, Yugoslavia, and Afghanistan, and are in the *Neoschwagerina craticulifera* Zone and *Neoschwagerina margaritae* Zone and its equivalents, which together make up the *Neoschwagerina* assemblage Zone. In Afghanistan, *Shikamaia (Alatoconcha) vampyra* occurs in both the *N. schuberti* Zone (= *N. craticulifera* Zone in other areas) and the *N. margaritae* Zone. These two zones are placed in the mid and upper parts of the Murghabian Stage, respectively (Leven 1967). In Yugoslavia, *Saikraconcha ogulineci* occurs in the *N. craticulifera* Zone (Kochansky-Devidé 1978), and in Tunisia, *S. tunisiensis* occurs in strata containing *Neoschwagerina* and *Yabeina*, correlated with the *Neoschwagerina* assemblage Zone (Toriyama 1973, p. 500) and with the Wordian and/or Capitanian stages of the Guadalupian (Newell *et al.*, 1976, p. 83). The concentration of younger Permian occurrences in the western Tethyan province is probably a result of more collecting in this area where younger Permian strata predominate over older Permian strata.

SHELL MICROSTRUCTURE

Alatoconchid shells have an inner shell layer of granular crystals, and an outer shell layer composed of large diameter simple prisms of calcite oriented perpendicular to the shell surface (text-fig. 3). These prisms form a thick (as much as 3 mm) layer over most of the shell, and are much larger than simple prisms occurring in modern bivalves (Taylor and Layman 1972). In *Saikraconcha tunisiensis* the prisms typically have diameters of up to 0.2 mm, and lengths of 3 mm, and in the byssal collar where the outer shell layer is greatly thickened they are nearly 1 cm long. This shell structure is similar to that found in the pinnid and inoceramid bivalves, but differs in the larger size of the prisms. Individual prisms extend across accretion surfaces and traverse the entire thickness of the prismatic shell layer, rather than being interrupted periodically at growth surfaces. Because of their size and coarse texture, these prisms disaggregate easily if the organic sheath around each crystal is destroyed. The sediments containing *S. tunisiensis* contain isolated prisms and bundles of prisms of this sort, much like inoceramid prisms, but larger. The coarse prismatic shell layer of the alatoconchids was



TEXT-FIG. 3. Shell microstructure of *Saikraconcha tunisiensis* n. gen. n. sp. A, coarsely prismatic outer shell layer, outer surface of shell towards top of photograph, and contact with inner shell layer at bottom of photograph, magnification $\times 70$; B, granular inner shell layer, with patches of larger granular crystals (probably due to recrystallization), magnification $\times 200$, from paratype, USNM 353923.

noted in the original descriptions of *Shikamaia akasakaensis*, *Saikraconcha ogulineci*, and *S. tunisiensis*, and has also been observed on *Shikamaia (Tanchintongia) perakensis* and *Saikraconcha (Dereconcha) kamparensis*. The presence of this shell layer could not be established for the available material of *Shikamaia (Alatoconcha) vampyra*, because of recrystallization.

The inner shell layer of the alatoconchids is composed of a mosaic of granular crystals of calcite. In most cases these are much smaller than the prisms of the outer shell layer, but patches of large granular crystals up to 2–3 mm diameter occur in some shells. The smaller of these crystals may be remnants of original shell material, but it is more likely that in the available specimens the inner shell layers have been completely recrystallized. The lack of correspondence between growth bands (shown by colour) and the areas of large and small granular crystals, together with the crystalline texture, suggest complete recrystallization has occurred. This shell layer was probably deposited as aragonite, which would normally be recrystallized in rocks of Permian age. In *Saikraconcha tunisiensis* there are visible traces of tiny, long crystallites oriented perpendicular to the shell surface, and Kochansky-Devidé (1978) described the microstructure of the inner shell layer of *S. ogulineci* as being finely prismatic.

Shell layers composed of large diameter crystals are very translucent, since there are few crystal boundaries to cause scattering of light. In alatoconchids this is the first shell material secreted by the mantle edge, and thus the growing margins of the shells are highly light-transmissive in a zone a few centimetres wide on either side of the plane of commissure. This may have been utilized to culture symbiotic algal zooxanthellae in the tissue of the animal, an adaptation known to be important in some modern bivalves, and possibly in the extinct rudists (Vogel 1975) and the extinct megalodontids (Fischer 1964, pp. 131–133).

RELATIONSHIPS AND EVOLUTION

The family Alatoconchidae is most closely related to the Myalinidae in the Ambonychiacea, as shown by the duplivincular ligament, thick shell wall, and shell shape. The alatoconchids appear to have had anisomyarian musculature, like their myalinid contemporaries. Runnegar and Gobbett (1975) placed the subgenus *Tanchintongia* in the Myalinidae, but this, and all other genera and subgenera discussed here, differ sufficiently from the myalinids to justify placement in a separate family. The strong, wing-like umbonal carina on juvenile and adult specimens, large shell size, thick coarsely prismatic outer shell layer, and distinct byssal groove warrant recognition of the group as a separate family. In addition, some genera possess a byssal collar, which is unknown in the Myalinidae.

Termier *et al.* (1973) suggested a placement of the Alatoconchidae in the Megalodontacea on the basis of hinge characters. The complex ligament and hinge teeth that they envisioned are now known to be incorrect, and the suggested relationship is invalid. Alate extensions of the hingeline on some juvenile specimens suggest a relationship to the Pteriidae or Bakevelliidae, and the coarsely prismatic outer shell layer suggests possible relationship to the Pinnidae or Inoceramidae, but the possibility of a close relation is precluded by the lack of ligament pits in alatoconchids, the possession of a duplivincular rather than multivincular or mytilid type ligament, and greater similarity of the total form to that of the myalinids. A coarsely prismatic outer shell layer is relatively rare in bivalves, but this feature cannot be taken by itself to indicate a close relationship.

Within the alatoconchids two main lineages can be defined by the character of the hinge. *Saikraconcha* has a simple duplivincular ligament occupying a relatively small ligament area, distinct byssal groove, and large byssal collar, while *Shikamaia* has a modified duplivincular ligament occupying only half of a large cardinal area, has a poorly developed to obsolete byssal groove, and lacks a byssal collar on adults. These differences are found in the Malaysian collection containing *Saikraconcha* and *Shikamaia*, suggesting that the two lineages were established early in the Permian, and persisted into the Late Permian. In both lineages there is a trend from an elongate shell outline for Early Permian species to a rounded shell outline for Late Permian species. Life orientation of the shell does not change during this trend, which culminates in a form and life orientation close to that of the modern genus *Corculum*.

SYSTEMATIC PALAEOLOGY

Family ALATOCONCHIDAE Termier, Termier and Lapparent 1973

Diagnosis. Large to very large equivalved shells with elongate or circular outline in dorsal view; shell wall thick, with massive infilling of umbonal cavity, but thin on leading edge; beaks commonly terminal; umbonal carina alate, compressed dorsoventrally and laterally produced, resulting in distinctive wing-like flanges formed by reflexed valve wall; very large flat ventral surface, bounded by umbonal carina; ligament duplivincular; byssal groove present, but non-functional in adults of some species; outer shell layer composed of very large simple prisms set perpendicular to shell surface.

Discussion. It has been called to our attention that the family name Alatoconchidae may not comply with provisions of the International Code of Zoological Nomenclature, Article 11e, which states that 'a family-group name must, when first published, be based on the name then valid for a contained genus', since *Alatoconcha* was inadequately described when first published, and was later placed in synonymy with *Shikamaia*. However, article 40 of the ICZN states that a family group name is not changed, even if a name giver is placed in synonymy, so the family name Alatoconchidae remains valid. The family name was validly proposed at first description, although both the generic and family concepts have greatly changed with subsequent redescription of *Alatoconcha*.

Genus SHIKAMAIA Ozaki 1968

Type species. By original designation, *Shikamaia akasakaensis* Ozaki 1968.

Diagnosis. Very large alatoconchids, lacking byssal collar on adults; with large cardinal area; ligament confined to ventral half of hingeline.

Description. Shells elongated in the anterior-posterior (apical-abapical) direction; beaks terminal; shell roughly triangular in anterior cross-section, and greatly flattened posteriorly; posterior margin pointed, and without gape; ventral surface of joined shells is flat and perpendicular to plane of commissure; beaks slightly upturned away from ventral surface; body cavity small because of massive deposits infilling umbonal cavity and outer edges of flanges; shell wall thick except on posterior margin; hinge lacking teeth; duplivincular ligament located on ventral half of large cardinal area; byssal groove on antero-ventral margin, obsolete on adults; prismatic outer shell layer thin.

Subgenus SHIKAMAIA s.s.

Discussion. Very little published information is available for the type species of the genus. Comparisons with other alatoconchid species have been facilitated, however, by unpublished information obtained from supplementary collections of K. Ozaki (written comm. 1982). The type lot consists of portions of very large shells with posterior shell form similar to that of *S. (T.) perakensis*, except that they are larger and heavier, and have an internal ridge along the dorsal margin of the shell not found in other species. The supplementary material collected by Ozaki reveals the characters of the anterior portion of the shell and shows the full form of the adult shell. *Shikamaia (Shikamaia)* has a very elongate form, and a smaller dorsal crest than other subgenera, is very compressed in a dorsal-ventral direction, and has a small byssal collar during the juvenile growth stage. This subgenus is more closely related to *Tanchintongia* than *Alatoconcha*, but can be distinguished from *Tanchintongia* by its smaller, less massive dorsal crest, presence of a small dorsal niche, and presence of an internal ridge along the dorsal margin of shell. Until the new material came to hand, there was no way to determine the degree of similarity between the two subgenera, but they are now known to be closely related.

Shikamaia akasakaensis Ozaki 1968

1968 *Shikamaia akasakaensis* Ozaki, pp. 28–33, text-figs. 1–5, pl. 7, fig. 1–2; pl. 8, figs. 1–3; pl. 9, figs. 1–2.

Description. Shell with very large wing-like flanges; width across posterior portion of shell as much as 25 cm, and thickness of flange as much as 5 cm; shell outline elongate, with a pointed posterior and anterior ends; length about three times width; dorsal crest small and low; shell wall of wing-like flange averaging 1 cm thick on large specimens; dorsal valve margin thickened internally beside plane of commissure; shell microstructure prismatic in outer shell layer; inner shell layer microstructure unknown.

Discussion. Collection of additional material shows that *S. akasakaensis* is a typical alatoconchid, although larger and heavier than other species. Growth lines on the type specimens show that the shell had a pointed end, and that they are from the posterior portion of the shell. Ozaki (1968) reported that the outer margins of the wing-like flanges are uneven, and undulating, but this appears to represent individual growth irregularities. The distinctive heavy internal thickening along the dorsal valve margin is also found on supplementary material. A few adults of other alatoconchid species show a minor thickening of the valve margin, but the condition is not as pronounced as in *S. akasakaensis*. In common with other alatoconchid species, the dorsal shell wall is thinner than the ventral shell wall, except at the thickened valve margin.

The great width of the type specimens (as much as 30 cm) indicates they reached large size. This is confirmed by specimens seen in outcrop (by K. Ozaki), which have lengths of 60 cm (but incomplete), and width of 20 cm, having a length to width ratio of at least 3 to 1. This indicates that adults reached lengths of 1 m, and possibly more.

This species must be redescribed before detailed comparisons with other species are possible, but it is distinct from all other alatoconchids. Many of the questions about it have been resolved with recently collected specimens, and additional collecting should provide enough material for a detailed description.

Subgenus *TANCHINTONGIA* Runnegar and Gobbett 1975

Type species. By original designation, *Tanchintongia perakensis* Runnegar and Gobbett 1975

Diagnosis. Elongate alatoconchids; wing-like flange and inflated portions of shell forming about equal areas of dorsal surface; pointed beaks projecting far beyond hingeline, and moderately diverging from each other.

Discussion. *S. (T) perakensis* is the best-known alatoconchid species, and is the only one for which early juvenile shell form is known. To the extent that any species or genus in the family can be considered typical, this one is the most representative. It has provided knowledge of the basic form, dorsal crest, wing-like flanges, byssal groove, musculature, hinge, and beak areas, that has made it possible to understand these features on fragmentary or poorly preserved specimens. The recognition of homologous features, such as the byssal groove and wing-like flange, in all species has made it possible to properly characterize the family, and define generic concepts.

Shikamaia (Tanchintongia) perakensis Runnegar and Gobbett 1975

Plate 62

1975 *Tanchintongia perakensis* Runnegar and Gobbett, pp. 316–320, text-figs. 1–2, pl. 45, figs. 1–5 (*non* figs. 6–7); pl. 46, figs. 1–8.

Studied specimens. Nearly thirty specimens in a single lot collected by D. Gobbett and C. T. Tan from the H. S. Lee mine, and housed in the Sedgwick Museum, University of Cambridge, Cambridge, U.K. (SM), and the Department of Geology, University of Malaya, Kuala Lumpur, Malaysia (UM), including the holotype and paratypes, SM G1874, G1875, G1877–1882, and topotypes UM 3070, 3394, 3399, and 4027, and fifteen other unnumbered specimens in the University of Malaya collection.

Description: Large equivalved shells; beaks terminal; length several times height or width; triangular transverse section through anterior part of articulated shell (height of triangle is in plane of commissure, and base of triangle coincides with ventral surface); posterior region flattened, resulting in nearly parallel dorsal and ventral surfaces; shell pointed at anterior and posterior ends, and widest and highest in middle (as much as 10 cm height and 20 cm width across both valves); greatest height and width located about one-third shell length from anterior end, with height decreasing abruptly towards posterior, and width tapering gradually towards a pointed posterior end; sharp umbonal carina, expanding posteriorly to form a wing-like flange as much as 10 cm wide; ventral surface of each valve wide, flat, and perpendicular to plane of commissure; umbones infilled with massive deposits as much as 3 cm thick; body cavity small relative to shell size; beaks not appressed; wide cardinal area between beaks and hinge-line; angle between hingeline and ventral surface varies from 15° to 40°, decreasing through ontogeny; hinge lacking teeth; sharply defined duplivincular ligament field covering part of cardinal area; incised ligament grooves aligned subparallel to hingeline except dorsally, where they curve posteriorly, becoming subparallel to dorsal margin of ligament field; narrow byssal groove present on anteroventral margin, directly beneath ligament area; coarsely prismatic shell laminae cross byssal groove at 45° angle, and weather out preferentially, forming a deep groove-like re-entrant on older part of valve; width of byssal groove varies from 3–4 mm on younger shells to 1 cm on large adults; shell wall thickness averaging 1 cm, but as much as 3 cm in apical area, and relatively thin (2 mm) on posterior margin; outer shell layer of coarse prisms, best developed in byssal area.

Discussion. *S. (T.) perakensis* is described from about thirty specimens, including eight specimens of the type lot, and three articulated ones. Runnegar and Gobbett's concept of the form of the shell is modified, especially for the body cavity and posterior regions. Their reconstruction of these regions was based on SM G1880, which is a fragment of the anterior portion of the body cavity, rather than the posterior end. Contrary to their opinion, the shell does not have a noticeable posterior gape, nor a byssal opening in adults. The statement concerning the umbonal septum (1975, p. 316) is based on a specimen assigned here to a different genus. On the other hand, the basic nature of the hinge and the presence of an obsolescent but prominent byssal groove were correctly determined, and the life orientation of the shell and life habits of the adults were clearly indicated. Additional material has greatly increased knowledge of ontogenetic changes in form and life habits.

Hinge. The hinge lacks teeth, and has a short duplivincular ligament. On juvenile shells the ligament extends along the entire hinge-line, but on large shells the ligament extends along only the anteroventral half of the hinge-line. Large shells have a well-defined ligament area on the ventral half of the cardinal area, marked with irregular ligament grooves aligned parallel or at a small angle to the hinge-line. The ventral margin of the ligament area is coincident with the byssal groove, and the dorsal margin is formed by a zone of convergent ligament grooves where the grooves curve sharply towards the body cavity and converge into a narrow zone aligned at a high angle to the hinge-line (see Pl. 62, figs. 1–2). Abapical convergence of ligament grooves to the hinge-line occurs in many

EXPLANATION OF PLATE 62

Figs. 1–10. *Shikamaia (Tanchintongia) perakensis* (Runnegar and Gobbett). 1, 2, UM 3399, dorsal and interior views of beak and apical portion of right valve, showing byssal groove along anteroventral margin, triangular ligament area, with large curved or winding ligament grooves that curve posteriorly at dorsal margin of ligament area (marked by arrow), and apical portion of body cavity. 3, 4, UM 3070, posterior and dorsal views of large articulated specimen, incomplete at both ends. 5–7, UM 4027, dorsal, ventral, and posterior views of articulated juvenile specimen, showing small byssal opening (marked by arrow), and strongly developed wing-like flange on early juvenile part of shell. 8, 9, UM 4027, external and internal views of left valve of juvenile, showing dorsal crest, and growth lines on dorsal and ventral surfaces. 10, UM 3394, ventral view of posterior portion of right valve, with plane of commissure at top of photograph and posterior termination of shell (abapical) to the right. The small angle between growth lines and outer margin of the flange (bottom of photograph) demonstrate a closed, pointed posterior end on the shell (refer to text-fig. 1). All specimens are from the same collection from which the holotype and paratypes were selected. All magnifications $\times 1$ except 3 and 4, which are $\times 0.5$. All from H. S. Lee mine, near Kampar, Kinta Valley, Perak, West Malaysia, H. S. Lee beds, Early Permian.



YANCEY and BOYD, Alatoconchidae—Permian bivalves

duplivincular ligaments, but such sharp curvature of ligament grooves has not been observed in other species. Whether this character is restricted to *S. (T.) perakensis* or is a feature of the ligament area of all species of *Shikamaia* is not determinable from the specimens presently available. Another unusual feature of the ligament is its limitation to only half of the hinge-line, in contrast to most duplivincular ligaments which have ligament grooves along the entire hinge-line. This shortened ligament may have arisen as an adjustment to the large size of the adult shell. The irregularity of the ligament grooves on some specimens is unusual, and makes one initially sceptical of their origin as ligament grooves. However, their ligament character is convincingly shown on several specimens because of the sharpness of the incisions, the consistent restriction of the grooves' area to the anteroventral half of the cardinal plate (also noted by Runnegar and Gobbett 1975), and the intersection of the younger grooves with the linear margin of the body cavity.

Byssal notch. Juvenile shells have a deep rounded notch crossing the shell margin very close to the apical end of the body cavity, which forms a circular or heart-shaped opening through the articulated valves as much as 0.5 cm in diameter. It passes through the shell at an angle of about 45° to the anteroventral margin of juvenile shells, and is aligned nearly parallel to the anterior-posterior axis of the shell (see Pl. 62, fig. 9). With growth the byssal opening is extended posteriorly by umbonal infilling, and forms a groove along the anteroventral margin of the valve that is noticeable on all shells, even on strongly eroded ones. In adults a byssal opening is not present (see Pl. 62, fig. 2), but the position formerly occupied by the byssal notch is marked by a zone of easily eroded shell material. The byssal groove is continually being formed as a result of erosion of this weak shell material, which is separated from the body cavity by a thin rim of dense shell material. The weak shell material contains many laminae of coarse, simple prisms set perpendicular to the growth surface, here aligned at 45° to the ventral margin of the shell; these prisms adhere weakly to each other and are susceptible to breakage. Consequently, the byssal groove that is characteristic of *Shikamaia* is secondarily formed, and not from a functional byssal notch. The byssal notch of juvenile shells is proportionally large enough to have contained a byssus capable of anchoring the shell, but the byssal area of an adult shell does not seem large enough to have contained a byssus adequate to support the mass of animal plus shell at this growth stage. The byssal notch was probably closed off by the time the shell reached a length of 10–15 cm.

Size and weight. Reconstructions show that the average length/width ratio for complete adult shells is about 3. Mature articulated individuals with widths of nearly 20 cm are shown in plate 45, figure 8, of Runnegar and Gobbett (1975), and single valves in our collection are almost 10 cm in width. The total length for these shells probably was close to 60 cm, and the dorsal crest extended as much as 10 cm above the ventral surface of the shell. Shell dimensions for typical adults were probably 10 cm height, 20 cm width, and 60 cm length.

The large size and thick shell wall produced a remarkably heavy shell. Many fragmentary valves (free of matrix) weigh over 50 g, and the beak areas alone of smaller specimens weigh up to 300 g. The greatest wall thickness is in the mid-region of the shell around the anterior end of the body cavity. The heaviest shell fragment studied weighed about 1 kg, suggesting about 4 kg for a single valve, and 10 kg total shell weight for an old individual.

Musculature. The animal had a large posterior adductor muscle, and was probably anisomyarian, like myalinids and mytilids. A large (approx. 4 cm²) muscle scar is visible on two shells near the posterodorsal end of the hinge-line. No other muscle scars have been identified, but the observed position of the muscle scar in a shell that is basically mytiliform favours the anisomyarian interpretation.

Subgenus ALATOCONCHA Termier, Termier and Lapparent 1973

Type species. By original designation, *Alatoconcha vampyra* Termier, Termier and Lapparent 1973

Diagnosis. Large alatoconchids with wide wing-like lateral flanges extending from anterior to posterior ends of shell; outline of shell margin subcircular rather than elongate; beaks incurved and

nearly touching; dorsal margin of cardinal area on each valve bowed out to enclose a wedge-shaped depression.

Discussion. *Shikamaia* (*Alatoconcha*) differs from other subgenera in characters of form; greater extent of flanges, more rounded outline, having a dorsal niche formed by the curved cardinal areas, and having umbonal cavities. In the original description, it was suggested that the shell had a parivincular ligament, a small secondary ligament, and a large tooth on the hinge. The narrow, arcuate groove interpreted by the authors of *Alatoconcha* as the scar of a parivincular ligament is identical in form and position to the byssal groove of *Tanchintongia*. The features originally interpreted as a secondary ligament pit and tooth appear to be based on imperfections of the fossil. As far as can be determined, the hinges of the two subgenera are the same.

A feature described for *Alatoconcha*, but rare or absent in other subgenera and genera in the family, is compartmentalization within the reflexed part of the valve ('arc-boutant' of Termier *et al.* 1973). Compartments are separated by curved lamellae, concave towards the commissure, which represent periodic withdrawal of the mantle from contact with the shell interior. These probably open to the outside on the posterior end of the shell, and appear to be an accidental rather than normal feature of the shell. They result from trauma to the animal, producing irregular growth, so that shell formation occurred as jumps rather than continuous growth.

Shikamaia (*Alatoconcha*) *vampyra* Termier, Termier and Lapparent 1973

Plate 63, figs. 1–4; text-fig. 4

1973 *Alatoconcha vampyra* Termier, Termier and Lapparent, pp. 75–80, text-figs. 1–6, pls. 13–14.

Type specimens. one large bivalved specimen (holotype) and several smaller fragments (paratypes) all housed in the Palaeontology collections of the Dept. of Earth Sciences, University of Lyon, Villeurbanne Cedex, France. All specimens are unnumbered.

Description. Medium-sized, equivalved shells, reaching lengths of 20 cm, widths of 15 cm, and height of 5 cm; flanges on the anterior portion of the shell are dorsally upturned, producing a curved ventral surface; beaks appressed; wedge-shaped dorsal niche present anterior to dorsal crest, formed by bowed-out cardinal area, and bounded by hinge-line, appressed anteroventral margin of cardinal area, and appressed beaks; hinge-line located on thin shell wall of cardinal platform, which forms wall of umbonal cavity; beaks partly infilled with massive deposits; shell wall thick, as much as 1 cm in beak area; hinge-line aligned at low angle with ventral shell surface; hinge lacking teeth, although a rudimentary bump or node may form at posterior end of body cavity; ligament unknown—probably duplivincular; prominent but narrow byssal groove located along anteroventral margin of cardinal area; byssal groove on large specimens closed off from body cavity by a thin, even rim of shell.

Discussion. *S. (A.) vampyra* is known from one 12 cm long, nearly complete, articulated specimen, and several small fragments of the posterior region of the shell. Termier *et al.* (1973) suggested that *S. (A.) vampyra* is related to the Megalodontidae, because of the strong umbonal carinae, suggested presence of large teeth, and a complex ligament. The feature that Termier *et al.* (1973) interpreted as a tooth is in fact a fragment of the opposite valve, and in that location the valves are not in contact with each other. The feature suggested to be a parivincular ligament groove ('rainure ligamentaire') is the byssal groove characteristic of all species of *Shikamaia*. The feature suggested to be a ligament pit ('fossette ligamentaire') is part of a shallow depression on the anterior end of the body cavity of one valve, and probably varies in prominence from specimen to specimen. Ligament grooves are not discernible on the holotype of *S. (A.) vampyra*, but the arcuate groove on the hinge is a key character in the interpretation of the hinge, and is homologous with the marginal byssal groove of *S. (T.) perakensis*. The dorsal and ventral directions chosen by Termier *et al.* (1973) must be reversed, as must the designation of left and right valves. Their comparison of *S. (A.) vampyra* with the outline of a bat in flight, as shown in the reconstruction drawing (their text-fig. 4) is misleading, and the fanciful name *vampyra* is inappropriate. The irregular form suggested in their text-figs. 1–4 is not characteristic of the shell, which is rather graceful in form. Breakage and deformation have created the irregularities, which were exaggerated in the illustrations.

The apical area and body cavity portions of *S. (A.) vampyra* are similar to those of *S. (T.) perakensis* except for the presence of the dorsal niche and umbonal cavities. The shell wall is as much as 1 cm thick, but is thin on the cardinal platform and the wing-like flanges. The shelf-like cardinal platform is thin on its leading (growing) edge, and makes a rather weak hinge for such a large shell. Shell walls on the flange vary from 1 to 3 mm in thickness, and the flange is about 0.5 cm thick. At the anterior end of the shell, the flange margin extends out nearly perpendicular to the plane of commissure. Growth lines on this part of the shell show that the old position of the plane of commissure has rotated outward 70° – 80° around a pole at the position of the beaks. This suggests a shell with rounded outline rather than one with high length/width ratio.

Genus SAIKRAONCHA new genus

Type species. Saikraconcha tunisiensis new species.

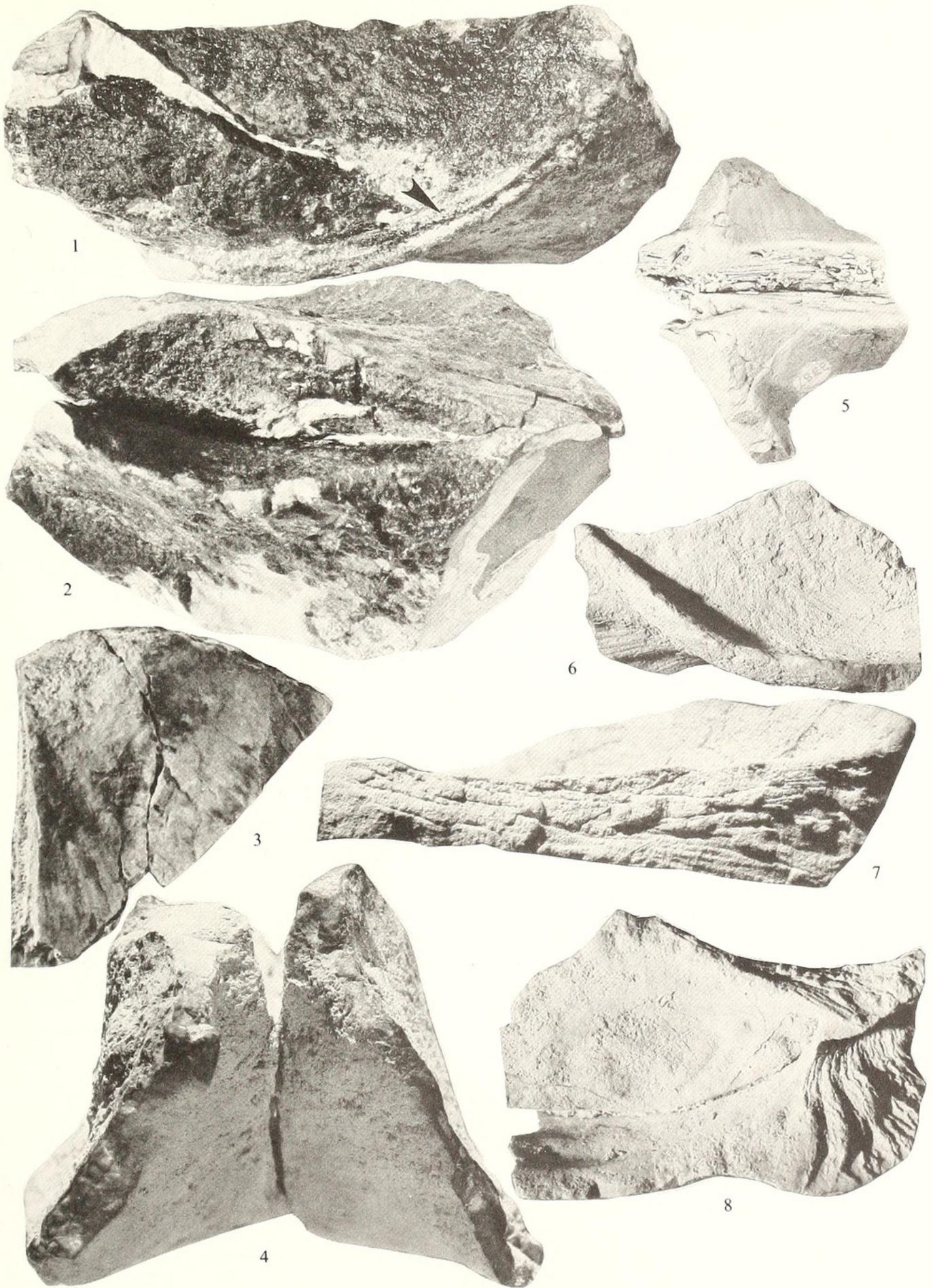
Diagnosis. Alatoconchids with prominent byssal collar on anteroventral margin; byssal groove narrow and deep, and opening into body cavity in adults; ligament area small and extending along entire anterodorsal margin of dorsal crest.

Discussion. The occurrence of an undescribed genus of alatoconchids first became apparent while examining the alatoconchids in the Malaysian collection from Kinta Valley, where two forms are present. The differences were overlooked at first, because very few juveniles of *Shikamaia (Tanchintongia) perakensis* are available, and there was much uncertainty about the amount of variability to be expected in alatoconchid species. The huge, massive specimens of *S. (T.) perakensis* dominate the collection retained at Cambridge (studied by Boyd), and the remainder of the Kinta collection (studied by Yancey) retained at University of Malaya. The authors of *Tanchintongia* based their description on the large, and common, form, although they included some specimens of the second form as paratypes of *Tanchintongia perakensis*, one of which was illustrated in their publication (Runnegar and Gobbett 1975, pl. 45, figs. 6–7). The two forms have greatly different hinges, and the second form is here placed in a new genus. Two other species of this genus occur in late Permian strata in the Mediterranean area, one in Tunisia and another in Yugoslavia. When first

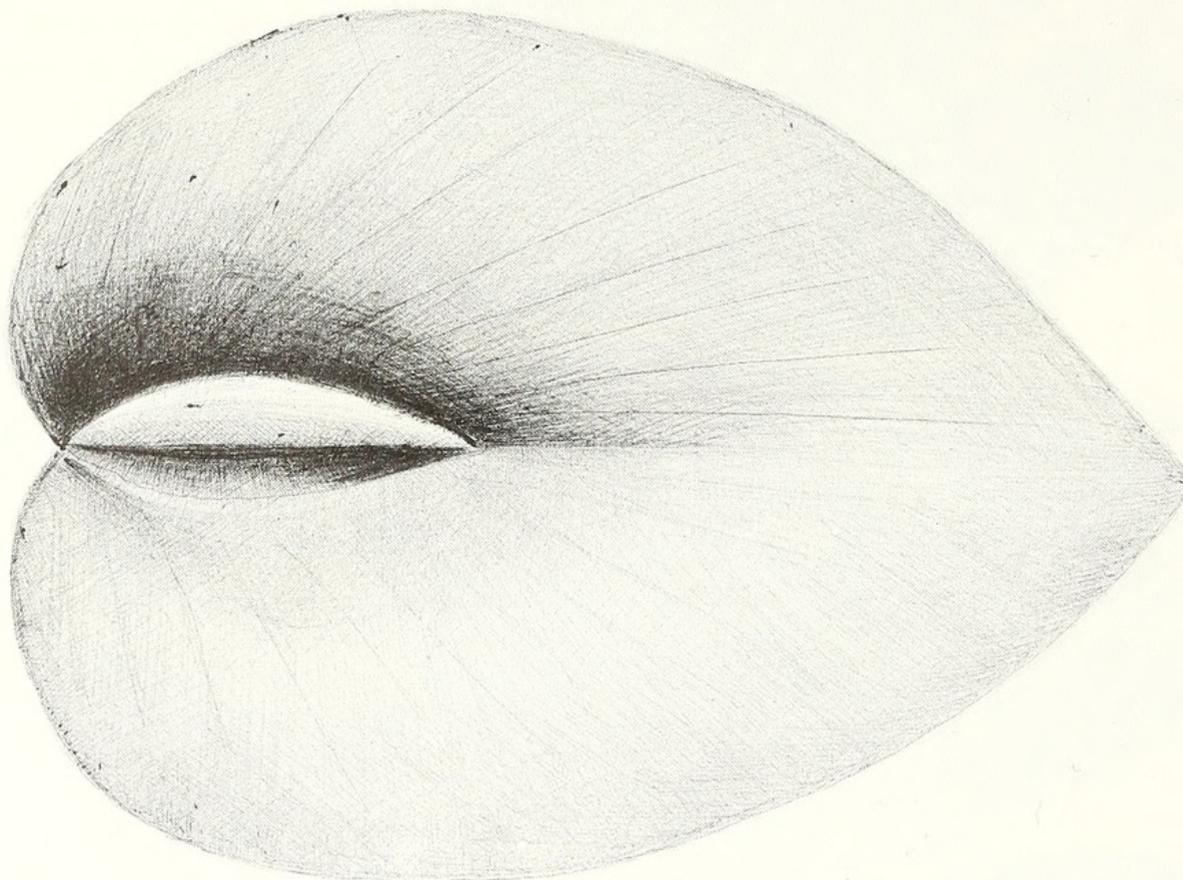
EXPLANATION OF PLATE 63

Figs. 1–4. *Shikamaia (Alatoconcha) vampyra* (Termier, Termier and Lapparent), holotype. 1, interior view of anterior part of the left valve, beak to right, with a portion of the dorsal margin of right valve still adhering to it (in upper left corner of photograph), showing byssal groove (marked by arrow) on ventral margin, glycerine-coated. 2, slightly oblique dorsal view of incomplete articulated specimen, showing large wedge-shaped dorsal niche, beaks are broken and wing-like flanges are missing, glycerine-coated. 3, ventral surface of anterior part of left valve, showing lateral extent of flange on anterior portion of shell, beak in upper left corner of photograph, and plane of commissure along left side of photograph, straight margin of lower right side is artificial, and part of a saw cut, glycerine-coated. The portion of the shell to the right of the fracture is not shown in the other figures, but is part of the holotype. 4, anterior view of incomplete articulated specimen, showing arched ventral surface of anterior prow region, and triangular cross-section of valves, beaks are broken and wing-like flanges are missing, coated with ammonium chloride. All magnifications $\times 1$ except 3, which is $\times 0.5$. From Al-e Say Pass, near Dacht-e Nawar, central Afghanistan, *Neoschwagerina margaritae* zone, upper Murghabian, Late Permian.

Figs. 5–8. *Saikraconcha (Dereconcha) kamparensis* n. gen., n. sp. 5, SM G2695, paratype, anterodorsal view of incomplete articulated shell, showing hinge-line and ligament areas. 6, 8, UM 3380, holotype, external and internal views of nearly complete left valve, magnification $\times 0.8$ and $\times 1.2$ respectively. 7, UM 3380, holotype, enlargement of hinge, showing duplivincular ligament grooves, magnification $\times 2$. All specimens coated with ammonium chloride. From H. S. Lee mine, near Kampar, Kinta Valley, West Malaysia, H. S. Lee beds, Early Permian.



YANCEY and BOYD, Alatoconchidae—Permian bivalves



TEXT-FIG. 4. Reconstruction of the shell form of *Shikamaia (Alatoconcha) vampyra*.

described, these were referred to *Shikamaia (Tanchintongia)* on the basis of large size and wing-like flanges. Further preparation of the Tunisian collection revealed a shell like that of the undescribed genus in the Malaysian collection.

During the course of this study the Tunisian specimens were carefully prepared to show the hinge, which differs in part from the interpretations presented by Kochansky-Devidé (1978) and Boyd and Newell (1979). The portion of the byssal collar between the ligament area and the byssal groove was the most baffling feature, and Boyd and Newell (1979, p. 8) noted its resemblance to a resilifer without specifically ascribing such a function to this feature, while Kochansky-Devidé (1978) interpreted the same feature on Yugoslavian specimens as part of the ligament area. This area was carefully prepared on three Tunisian specimens, and the possibility that it is a resilifer or ligament area can be ruled out, on the basis of no ligament grooves, too rough a surface for ligament attachment, and truncated shell layers exposed on this surface. It is a large byssal collar. With the identity of this feature resolved, the hinge is revealed to be of simple form, while the byssal area has complex form.

The two Mediterranean species are the youngest alatoconchids known, and are also the most unusual in form. Several individuals of *Saikraconcha tunisiensis* have almost wavy, or unusually curved, lateral flanges, instead of the nearly flat flanges of most other species of alatoconchids, and they are the most dorsoventrally compressed of the alatoconchids.

Life orientation for species of this genus is interpreted to be the same as for *Shikamaia*. The very flattened form dictates a horizontal orientation for the wing-like flanges, and the functional byssal opening and thickened shell on the same side of the flanges as the byssal collar indicate that the collar was ventral, and the crest was dorsal. This orientation is opposite to that suggested by Kochansky-Devidé (1978) for *Saikraconcha ogulineci* (Kochansky-Devidé), but its similarity to the better-known *S. tunisiensis* provides compelling reasons for reinterpreting the life orientation of *S. ogulineci*.

Derivation of name. From an arbitrary combination of the word Saikra, name of a village and hill in the Djebel Tebaga region, and the term *concha* as used in *Alatoconcha*, the name given for the family name.

Subgenus SAIKRACONCHA s.s.

Saikraconcha tunisiensis, new species

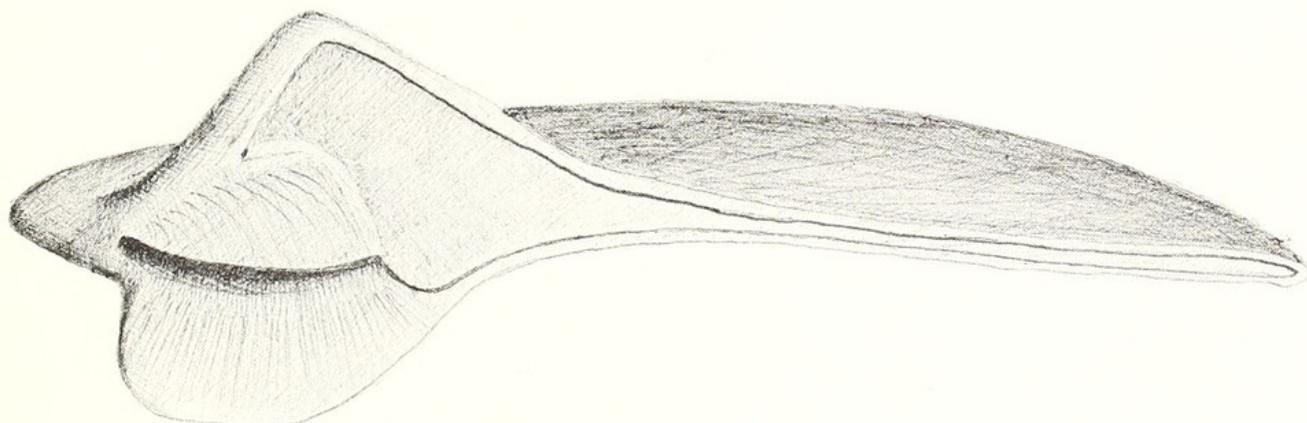
Plate 64, figs. 7–11; text-fig. 3, 5

1979 *Shikamaia ogulineci*, Boyd and Newell, pp. 7–12, text-figs. 8–14.

Type specimens. Twenty-two specimens (most are fragmentary) in a single lot collected by D. Boyd from locality G16 of Newell *et al.* (1976), and housed in the U.S. National Museum, Washington, D.C. Holotype, USNM 258957; Paratypes, USNM 258956, 258958–258962, and 353915–353930.

Diagnosis. Large shells with well-rounded outline, and very flattened along dorsal–ventral axis; umbonal septum on anteroventral margin, between ligament area and byssal notch; large byssal collar; beaks non-terminal, and ventrally down-turned.

Description. Large rounded shells, with width about the same as length; very flattened along dorsal–ventral axis except at anterior end, where a sharp crest occurs on dorsal surface, and a large byssal collar extends below ventral surface; very sharp umbonal carina on anterior end of valves, extending into wing-like flange with limbs 1 cm or less apart; width of flange as much as 15 cm from plane of commissure; flange interior partly infilled in early portions of shell; dorsal crest small, and formed by hinge-line extending away from plane of wing-like



TEXT-FIG. 5. Reconstruction of right valve of *Saikraconcha tunisiensis*.

flanges at a high angle (50° – 70°); ligament duplivincular, with faint, rectilinear ligament grooves, approximately 0.3 mm apart; byssal notch on anteroventral margin, which remained open throughout ontogeny; byssal groove, roughly semicircular in cross-section in each valve, and about 0.5 cm deep in larger valves, extending across middle of wide byssal collar projecting below ventral surface of shell; byssal collar is curved, and with counterpart on opposite valve forms a spout-like opening, bounded apically by appressed beaks; inner surface of byssal collar rough; portion of byssal collar between byssal groove and ligament area covered with curved growth lines, and projects internally along plane of commissure to form a small, thick (as much as 1 cm), blunt umbonal septum; shell wall thick (0.5–2.0 cm) except at distal edges; dorsal shell wall consistently thinner than ventral shell wall; shell wall with an outer shell layer (as much as 2 mm thick) of very coarse (as much as 0.1 mm diameter), simple prisms set perpendicular to shell surface; inner shell layers with a mosaic of granular crystals, probably recrystallized from fine prismatic crystallites.

Discussion. This species is known from a single locality in the Permian strata of southern Tunisia (at the base of unit 16, of measured section G, described in Newell *et al.* 1976, p. 104). As is the case with all other alatoconchid localities, no complete valves are available. The dorsal parts of the valves are lacking in nearly all cases, but the apical region is fairly well determined. The abapical configuration is largely conjectural, but probably is composed exclusively of flat flange; flange margins probably converge abapically without gaping.

The shell is strongly compressed, and umbonal carinae flare widely to form flat, sharp-edged, wing-like flanges perpendicular to the plane of commissure. These give the shell a nearly circular (or heart-shaped) outline in dorsal view. With only small projections perpendicular to the plane of the flanges, the shell approaches *Corculum* in overall form although larger in size. On the anterior end the flange margins meet the plane of commissure at an obtuse angle, producing a V-shaped indentation of the shell margin at the apical end.

The dorsal shell wall of the flange is thinner than the ventral one, and has broken away in nearly all of the collected specimens. This has produced some unusual appearances that have complicated the description and interpretation of this species. On one specimen, breakage of the dorsal shell surface during life of the animal was repaired by withdrawing the mantle from the edge of the flange, and secreting a thinner shell layer between the shell break and the plane of commissure. This is similar to the abrupt withdrawal of mantle edge reported by Termier, *et al.* (1973), but here can be shown to be due to shell damage and injury.

Shell microstructure. Individuals of this species have the best preserved shell microstructure of any species in the family, and in *Saikraconcha tunisiensis* the outer shell layer is quite thick compared to that in other species. The shell has an outer layer (as much as 2 mm thick) of very coarse, simple calcite prisms (as much as 0.1 mm diameter) oriented perpendicular to the shell surface, and an inner shell layer (as much as 2 cm thick). In the outer shell layer each prism crosses growth surfaces and extends across the entire shell layer. Each prism is approximately of equal diameter throughout. They are packed like columns in columnar-jointed rock, and are rather easily separated from each other.

The inner shell layers are recrystallized, but show traces of original microstructure. The present shell fabric is a granular mosaic of fine to coarse crystals, with traces of fine prisms orientated perpendicular to the shell surface, and interrupted by growth lines. The size of these prisms or fibres cannot be determined accurately because of recrystallization, but they are considerably smaller than prisms of the outer layer. They were probably aragonitic and more susceptible to extensive recrystallization than the outer-layer prisms, which were probably originally calcite.

Saikraconcha ogulineci (Kochansky-Devidé, 1978)

1978 *Tanchintongia ogulineci* Kochansky-Devidé, pp. 213–218, text-figs. 1–3.

Diagnosis. Large ovoid shells; beaks terminal; umbonal septum present; large byssal collar.

Description. Large shells attaining width of 30 cm; length unknown, but probably greater than width; wing-like flanges relatively narrow, and slightly undulose; umbonal septum present between byssal notch and ligament

EXPLANATION OF PLATE 64

Figs. 1–6. *Saikraconcha (Dereconcha) kamparensis* n. gen., n. sp. 1–5, UM 3372, paratype, ventral (beaks at right), side (exterior of right valve), anterior, posterior, and dorsal (beaks at left) views of articulated, incomplete juvenile specimen, with posterior portion and nearly all of byssal collar missing, showing outline of wing-like flanges and growth lines. 6, SM G1876, paratype, anterior view of left valve, showing prominent byssal groove just below beak (this specimen was illustrated by Runnegar and Gobbett 1975, pl. 45, figs. 6–7). All magnifications $\times 1$. All specimens coated with ammonium chloride. All from H. S. Lee mine, near Kampar, Kinta Valley, West Malaysia, H. S. Lee beds, Early Permian.

Figs. 7–11. *Saikraconcha tunisiensis* n. gen., n. sp. 7–9, USNM 258957, holotype, anterior, dorsal, and ventral views of incomplete articulated young shell, lacking dorsal and posterior regions, dorsal view showing body cavity with distinct byssal opening emerging between valves, anterior view showing downturned beaks, and ventral view showing ovoid opening formed by byssal collars. 10, USNM 258957, holotype, hinge view of anterior portion of incomplete left valve, anterior to right. 11, USNM 258957, holotype, hinge view of right valve, anterior to left, with encrusting coral growing on anterior end of byssal groove and on beak. All magnification $\times 1$. All specimens coated with ammonium chloride. From locality G16 of Newell *et al.* (1976), east end of Djebel Tebaga Range, near Medenine, Tunisia, Saikra biohermal complex, Late Permian.



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area; large byssal collar projecting ventrally, with ovoid opening about twice as long as wide; beaks appressed together, and located at anterior end of shell; ligament probably duplivincular.

Discussion. *S. ogulineci* is closely related to *S. tunisiensis*, but differs from it in shell proportions, and placement of the beaks. Kochansky-Devidé (1978) described it as being about twice as long (anterior-posterior) as wide, but this was for a reconstruction, which was probably influenced by the illustrated reconstruction of *Shikamaia (Tanchintongia) perakensis* published by Runnegar and Gobbett (1975). The semicircular outline of the flanges is closer to the forms of *Saikraconcha tunisiensis* and *Shikamaia (Alatoconcha) vampyra*, relatively wide shells, than to the wedge-shaped anterior portions of the elongate *S. (T.) perakensis* and *Saikraconcha (Dereconcha) kamparensis*. The two Mediterranean species of *Saikraconcha* differ most noticeably in the curvature of the beaks. *S. ogulineci* has beaks which touch at the anterior end of the shell. The beaks of *S. tunisiensis* are ventrally downturned, and are not terminal. The two species may attain similar size, reaching widths of about 30 cm, with *S. ogulineci* being more elongate than *S. tunisiensis*. Kochansky-Devidé (1978) estimated a length of 65 cm for *S. ogulineci*, based on the assumption of it being twice as long as wide, but the shell is probably less elongate than shown in her reconstruction.

A slightly undulose character of the flanges was noted in the original description of *ogulineci*: loosely translated 'In side view, the flank edges are somewhat wavy'. This is apparent in both *S. ogulineci* and *S. tunisiensis*, and is puzzling since it seems to be irregular, and without function. The character of the byssal collar and byssal groove are well described by Kochansky-Devidé (1978), but are here reinterpreted. She suggested that the wrinkled growth lines on the interior of the byssal collar were the result of ligament attachment, and inferred a divided ligament area traversed by the byssal groove. This is most unlikely, and by comparison with *S. tunisiensis* it is apparent that the ligament area is confined to the outer edge of what she referred to as a 'keel'. Since this feature projected upward, the term keel is inappropriate, and we refer to it as the crest. Kochansky-Devidé oriented the shell with the beaks upturned, and consequently had the byssal collar upturned. Reversing this orientation brings the byssal area into a more logical location, and better positions other shell features.

DERECONCHA new subgenus

Type species. *Dereconcha kamparensis*. new species

Diagnosis. Shell small and elongate; lacking umbonal septum; having prominent byssal collar, all of which is ventral to byssal groove.

Discussion. This subgenus differs from *Saikraconcha (Saikraconcha)* in lacking an umbonal septum. The byssal opening is located at the apical end of the bodycavity, adjacent to the ligament area, and the byssal groove runs along the dorsal margin of the byssal collar, rather than across the middle of the collar.

Derivation of name. From an arbitrary combination of the first four letters of the name Derek Gobbett, and the term *concha* as used in *Alatoconcha*, the name-giver for the family name. Through the efforts of Derek Gobbett, formerly of the University of Malaya, and Tan Chin Tong, University of Malaya, a large collection of alatoconchids was assembled during many collecting trips. At present this is the best collection of alatoconchids available.

Saikraconcha (Dereconcha) kamparensis new species

Plate 63, figs. 5-8; Plate 64, figs. 1-6

1975 *Tanchintongia perakensis* Runnegar and Gobbett, pl. 45, figs. 6-7 (not figs. 1-5 on pl. 45, nor any of pl. 46).

Type specimens. Seven specimens in a single lot of specimens collected by D. Gobbett and C. T. Tan from the H. S. Lee mine, and housed in the Department of Geology, University of Malaya, Kuala Lumpur, Malaysia (UM), and the Sedgwick Museum, University of Cambridge, U.K. (SM). Holotype UM 3380, paratypes

SM G 1876 (this was illustrated by Runnegar and Gobbett 1975), 2695, 2697, UM 3372, and one more unnumbered specimen in the University of Malaya collections.

Diagnosis. same as for subgenus.

Description. Small to medium-sized alatoconchids, elongated in anterior-posterior direction; maximum shell dimensions probably 20 cm long and 10 cm wide; sharp umbonal carinae expand laterally to form narrow wing-like flanges; anterior margin of flange forms 45° angle with plane of commissure; reflexed shell wall of flange forms acute angle in transverse section, rather than parallel-sided fold; hinge-line inclined about 45° to ventral surface, forming large dorsal crest on anterior end of shell; beaks upturned and terminal, producing a prow-like apical end; prominent byssal groove immediately below beak and ligament area, entering shell at anterior end of body cavity; byssal opening rounded, with a heart-shaped cross-section in articulated valves; large byssal collar projecting ventrally below byssal groove, with inner surface formed by irregular, shingled growth layers; ligament area triangular, and located on anterodorsal margin, bounded anteriorly by beak and byssal groove; ligament duplivincular, and consisting of several to many fine, long grooves, almost parallel to hinge-line; shell wall typically 0.5 cm thick, except on growing edges, but as much as 1 cm thick where heavily infilled in beak areas; ventral shell wall thicker than dorsal shell wall; thin outer shell layer of coarsely prismatic calcite, with prisms oriented perpendicular to shell surface; outer prismatic shell layer thickened on byssal collar.

Discussion. This is the smallest of the described alatoconchid species, but clearly reveals its alatoconchid affinities in the wing-like flanges, coarsely prismatic outer shell layer, and its large byssal collar. It is the least specialized alatoconchid, and is probably most closely related to the myalinids, from which the alatoconchids are thought to be derived. The presence of an open byssal notch on the available specimens suggests that it remained attached by byssus throughout life. It is probable that specimens were attached to the very large shells of *Shikamaia (Tanchintongia) perakensis*, which occur commonly in the same deposit in which *Saikraconcha (Dereconcha) kamparensis* was collected.

Derivation of name. Named after the town of Kampar, in the Kinta Valley in the state of Perak, Malaysia. Kampar is near the H. S. Lee mine from which the alatoconchids were collected.

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