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XIII.

DINOFLAGELLATA OF THE SAN DIEGO REGION, II. ON *TRIPOSOLENIA*, A NEW GENUS OF THE DINOPHYSIDAE.

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The plankton taken in deeper waters off San Diego during the past four years has contained a number of individuals of species of the *Dinophysidae* related to *Amphisolenia*. The relative variety of the forms and their less accessible habitat probably account for the fact that they have not been observed by other investigators, though it is not improbable that Schütt's ('93) *Amphisolenia tripos* (*nomen nudum*) is a member of this genus.

The five forms here described, together with three others described elsewhere (Kofoid :06), constitute a compact group of related species having in common a set of distinctive characters which delimit them from the known species of *Amphisolenia*, to which genus they are all more closely related than to any other of the *Dinophysidae*.

Their relationship to *Amphisolenia* is indicated by the differentiation of the body into the following regions: An expanded, rounded, or flattened head girdled by the transverse furrow, an elongated slender neck terminating posteriorly in the expanded cytopharynx, an expanded midbody containing the nucleus, and an antapical prolongation. The distinctive characters of the genus are (1) the form of the midbody, which is strongly compressed laterally, and (2) the presence of a pair of nearly equal and usually nearly symmetrical antapical horns, both of which arise from the midbody.

The *axial relations* in *Triposolenia* differ from those of other *Dinophysidae* owing to the obliquity of the neck and to the dorso-ventral asymmetry of the antapicals. In *Dinophysis* and *Phalacroma* the main (antero-posterior) axis passes through the center of the epitheca, the center of the hypotheca and the antapex in nearly a straight line. The bilateral asymmetry in these genera, if any, is slight. In *Amphisolenia* the main axis is straight, or nearly so, except in some species in the distal part of the single antapical horn. This is often bent to the left distally or curved in the dorso-ventral plane in bifurcated or branched species such as *A. thrinax* and *A. bifurcata.* The epitheca, neck, midbody, and a large part of the antapical horn lie in the straight line of the main axis. The species of the genus are thus predominantly linear in type.

In *Triposolenia,* however, the main axis is not a straight line, for there is both bilateral and dorso-ventral asymmetry. Assuming the axis of the midbody as a base of reference because of its relation to the balanced antapicals and to the plane of the girdle, we find that the anterior process is always displaced ventrally, in *T. ramiciformis* and *T. exilis* to the very margin of the midbody, in other species to a very slight extent. Its axis, moreover, is always inclined 10°–20° ventrally from the main axis. The neck, on the other hand, is displaced dorsally on the anterior process and is inclined dorsally from 10°–35° from the axis of the midbody and is in addition not infrequently curved in the dorsal direction. The plane of the girdle is nearly perpendicular to the axis of the midbody, at least more nearly so than to the axis of the neck. Presumably the axis of rotation in locomotion is approximately perpendicular to the plane of the girdle and is therefore coincident with or at least nearly parallel to the axis of the midbody.

The antapical extensions of the body among the *Dinophysidae* are feebly developed except in *Amphisolenia* and *Triposolenia.*

In *Phalacroma, Ornithocercus,* and *Histioneis* they consist merely of reticular extensions from the thecal wall. In the two genera first named, however, the thecal wall itself and the protoplasmic contents are prolonged posteriorly in well defined antapical horns, one in *Amphisolenia* and two in *Triposolenia.*

The pair of processes in *Triposolenia* exhibits certain constant relations which give to the symmetry of the organism a tripartite character that is unique among the *Dinophysidae*, though forms exhibiting a superficial resemblance are seen in the genus *Ceratium* and in *Peridinium.* In both of these genera, however, the antapical horns are right and left, that is, the bifurcation is bilateral, while in *Triposolenia* the horns are dorsal and ventral, and the bifurcation is sagittal. The only other instances of sagittal bifurcation among the Dinoflagellates are found also in the family *Dinophysidae*, in *Amphisolenia bifurcata* (Murray and Whitting, '99), *A. thrinax* (Schütt, '93), and *A. quinquecauda,* and in *Phalacroma ultima.* The bifurcation is, however, but feebly expressed in these species as compared with its development in *Triposolenia.* The tripartite character of this genus is shown in the proportionate development of the anterior process and the pair of antapical horns. The distance of the apex of the epitheca from the center of the midbody is approximately equal to that of the antapices of the horns from the same point. The proportionate development of the two antapicals and the anterior process is equally evident in the short-horned forms of the San Diego region, and the long-horned ones of the warmer waters of the tropics. Elongation of the anterior process is coincident with elongation of the antapicals and is present throughout all types of curvature and origin of the horns. In species with antapicals arising from the posterior angles of the midbody this equality is less marked than in those with the pendant midbody, the anterior process being a trifle shorter in the first named group. The ventral horn is also a little longer than the dorsal in all the species, an asymmetry which finds a parallel in the uniformly shorter right horn of the bifurcated species of *Ceratium* and *Peridinium.* The ventral antapical of *Amphisolenia* and the right one of *Ceratium* and *Peridinium* lie on the side nearest to the longitudinal flagellum and to the axis of rotation and of locomotion. Elongation in the axis of locomotion is a common phenomenon among organisms. It may be that the dorsal deflection of the head balances the deficiency in the length of the dorsal antapical.

The balanced relationship of the two antapicals to each other and to the midbody is as striking as the similar relationship of the anteriorly deflected horns of the long-horned forms of *Ceratium* such as *C. vultur* Cleve, and *C. patentissimum* Ost. and Schm. This balance is shown in their approximately equal development and similar spread from the axis and in the correspondence in the reversed curvatures of the two horns. This balance is only approximate, however, appearing at its highest development in *T. truncata* and *T. bicornis* and progressively encroached upon in *T. fatula* and *T. ambulatrix*, where the dorsal horn is deflected dorsally without corresponding ventral deflection of the ventral horn. It is noteworthy that in both of these species the dorsal deflection of the anterior process is decreased as if to counterbalance the increased dorsal deflection of the dorsal antapical.

This coördination in the matter of the proportionate development of the three processes from the midbody and the balanced relationship of the antapicals throughout the species of the genus suggests an important function in orientation for flotation and locomotion.

The body as in other *Dinophysidae* is composed of two valves, a right and left, which separate along a sagittal suture line. The suture in *Triposolenia* is not structurally marked except by a faint line, or a few scattered pores along the ventral side of the neck or in the tubercles on the major flexures of the antapicals. The *epitheca* as in *Amphisolenia* is reduced to a small dome above the girdle, while the *hypotheca* constitutes the greater part of the organism. Neither girdle plates nor suture are apparent.

The *midbody* (*mb.* Pl. 15, fig. 1) is a centrally located enlargement, strongly compressed laterally, and having a triangular, elliptical, oblong, or ovoidal outline in lateral view. Its altitude is about 0.25, its transdiameter 0.1–0.04, and its dorso-ventral diameter 0.35–0.12 of the total length. It is broadly rounded on the margins, which are three in number, an antero-dorsal, an antero-ventral, and a post-margin, the three being subequal in all species except those with pendant midbody. The slight inequality of the sides is constant in that the antero-ventral margin is in all species the shortest and the post-margin the longest. This inequality results from the fact that the anterior process in all species has its origin on the ventral side of the axis of the midbody.

The species of *Triposolenia* fall in two distinct groups or subgenera with reference to the form of the midbody. In the *truncata* group (Subgenus *Posterocornia*) the margins of the midbody are approximately equal and the horns originate on the posterior angles. In the *ramiciformis* group (Subgenus *Ramiciformis*) the two anterior margins are very unequal, the antero-dorsal being the longer and nearly horizontal, the antero-ventral being practically obliterated, while the post-margin is extended in a pendant lobe with oblong or subrectangular outline. The nucleus and the greater part of the protoplasm of the organism is found in this pendant region.

The *anterior process* (*a.p.* Pl. 15, fig. 1) is an extension of the midbody in the antero-ventral direction at an angle of 10°–20° from the axis. Its length does not exceed and is usually less than the altitude of the midbody. It is a stout, laterally compressed process about twice as thick dorso-ventrally as the neck. It expands abruptly on the ventral side at the cytopharynx (*c'ph.* Pl. 15, fig. 2) about the flagellar pore (*f.p.* Pl. 16, fig. 6). Its point of origin in species with pendant midbody (Pl. 17, figs. 7, 8) is shifted to the ventral side so that the ventral horn and anterior process bifurcate from a common projection of the midbody.

The *neck* (*n.* Pl. 16, fig. 6) is a slender cylindrical extension of the anterior process, whose length to the base of the head is 0.8–1.75 of the altitude of the midbody. It is straight or curved dorsally, of uniform calibre throughout or constricted distally (Pl. 17, fig. 7) and is more or less, 10°–35°, deflected dorsally from the axis. It passes abruptly into the expanded head just below the posterior collar of the girdle.

The *head* (*hd.* Pl. 15, fig. 2) is composed of the epitheca and the expanded region at the end of the neck. It is encircled by the broad transverse furrow which covers nearly two-thirds of its axial length. Its form varies much in the different species. It is laterally compressed and its transdiameter is not much greater than that of the neck. Its dorso-ventral diameter is more extended and its anterior face is rounded in most species, but concave in *T. truncata* (Pl. 16, fig. 5).

The *antapical horns* (*a.h.* Pl. 15, fig. 2) are latero-posterior extensions from the midbody, of approximately circular cross-section, and curved from a lateral direction at their origin to a posterior one distally. The dorsal horn is always a little shorter than the ventral and the two horns stand in a balanced relation to the axis of the midbody. The curvature is in some cases localized in a major flexure (*m.f.* Pl. 17, fig. 7) and in others, as in *T. truncata,* is distributed. The distal ends of the horns exhibit in lateral view in some species a slight sigmoid curvature, the antapices being deflected outward. The tips are without spinules and rounded (*T. exilis* Pl. 17, fig. 8), or truncate with dorso-ventral spinules (*T. truncata* Pl. 16, fig. 5), or with lateral spinules (*T. depressa* Pl. 16, fig. 3). In all species but *T. truncata* the outer margins of the major flexures or adjacent regions bear 2–4, rarely 1–2, or 5–7 small elevations or tubercles (*t.* Pl. 15, fig. 2), each pierced by a pore. They lie close to the sagittal suture and are conical elevations deflected posteriorly. In addition to the curvature in the dorso-ventral plane there is in all species a slight bilateral asymmetry, in that the antapical horns do not lie in the sagittal plane of the midbody but are bent to the right slightly in the middle or anterior regions and distally to the left, the dorsal horn exhibiting more of the distal curvature than the left.

The *thecal wall* in this genus, as also in most species in *Amphisolenia,* is hyaline and apparently structureless. It is of nearly uniform thickness except on concave faces of the horns, where, as in *Ceratium,* the wall is somewhat thickened, especially in the more robust individuals. Under the highest magnification the wall is very faintly and minutely spotted or flecked, as if in the incipient stages of pitting or reticulation. In but a single species, *T. truncata,* are these structures developed into plainly visible pits and reticulations. The pores are found only in the tubercles and along the ventral suture on the neck.

The *transverse furrow* (*tr.f.* Pl. 16, fig. 6) encircles the head as a wide equatorial band, which is slightly if at all impressed. Its floor is flattened in *T. bicornis* (Pl. 15, fig. 2), slightly concave in *T. depressa* (Pl. 16, fig. 3), or convex in *T. ramiciformis* (Pl. 17, fig. 7). There is no appreciable displacement distally in the furrow, that is, it does not form a spiral about the head.

The *anterior list* or collar (*a.l.* Pl. 16, fig. 6) is a flaring hyaline sheet with 12–20 equidistant ribs. There are two prominent ventral ribs at the ventral suture. The plane of both lists is oblique to the neck, being directed ventro-posteriorly, slightly beyond the perpendicular to the axis of the midbody. The anterior list flares obliquely anteriorly at an angle of 10° or more and is frequently concave posteriorly. On account of the posterior displacement of the flagellar pore the *posterior list* (*p.l.* Pl. 16, fig. 6) of the transverse furrow has an unusual form in both *Triposolenia* and *Amphisolenia.*

Instead of forming a simple circle about the girdle as in *Peridinium,* the posterior list turns abruptly posteriorly at the ventral suture and continues posteriorly along the ventral side of the neck in two parallel wings to the flagellar pore forming the pseudo-longitudinal furrow. The transverse flagellum (*tr.fl.* Pl. 16, fig. 6) runs anteriorly to the collar in this channel. The right list is not so high as the left and both rise from the thickened ridges on the neck. Posteriorly the two fins diverge to enclose the flagellar pore (*f.p.* Pl. 16, fig. 6) which lies in the pharyngeal enlargement. The height of the left fin increases at the pore and it swings in toward the median line behind the pore. In the region of the sagittal plane there is usually present a suture spine (*s.sp.* Pl. 16, fig. 6) beyond which the fin continues posteriorly for a short distance along the anterior process, and dies out within a short distance of the pore. This spine is doubtless homologous with the midspine of the ventral fin or left longitudinal list of *Dinophysis,* which Stein ('83 Taf. 20, fig. 19) has shown to be located near the suture line in *Dinophysis.* It appears from Stein's figure and from other evidence in my hands not yet published, that the ventral fin in the *Dinophysidae* lies on the left valve anterior to the midspine and *on the right valve* posterior to this spine. In some genera this spine is frequently doubled.

In any case this spine in *Triposolenia* lies near the suture and the continuation beyond the spine is also near the sagittal line and may well belong to the right valve. Not having seen *Triposolenia* in the stage of division it cannot be stated positively that the ventral fin would be parted at this spine and that the anterior and posterior moieties would go to the left and right valves respectively, but the homologies here indicated make such a division probable in this genus. The right list continues but a short distance beyond the pore, and lies on the side of the cytopharyngeal enlargement. In *Peridinium* and *Dinophysis* the longitudinal furrow lies posterior to the flagellar pore. Its homologue therefore in *Triposolenia* is the very short extension of the two lists posterior to the pore. The long anterior section may be regarded as a posterior extension of the lists of the transverse furrow affording a channel for the passage of the transverse flagellum (*tr.fl.* Pl. 16, fig. 6) from the pore to the girdle, and it may therefore be regarded as a pseudo-longitudinal furrow resulting from the migration apart of the transverse furrow and the flagellar pore and the extension of the lists in this region of migration.

The *transverse flagellum* (*tr.fl.* Pl. 16, fig. 6) arises in the flagellar pore and passes anteriorly between the longitudinal lists and encircles the head from left around to right as in other girdled Dinoflagellates. The longitudinal flagellum I have not seen in any species thus far examined. The rudimentary longitudinal furrow is suggestive of a possible reduction to a rudimentary state.

The *flagellar pore* (*f.p.* Pl. 16, fig. 6) is a large opening on the antero-ventral end of the cytopharyngeal expansion. Its left lip is somewhat higher than the right and it is therefore directed anteriorly and to the right.

The protoplasmic contents are very hyaline and coarsely granular and contain a compressed ellipsoidal nucleus (*nu.* Pl. 15, fig. 2), with a moniliform chromatin reticulum. Near the nucleus is found a pusule (*pus.* Pl. 15, fig. 2) which opens by a slender canal (*can.* Pl. 15, fig. 2) into the flagellar pore. One or more accessory pusules (*ac.pus.* Pl. 15, fig. 2) may lie near it in the plasma. Occasionally the plasma is crowded with highly refractive ellipsoidal plasmosomes of amyloid character. In many individuals it is possible to find small irregular, pale, yellowish-green chromatophores (*chr.* Pl. 15, fig. 2) with a peripheral distribution in the cell. No species appears to possess these structures with a characteristic pattern in either form or distribution.

Reproduction, either sexual or asexual, has not been observed.

Surface temperatures of the Pacific in the San Diego region range from 14°–24° C. with a predominant temperature of 18°–20° C. throughout much of the year. At 100 fathoms the temperature has been found to range from 9.75°–13° C. No seasonal restrictions in the distribution of the species of *Triposolenia* appear in the scanty data of their occurrence in the waters off San Diego. The more common species, *T. bicornis, T. truncata,* and *T. ramiciformis,* are found in both summer and winter plankton. *T. depressa* and *T. exilis* have thus far been found very sparingly in the San Diego plankton.

Triposolenia gen. nov.

Dinophysidae with subequal valves, transverse girdle encircling a small head, neck elongated, oblique to anterior process which arises obliquely from a laterally compressed enlarged midbody. Two antapical horns, spreading, curved, approximately balanced, the dorsal a trifle shorter than the ventral. The antapical tips simple, with or without spinules or projecting tubercles or major flexures, often with a distal sinistral deflection, thecal wall structureless or pitted. Lists hyaline, ribbed, not excessively developed. Chromatophores yellowish green, if present. In oceanic plankton of warm-temperate and tropical seas in the deeper levels, rarely at the surface.

Types of the species here described are in the collections of the Zoological Department of the University of California.

Posterocornia subgen. nov. Antapicals arising from posterior part of centrally located midbody.

Ramiciformia subgen. nov. Antapicals arising from anterior part of pendant midbody.

KEY TO THE SPECIES OF TRIPOSOLENIA.

1. Antapical horns balanced, nearly symmetrical 2
1. Antapical horns asymmetrical, the dorsal one quite oblique 3
3. Neck uniform anteriorly .... *T. ambulatrix* Kofoid*
3. Neck constricted anteriorly, deflected dorsally........ *T. fatula* Kofoid*
2. Wall of midbody plainly pitted .... *T. truncata*
2. Wall of midbody not pitted 4
4. Antapical horns arising from antero-lateral angles of pendant midbody 5
4. Antapical horns arising from postero-lateral angles of midbody........ 6
5. Midbody slender, neck not very oblique to its axis .... *T. exilis*
5. Midbody stout, neck oblique to its axis .... *T. ramiciformis*
6. Midbody subtriangular in lateral view, post-margin not strongly convex, anterior margins convex .... *T. bicornis*
6. Midbody subelliptical in lateral view, post-margin strongly convex .... *T. depressa*
6. Midbody trianguar in lateral view, anterior margins concave .... *T. longicornis* Kofoid*

Triposolenia truncata sp. nov.

Pl. 10, fig. 5.

This is the most robust of the eight known species, with stout neck and stout antapical horns somewhat regularly convex outwardly, with truncate ends bearing at each terminal angle a short spinule. There are no tubercles on the antapicals. The epitheca is concave anteriorly, and the thecal wall is pitted.

The midbody is laterally compressed, subtriangular in lateral view, with the three margins nearly equal in length and nearly equally convex, the convexity of the ventral margin decreasing as it approaches the neck. The posterior margin is often a little longer than either the dorsal or ventral one, and the ventral margin a trifle shorter than the dorsal one.

The antapicals are symmetrical, their regions of major flexure and their tips being respectively equidistant from the center of the midbody. They are also approximately equal to the anterior projection, but the distance in a direct line from the center of the midbody to tip of the antapicals exceeds that to the most distant portion of the head. If, however, the distance be measured along the axis to the dorsal edge of the transverse list, the length of the anterior process equals that of the posterior ones. This

* Bull. Mus. Comp. Zool., 1906.

proportion is preserved alike in slender and in more robust individuals. There is thus apparently a correlation in the development of the three regions.

The length of the antapicals is 2.5–3.25 times the distance from the center of the midbody to their bases. Their curvature is greatest in the middle third of their course and is sometimes slightly localized in a knee, though the curvature as a whole is more uniform than in the other species. The distance between the tips is 2–2.25 times that between the bases and that between the outer margins of the knees 1.15–1.2 times that between the inner spinules of the tips. The ends are squarely truncate and each bears on the dorsal and ventral angles at the suture line a pair of slender divergent spinules not over half the diameter of the antapicals in length. Sometimes the outer spinule alone is present and is larger than usual. The dorso-ventral diameter of the antapicals at the tips is 0.5–0.7 that of their bases and the mean diameter varies from 0.1 of the total length in robust individuals to 0.06 in more slender ones. Their length varies from 1.6 to 1.8 times the diameter between their bases and 1.5 to 1.7 times the altiude of the midbody measured from the base of the anterior process to the middle of the posterior margin. The distal fourth of the antapicals is deflected slightly to the left.

The anterior prolongation consists of the head, neck, and a short extension of the midbody to the flagellar pore, the latter forming 0.3–0.4 of the total length of the process. The region of the cytopharynx is strongly protuberant ventrally, but the projection recedes more or less before its junction with the midbody. The diameter at the cytopharynx is nearly twice that of the neck.

The head is elongated, depressed, and slightly oblique, and its long axis is 0.6 of the length of the neck. The anterior face of the epitheca is quite concave, and the transverse furrow is somewhat impressed. The transverse lists are low, spreading, and the anterior one is faintly ribbed with 10–12 ribs. The longitudinal lists embrace the flagellar pore. The left one is continued beyond the pore nearly to the midbody, and has a suture spine below the pore and several accessory spines distally.

The thecal wall is pitted (pores?) profusely, but more sparingly towards the tips of the antapicals and the base of the anterior process. On the neck the pits gradually widen to a coarse reticulum 2–4 meshes wide on each valve.

The nucleus is very small (in some cases observed) and is located posteriorly. There are a few irregular chromatophores, or numerous ellipsoidal ones gathered along the ventral margin.

This species, in the individuals thus far observed, is quite uniform in dimensions and proportions, except in the diameter of the three processes from the midbody. These vary considerably in thickness but less in length, thus giving to the organism different degrees of robustness with little change in the other dimensions than the diameter of the processes.

Taken in plankton from 180–30 fathoms to surface off San Diego, but always sparingly.

Dimensions: Length, 113–145 μ; distance between knees of antapicals, 83–115 μ; distance between tips of antapicals, 70–106 μ; distance from apex to middle of posterior margin of midbody, 77–97 μ; length of neck, 25–28μ; dorso-ventral diameter of midbody, 33–40 μ.

This is the type species.

Triposolenia depressa sp. nov.

Pl. 16, figs. 3, 4.

A small species with midbody elliptical in lateral view, convex margins, and antapicals of *T. bicornis* type with truncated spinulate tips.

This is the smallest of the known species of the genus and is characterized by the foreshortening of the antero-posterior axis of the midbody which gives to it an ellipsoidal form with its major axis in the dorso-ventral position. The three margins are all strongly convex and the antero-ventral is somewhat shorter than the others. The antero-posterior axis is 0.25 of the total length and 0.8 of the dorso-ventral axis of the midbody. The anterior process is very short and oblique, with well marked cytopharyngeal swelling. Its length is about 0.5 of the antero-posterior axis of the midbody. The neck is short and straight or very slightly curved dorsally toward the head, and obliquely deflected dorsally 35° from the axis of the anterior process. Its length is about 0.25 of the total length. The head is capitate with flat or impressed furrow and low convex epitheca.

The antapicals arise from the postero-lateral regions of the *bicornis* group. The ventral is a little longer than the dorsal. They diverge postero-laterally for a short distance and then bend somewhat abruptly in a localized major flexure to a posterior direction. The greatest distance between horns is 3.5 and between the tips 3 times the altitude of the midbody. Distally they exhibit a slightly developed sigmoid flexure in lateral view. In dorso-ventral view both horns are bent to the right proximally and distally to the left, the dorsal horn having more distal curvature than the ventral. The antapical tips are truncated in dorsal or ventral view, with minute lateral terminal spinules. In lateral view the tips are somewhat rounded. There are several scattered tubercles on the outer margins of the horns.

The thecal wall is hyaline, structureless, with a few pores along the midventral line of the neck and in the tubercles of the antapicals.

A large nucleus is found in the midbody, along with principal and accessory vacuoles and a few minute scattered spheroidal chromatophores.

Dimensions: Lenth, 100–122 μ; altitude of midbody, 22–28 μ; length of antapicals, 48–70 μ.

Taken in a vertical haul from 95 fathoms off San Diego.

Triposolenia bicornis sp. nov.

Pl. 15, figs. 1, 2.

A species resembling *T. truncata* but less robust, with longer antapicals, with tuberculated major flexures and rounded tips and capitate head with convex epitheca.

The midbody resembles that of *T. truncata*, with the exception that its margins are often more convex, giving it a slightly more rotund appearance.

The antapicals arise in the same manner as in *T. truncata* and exhibit the same balanced relation with respect to each other and the same proportion to the anterior process. Both antapicals and anterior process are shorter in robust forms and longer in the more delicate ones.

The horns have the same proximal curvature as in *T. truncata*, but the major flexure is somewhat farther removed from the midbody. Distally the horns are incurved, and then exhibit the outward curvature near the tips, which is also found in *T. ramiciformis*. There is some curvature to the left distally in both horns. There are 3–6 irregular tubercles on the outer margins of the horns below the major flexures. The ventral horn is usually a trifle longer than the dorsal one. In length the horns are 1.6–3 times the distance between their bases, or 12–40 times their width.

The anterior process is straight or concave dorsally, the projection from the midbody to the flagellar pore being one-fourth to one-third of its total length. There is usually considerable dorsal curvature in the neck and more or less protuberance of the region of the cytopharynx. The head is subcapitate, with slightly impressed furrow. The transverse lists are low and spreading with 20–24 delicate ribs. The longitudinal lists are salient at the junction with the transverse one, almost decurrent on the neck and again salient as they surround the flagellar pore. A suture spine is found in the left list just posterior to the flagellar pore. The thecal wall is structureless. Pores occur in the tubercles.

This species is the most common one in the genus at San Diego, but is never abundant as compared with many other Dinoflagellata. It varies in size, in the curvature of the antapicals and the neck and in their length and thickness. The number and location of the tubercles is also subject to considerable variation.

The nucleus is ellipsoidal and usually located near the posterior face of the midbody. An attraction sphere is found on the anterior face of the nucleus. One or two pusules are present along the ventral wall, each with efferent canal leading to the flagellar pore. The chromatophores are small, irregular, almost colorless, with superficial distribution.

Dimensions: Length, 120 to 185 μ; distance between knees of antapicals, 70 to 130 μ; between tips, 60 to 112 μ; altitude from apex to middle of posterior margin of the midbody, 75 to 110 μ; altitude from apex to middle of posterior margin of the midbody, 75 to 110 μ; altitude of midbody to base of anterior process, 30 to 50 μ; dorso-ventral diameter of midbody, 32 to 48 μ; length of horns, 45 to 95 μ; rarely 130 μ.

Taken frequently in small numbers in vertical hauls from 135–30 fathoms to the surface, and rarely in surface catches off San Diego.

Triposolenia ramiciformis sp. nov.

Pl. 17, fig. 8.

A grotesque species of slender habitus, with midbody pendant from the base of the dorsal antapical horn, convex epitheca and capitate head, elongated neck, and elongated basally spreading antapicals, with tuberculate major flexures and pointed ends.

The midbody of this species is laterally compressed, sack-shaped in lateral view with broadly rounded antapex, usually tapering but little till near the antapex, though several specimens have been seen in which the midbody tapers gradually from the base of the antapicals to the more narrowly rounded apex. The length of the midbody along its major axis is 1.67 (1.5–2.0, rarely 2.5) times the mean dorso-ventral diameter and 1.15 (1.1–1.3, rarely 1.7) times the distance between the bases of the horns. The main axis of the midbody is oblique to that of the neck, the angle of divergence being 12°–25°.

The two antapicals emerge from the midbody, not from the posterior part as in *T. truncata* and *T. bicornis*, but from the anterior angles. The ventral horn and the anterior projection emerge together from the ventro-anterior angle and the dorsal one from the dorso-anterior angle. The ventral horn is slightly anterior to the dorsal one, so that the anterior margin is somewhat oblique to the main axis of the midbody. It usually has a small convexity nearer the base of the dorsal horn.

The two horns are subequal and subsymmetrical with respect to the midbody, the ventral is usually a little longer than the dorsal. In length the ventral horn is 2.9 (2.5–3.3), and the dorsal 2.7 (2.5–3.2) times the altitude of the midbody in its main axis. In a few cases the dorsal horn is the longer. The horns are of fairly uniform caliber throughout, the length of the ventral being 24–28 times its width. The tips are bluntly pointed.

From their origin the horns diverge latero-posteriorly, leaving the midbody almost at right angles to its major axis and curving posteriorly within 1.5 altitudes of the midbody from their origin. This major flexure is usually gradual, but may be more or less abrupt. At the level of the posterior third of the midbody the horns have a direction nearly parallel to its major axis and are then slightly incurved while the ends are again slightly outwardly curved. In the region of the major flexure and below it each horn bears on its outer surface 2–5 low tubercles.

The anterior process rises from the midbody above the base of the ventral horn in a direction nearly parallel to its ventral margin. Above the pharynx the slender, straight, or slightly curved neck is bent dorsally at an angle of about 30°. The region of the flagellar pore is quite protuberant, its dorso-ventral diameter being fully twice that of the adjacent neck. The head is capitate, its dorso-ventral diameter being 1.5–2 times the width of the head. The neck is about 0.75 of the total length of the anterior process. The epitheca is convex and the transverse furrow scarcely impressed. The transverse lists are low, spreading with many fine ribs. The longitudinal lists are salient about the flagellar pore and the left bears a prominent suture spine.

The thecal wall is hyaline, structureless. A few pores can be found in the ventral sagittal suture of the neck, and in the tubercles of the major flexures.

The nucleus is lenticular in form, laterally compressed, and lies in the posterior part of the midbody. Chromatophores, few, irregular in form, yellowish green.

Dimensions: Length, 152–160 μ; altitude of midbody in main axis, 37–43 μ; length of anterior process, 56–72 μ; length of posterior horns, 95–140 μ.

Taken sparingly in vertical hauls from 100 fathoms off San Diego.

Triposolenia exilis sp. nov.

Pl. 17, fig. 8.

This is a species of the *T. ramiciformis* type with pendant midbody. It differs from that species in having a narrower midbody, a less oblique and more curved neck and antapical horns less widely spreading.

The midbody is long and narrow, its dorso-ventral diameter taken midway of its length, being 0.4 of its axial length. Its dorsal and ventral margins are subparallel, tapering but little posteriorly. The antapex is bluntly rounded, being almost truncate. The length of the midbody equals that of the head and neck, equals the distance from its antapex dorsally to the dorsal horn, is a little more than the corresponding distance to the ventral horn and is somewhat less than 0.25 of the total length. The anterior process extending from the midbody to the flagellar pore has the usual size and proportions. The neck is nearly parallel to the general trend of the antapicals and the long axis of the midbody, being bent dorsally in a gentle curve about 12° from a parallel to the axis. The head is spheroidal with a convex epitheca.

The antapicals arise as in *T. ramiciformis*, but begin at once to curve posteriorly in an arc which brings them to an antero-posterior direction within the length of the midbody, thus nearly obliterating the localized major flexure seen in *T. ramiciformis*. The sigmoid posterior curvature of the antapicals is freely developed. The tips are rounded, without spinules. There are 2–3 feebly developed tubercles on the dorsal and ventral margins respectively of the dorsal and ventral horns within the level of the midbody. The lateral curvature in the antapicals has not as yet been determined. The length of the dorsal and ventral horns is 2.1 and 2.3 times the axial length of the midbody respectively. The inequality in the antapicals is greater than in any other species here described. The distance between the antapicals at the level of the antapex of the midbody and at the tips are respectively 1.8 and 1.6 times the axial length of the midbody.

The thecal wall is hyaline and not pitted nor reticulate. The transverse lists are faintly and sparingly ribbed and the longitudinal ones are without structural differentiation. A faint suture spine is located posterior to the flagellar pore.

Dimensions: Length, 165 μ; altitude of midbody, 45 μ; length of anterior process, 61 μ; length of antapical horns, 94 and 103 μ.

Taken in vertical haul from 100 fathoms off San Diego in July.

The following tabular comparison of characters will facilitate the separation of *T. ramiciformis* and *T. exilis*.

	Obliquity of neck	Ratio of length and dorso-ventral diameter of midbody	Distance between antapicals at level of tips	Distance between antapicals at level of midbody	Major flexure
T. exilis	12°	3.2:1	1.6 lengths of midbody	1.6 lengths of midbody	Diffused
T. ramiciformis	24°	3.1:1	2 lengths of midbody	2.5 lengths of midbody	Localized

Zoological Laboratory, University of California,
October 3, 1906.

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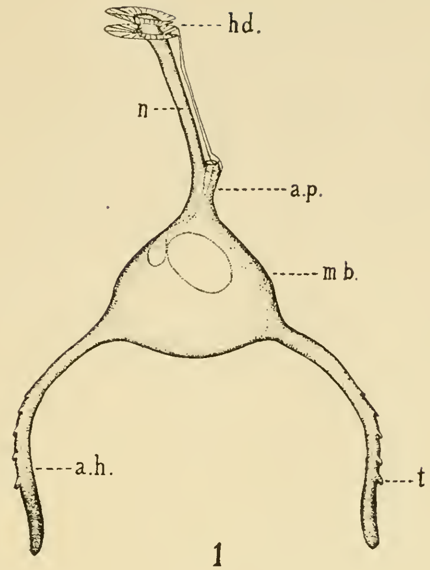
PLATE XV.

Fig. 1. Right side of *Triposolenia bicornis* sp. nov. × 514.

Fig. 2. Cell contents of *T. bicornis*, viewed from the left side. × 740.

ABBREVIATIONS.

ac.pus.—accessory pusule.
a.h.—antapical horn.
a.p.—anterior process.
can.—efferent canal.
chr.—chromatophore.
c'ph.—cytopharynx.
f.p.—flagellar pore.
hd.—head.
mb.—midbody.
m.f.—major flexure.
n.—neck.
nu.—nucleus.
pus.—pusule.
t.—tubercle.



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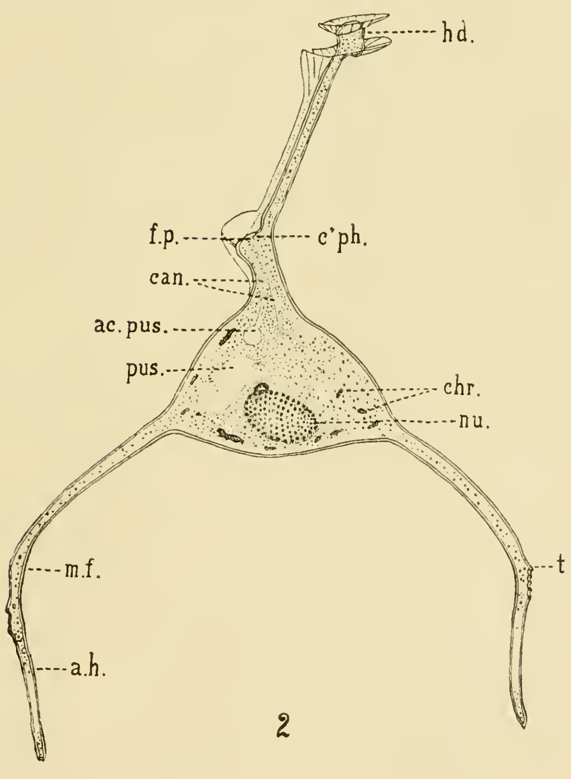

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PLATE XVI.

Fig. 3. Right side of *Triposolenia depressa* sp. nov. × 506.

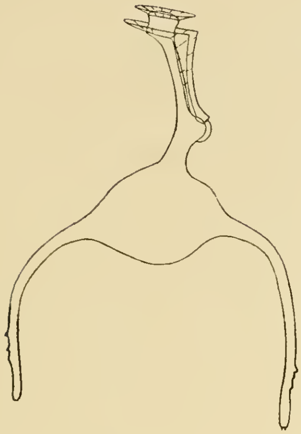
Fig. 4. Dorsal view of the same. × 506.

Fig. 5. Right side of *T. truncata* sp. nov. × 506.

Fig. 6. Anterior part of *T. bicornis*. × 1200.

ABBREVIATIONS.

a.l.—anterior list.
d.a.h.—dorsal antapical horn.
f.p.—flagellar pore.
n.—neck.
p.l.—posterior list.
tr.f.—transverse furrow.
tr.fl.—transverse flagellum.
s.sp.—suture spine.
v.a.h.—ventral antapical horn.



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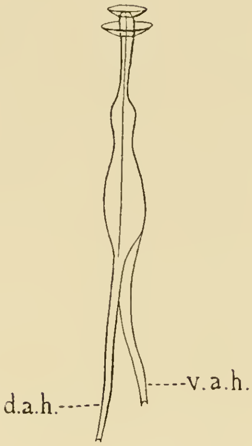

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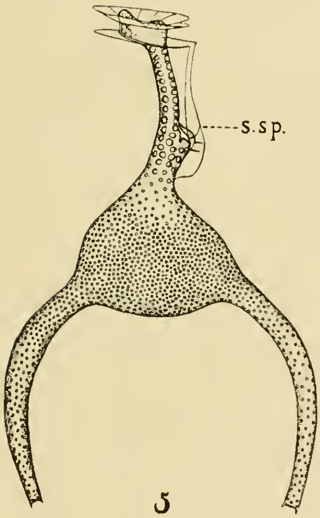

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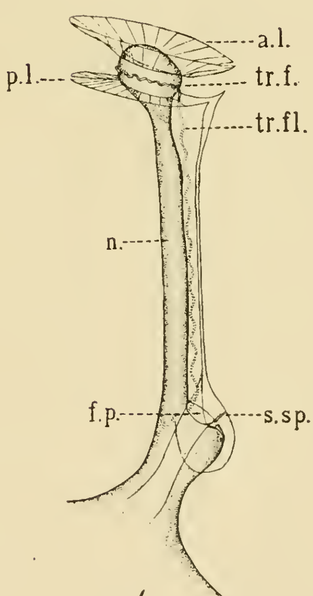

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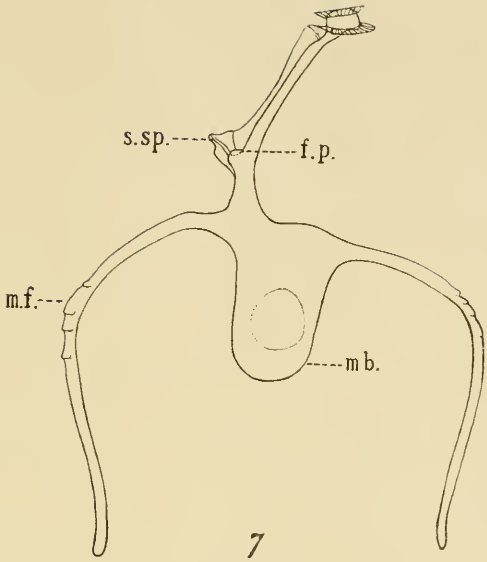
PLATE XVII.

Fig. 7. Left face of *Triposolenia ramiciformis* sp. nov. × 487.

Fig. 8. Right face of *T. exilis* sp. nov. × 487.

ABBREVIATIONS.

f.p.—flagellar pore.
mb.—midbody.
m.f.—major flexure.
s.sp.—suture spine.



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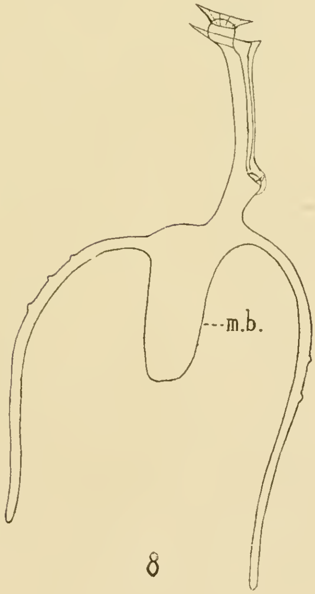

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UNIVERSITY OF CALIFORNIA PUBLICATIONS
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A DISCUSSION OF SPECIES CHARACTERS IN TRIPOSOLENIA.

I.—The Nature of Species Characters.

II.—The Adaptive Significance of Species Characters.

III.—The Coincident Distribution of Related Species.

BY

CHARLES ATWOOD KOFOID.

I. The Nature of Species Characters in the Genus Triposolenia.

The genus *Triposolenia* is sharply set off from other genera of the *Dinophysidae* by the pronounced form of its midbody and the relation which this bears to the balanced antapical horns and to the anterior process. As yet no species have been found which will afford a transition between *Triposolenia* and the most nearly related genus *Amphisolenia* which has a fusiform midbody and a single simple or branched antapical horn.

The characters by which the species of *Triposolenia* may be distinguished from each other are principally the form of the midbody, the origin of the antapical horns, as well as their curvature, spread and tips, the curvature and obliquity of the neck, and the shape of the head, especially of the epitheca. The structures least modified are the anterior process, the lists and collars.

Differentiations of the thecal wall appear only in *T. truncata*. Differences in position of nucleus and vacuoles and in the number, form, and color of the chromatophores and plasmosomes appear to have little significance in the matter of specific distinctions.

The *size of the organism* is also of aid in distinguishing the species. This is shown very strikingly on a comparison of drawings of numbers of individuals of the several species made to the same scale. It appears at once that *T. depressa* and *T. truncata* are small species, that *T. bicornis*, *T. ambulatrix*, and *T. exilis* belong to a series of medium sized species, and that *T. ramiciformis* and *T. longicornis* are the largest ones. Variations in the length of the antapicals and of the neck are the principal cause of fluctuations in the size. In the cases *T. bicornis*, *T. truncata*, *T. ramiciformis*, and *T. longicornis* where a number of individuals have been measured, the extreme measurements are usually relatively rare and most of the individuals lie very near the mean. There is thus a norm in the matter of size for each species.

It comes frequently to be a matter of experience to one who examines many organisms with a view to assorting them according to their kinds, that differences are detected *en mass*, without analysis of the individual differentials which together constitute the facies or *ensemble* of characters which is diagnostic of the species. In a relatively simple organism such as *Triposolenia* these individual structural characteristics of the species may be readily isolated and a comparison of their assemblages and relations affords some data bearing on the nature and origin of species.

The accompanying table of species characters of the eight known species in this genus has been drawn up to include those characters which are most easily defined or simply expressed. Others, principally in the more complex matter of proportions of various parts, might be added to the list.

It might be supposed that in so simple an organism as *Triposolenia* species might be separated by single characters. An examination of the table and the plates will suffice to show that this is decidedly not the case. For example, *T. truncata* differs from its nearest relatives, *T. bicornis* and *T. depressa* in *size, shape of head and epitheca, length, curvature, and angle of the neck, proportions of the anterior process, shape of the midbody* (from *T. depressa* only), *proportions, curvature, and spread of the antapicals as well as in their tips.* There is, indeed, scarcely an element of the organization which on close examination does

SPECIES CHARACTERS IN TRIPOSOLENIA.

		Midbody				Antapical horns		
Species	*Length in μ*	*Form in lateral view*	*Margins*	*Head*	*Epitheca*	*Origin*	*Major flexure*	*Tips*
truncata	128 (113-145)	subtriangular	moderately convex equal	much flattened	concave	posterior	slightly localized	truncate spinulate
depressa	100-122	subelliptical	strongly convex nearly equal	elongated capitate	convex	posterior	distributed	nearly truncate spinulate
bicornis	150 (130-176)	subtriangular	slightly convex nearly equal	flattened spheroidal	slightly convex	posterior	localized	pointed
ambulatrix	158	irregular oval	diversely convex unequal	spheroidal	convex	posterior	distributed	blunt and spinulate
fatula	175-190	triangular	concave anteriorly unequal	spheroidal	convex	posterior	distributed	spinulate
longicornis	230 (210-240)	triangular	very slightly convex equal	flattened	flat	posterior	distributed	rounded
exilis	150	elongated	sides nearly parallel	flattened capitate	slightly convex	anterior	localized	blunt
ramiciformis	159 (154-175)	nearly oval	not parallel	flattened capitate	slightly convex	anterior	localized	blunt

not exhibit a difference in the species in question. These differences are not so pronounced between *T. bicornis* and *T. depressa* as between *T. exilis* and *T. ramiciformis*, nevertheless it is evident that even these more nearly related couples are distinguished at once by a complex of characters rather than a single one or even a few. The differences between *T. exilis* and *T. ramiciformis* are discussed under the description of the former. The differences between *T. bicornis* and *T. depressa* are in size, form of midbody, proportions of neck and of cytopharyngeal region, and in the tips of the antapicals. The elementary characters of the organism are thus fundamentally and extensively different in their form and relations in the different species in this genus. It is as though they had been thoroughly shaken up and readjusted in the case of each species, when nature cast the die.

The individual species characters are all subject to variations of the fluctuating kind, in varying degrees of amplitude. Thus the length of neck and the convexity of the margins of the midbody are quite variable. Variation is least evident in the anterior process, and the head. The greatest variation is perhaps found in the antapicals, in their length, in the spread, degree, and localization of their curvature, in the number and distribution of the tubercles and in the form of their tips. *Triposolenia* is probably a divergent member of the *Dinophysidae*, and it may be that the antapical horns, especially the dorsal one, are phylogenetically recent structures. They are also peripheral in location, though no more so than the head in which fluctuating variations are less evident.

These fluctuating variations often cause an individual of one species to approach another in some one or even several characters, as, for example, *T. truncata* falls within the size limits of both *T. depressa* and *T. bicornis*, but approach in size is not accompanied by a proportionate change in the same direction in *all other differential characters.* Again the antapical tips of *T. depressa* are sometimes partially truncated, but there is no coincident fluctuation in the pitting of the thecal wall or flattening of the epitheca characteristic of *T. truncata;* in other words, variation is not total in the direction of a given species.

II. The Adaptive Significance of Specific Characters.

In view of the current discussion among biologists of the adaptive significance of diagnostic characters which separate species and of the efficiency of natural selection in the origin of these characters, individually or in their totality, it is a matter of interest to consider what light the organisms with which we are here dealing throw upon this vexed question. The relative simplicity of their organization and the fact that the specific distinctions are comparatively few, probably less than a dozen being revealed in the theca on the closest scrutiny, and further that they are expressed in the more permanent exoskeleton or thecal[1] wall where they are preserved in fixed form for comparison, and of still greater significance the fact that they have had their origin in the surface waters of the sea, a region of relative environmental uniformity and possibly the primitive home of organisms (Brooks '95), all conspire to reduce the problem to its lowest terms and to lend an unusual interest to its consideration.

The problem is here freed from the complexities which attend its consideration in the higher organisms where multiplicity of parts makes difficult the expression of the total specific differences, where the mobility and contraction of the organism or its constituent parts renders impossible a precise definition of all the diagnostic characters, and where the period of growth is long continued and the total form-cycle of the individual in which the species characters are expressed is more extended in time and of greater amplitude in its modifications. Incomplete as our conception of the ensemble of specific characters in *Triposolenia* must be, the conditions are such as to afford a nearer approach

[1] It is of course probable that all of these skeletal characters exhibited in the non-living cellulose skeleton are the expression of the many coördinated internal metabolic processes of the nucleus and cytoplasm of the cell, processes which, moreover, are of an ephemeral nature in the cyclic process which culminates in the new formation of the half-theca at the time of cell-division when the parental theca is parted in the sagittal plane and each daughter cell reproduces the lacking half of the thecal wall. Sexual reproduction is as yet unknown in this family and, indeed, has been rarely observed in the Dinoflagellates as a whole, and is as yet unrecorded among the marine species. Judging from the trend of discoveries in the life-histories of the Protozoa its occurrence is to be expected generally among the Dinoflagellates. Should it occur it is probable, from the observations of Zederbauer (:04), that complete formation of a new theca about the zygote or its offspring will be found to take place after union of the gametes.

to a comprehension of the total organism than can be attained in a more complex organism living in a more diversified environment and descended through a more diversified ancestry.

Are the diagnostic characters of the species of *Triposolenia* adaptive? Do they have a survival value to the organisms which possess them? Does the survival value attach itself to the sum total of the species characters or to but one or several, and are the remaining ones in this case to be "explained" as a result of coördination?

If the differentiation of the species in this genus is the result of a struggle for existence it necessarily follows that a survival value attaches to the *differential* characteristics, either to their sum total, which in the case of *Triposolenia* we find to include a considerable number of correlated elements, or to one or more of the individual structural characters to which all the others must then be linked in some necessary relation that is expressed by the term coördination. In assigning natural selection as the cause of the species characters in *Triposolenia* we are at once confronted by the difficulty of finding any evidence of the *differential* survival value of any of the characters in question. Presumably competition is severest between individuals of the same or closely related species and species of related genera. It is, however, impossible to establish the fact of any advantage accruing to one of these species over its nearest allies by reason of its structural distinctions and difficult to find any satisfactory basis for a logical inference or conclusion to that effect.

The structural adaptations in *Triposolenia* are evidently directed toward the development of a specific skeletal surface sufficient for the necessities of flotation, the distribution of skeletal matter with reference to orientation, and to the exposure of the protoplasmic contents to the action of light and of substances in solution in the water. It is conceivable, and indeed probable, that *all* the types of midbody, of form, proportions and curvatures of the antapicals and neck are adaptive, or at least are not unadaptive in these directions, and that the pitted surface of *T. truncata* is adaptive in compensation for its shorter horns, but the various forms of head and antapical tips and the distributions of tubercles are less clearly of utility. That *all* of these specific types are fitted to survive is witnessed by the coincident occurrence of at least five of the species in the San Diego area, and it is not improbable that prolonged search will bring the other three to light in that region. While it is not probable that all of the species are *all equally well adapted to survive* it is evident that they have been and are *sufficiently* well adapted to maintain themselves.

It is conceivable that all variations or mutations which have weakened the coherence of the parts or increased or decreased the specific gravity or specific surface beyond certain limits would result and may have resulted in the extinction of these unfit individuals which have passed the "dead line" into the territory where selection becomes operative. It is equally probable that many types of form and proportions of the structural elements of *Triposolenia* might occur and may have occurred upon which selection is entirely inoperative by reason of the fact that they lie within the circle of permissable adaptive changes at whose circumference natural selection lies in wait. For example, it is impossible to see how natural selection can account for the triangular, elliptical and the two pendant types of midbody in *Triposolenia.* All afford approximately equal form resistance, specific surface, and exposure for metabolism. That one type is about as effective as another, or at least sufficiently effective, is evidenced by their continuance in a common environment. The same statement might be made with reference to other diagnostic structural features of the several species. In *Triposolenia* we have an illustration of the occurrence of a number of types of structure, apparently of specific rank, types defined by a number of structural elements rather than by a single one or a few, types, moreover, which are apparently not linked together by coincident variations of the fluctuating nature of all the characters involved, and these types, or species as I believe them to be, all appear to lie within the circle of permissible adaptive modifications where natural selection is inoperative. The utility of each of the complexes of characters is sufficient for their preservation without the necessity of calling in natural selection to account for their differentiation and continuance. It is not difficult to imagine a number of types of *Triposolenia,* modifications of the structural elements which the genus presents, which may occur as additional species, and it requires no gift of prophecy to predict that continued exploration of the sea will bring to light additions to the genus.

If then natural selection does not originate the specific characters of *Triposolenia* we are forced to seek some other explanation of the complex of structures found in the organization of each species. The mutation theory of De Vries (:05) affords a conception of the origin of these species which avoids the difficulties attendant upon the absence of differential survival values of the specific characters and also lends itself readily to the view here advocated that specific distinctions involve not a few but many characters of the organism.

III. The Coincident Distribution of Related Species of Triposolenia.

The data available for the critical determination of this question are inadequate at present. In the first place the individuals are always relatively rare, 1–6 representing the number of individuals usually found in a haul of a 14-inch net. Again, closing net catches have not been examined in sufficient numbers and from sufficient localities to determine the *vertical* distribution of the species. It is possible that there may be a differential vertical distribution and that temperatures may form barriers between the species. I have no conclusive evidence on this point at present. The programme of the San Diego Station includes an investigation of the vertical distribution and movements of the plankton. It is hoped that precise evidence on this matter of temperature barriers and vertical distribution will be forthcoming. The facts are as follows: All species except *T. ambulatrix* and *T. longicornis* have been found within an area of a few square miles off San Diego in hauls within 100 fathoms of the surface. A number of hauls from 200–300 and even 400 fathoms have been made, but they do not show any increase in the number of individuals of *Triposolenia*. The hauls have been made in most cases by lowering the nets to the desired level and towing for 10–60 minutes and then bringing the open net to the surface. This affords an assumption in favor of a considerable part of the contents coming from the deeper levels since the net does not filter on the descent and has its filtration efficiency reduced during its ascent. The individuals of the various species of *Triposolenia* have been found with a single exception only in the hauls from below the surface, and principally in those from the 70–130 fathom levels. Frequently several species have been found in a single catch. Representatives of this genus are extensively distributed throughout the Eastern warm temperate and tropical Pacific. It is not improbable that Schütts' ('95) *Amphisolenia tripos* (*nomen nudum*) from the Gulf Stream is a member of this genus. The investigations of Cleve ('01 and '02) and others have shown the cosmopolitan nature of the distribution of the pelagic Dinoflagellates. My own observations on the plankton of the Pacific confirm this view. *Triposolenia* is not a genus restricted in its distribution and the species here described are not local forms. They will be found, beyond question, widely distributed in the warmer seas. Over against the possibility of barriers of temperature separating them in their vertical distribution should be placed the probability of some vertical movement as a result of vertical currents (see Holway :05) and also as a result of heliotropism, the latter varying with the amount of carbonic or other acids in the water (Loeb :03). In any case the coincident distribution of closely related species is a common feature among the pelagic protozoa with which I am familiar, *e.g.*, among the Coccolithophorida, the Silicoflagellata, other Dinoflagellata, the Radiolaria, and the Tintinnidae. That these primitive animals should have attained so high a degree of specific differentiation in the presence of so great environmental uniformity, in the relative absence of barriers, is a fact of profound significance to be taken into account in any discussion of the process of organic evolution.

Zoological Laboratory, University of California,
October 3, 1906.

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ON THE SIGNIFICANCE OF THE ASYMMETRY IN TRIPOSOLENIA.

BY

CHARLES ATWOOD KOFOID.

The appearance in *Triposolenia* of an asymmetry caused by the deflection to the left of the posterior ends of the antapicals and a similar asymmetry in a number of species of *Amphisolenia* (Kofoid :06) leads to a consideration of the significance of this somewhat widespread phenomenon. Had it appeared as one of the characters of a single species, or even of several, it would be dismissed as one of those usual chance vagaries of structure which so often crop out in the diagnostic features of a species. Its occurrence in the two genera named and suggestions of an analogous structural feature in some other genera of Dinoflagellates is indicative of a more profound relationship to the welfare of the organisms in which it appears.

Locomotion in this genus, as in other Dinoflagellates, is brought about by the combined action of the two flagella. The transverse flagellum causes rotation about the antero-posterior axis of the body, or rather about the axis of the spiral of progression, while the longitudinal flagellum is the principal organ of propulsion, though it may also assist in the rotation. The combined effect of the activity of the two flagella is to cause the organism to move forward in a spiral course about a more or less straight line of progression as shown in Fig. A. The rotation may be in either direction, that is, dexiotropic or leiotropic. A more precise definition of the motion is possible by using the axes and poles of symmetry of the organism. The dexiotropic rotation

Fig. A. Diagram of locomotion in Triposolenia.

of an organism with its antero-posterior axis in a horizontal position is brought about by a turning of its body on this axis in the direction of its left over to its right, and the leiotropic by turning in the opposite direction, to wit, from its right over to its left. In the Dinoflagellates generally the rotation is predominantly from left over to right and structural differentiations which favor this predominance in the direction of rotation are not infrequent, such, for example, as the distal displacement of the girdle giving to it the form of a descending right spiral. Such differentiations usually result in some bilateral asymmetry. The only structural character of this sort in *Triposolenia* appears to be the asymmetry in the lists about the flagellar pore.

As Jennings[1] has clearly shown, this rotation upon the axis, with resulting spiral course of greater or less radius, is a most effective means of securing progression in a definite direction. The radius of the spiral is largely influenced by the degree of asymmetry of the organism, being greater as the asymmetry increases.

There is in *Triposolenia*, however, a form of bilateral asymmetry which, though it may be coördinated with the spiral rotation of the organism, is nevertheless also a most perfect adaptation to flotation in that it serves to orient the body during passive descent in response to gravity, in the position of greatest resistance. I refer to the distal deflection of the tips of the antapical horns to the left.

The principal necessity which confronts pelagic organisms is that of keeping within range of the food supply, which for most organisms means keeping within a certain distance of the surface of the sea. In the case of *Triposolenia* the organism is dependent to some extent upon illumination for its synthetic processes. The degree of light necessary is apparently not great since its center of distribution appears to be nearer the hundred fathom line than to the surface. The constant action of gravity tends to draw the organisms below the levels of optimum illumination. It is essential, then, to the welfare of the organism that its locomotor activities should preserve its location in the region of optimum

[1] Jennings, H. S.: On the Significance of Spiral Swimming of Organisms. Am. Nat., Vol. 35, pp. 369-378, 11 figs., 1901.

illumination. This could be accomplished by the mode of locomotion above described, provided that the organisms were oriented with their heads uppermost. The form of the midbody, especially in the pendant type, and of the antapicals, is strongly suggestive that they may serve as organs of orientation. If they have this function it may result either from a greater specific gravity posteriorly, or from a smaller specific surface in the same region, or it may be from both. The lists suffice to give the anterior part a greater specific surface than is found posteriorly, and in the passive sinking of the organism this difference would tend to hold the anterior end uppermost. Treatment with osmic acid reveals an accumulation in the head and neck of fatty or oily substances which turn a darker brown than the cell contents elsewhere in the body. The presence of these lighter substances here would also tend to keep the anterior end uppermost. Furthermore, it may be that these organisms exhibit a positive heliotropism for certain intensities of light, as do some other Dinoflagellates, and that this reaction would result habitually in their active orientation with the anterior end uppermost in levels of optimum illumination. The orientation of the body may thus be passive, as a result, when the organism is sinking, of the molecular friction of the water on the greater specific surface of the anterior end, or as a result of its smaller specific gravity, or it may be active, resulting from positive heliotropism. In any case, given this orientation, locomotion will result in movement toward the surface away from the ceaseless pull of gravity.

There is one disadvantage to the organism in this orientation in that its form resistance to the pull of gravity is small. Indeed the area of the water displaced by *Triposolenia* in sinking while in a vertical position is the least possible, being less than with the dorsal or ventral edge below, and very much less than it would be if the organism lay on either side. In the case of *T. depressa* the displacement area in the vertical position is about 390 square micromillimeters, with the ventral edge below it is 540 square micromillimeters, while on one of the lateral faces it is about 1,200, or nearly three times as great.

It is obvious that passive sinking as a result of the pull of gravity, if long continued, would carry the organism below the limit of optimum illumination, or even beyond possible photosynthesis. The return to the optimum levels can only be made at some expense of energy. Any structural provision, therefore, which lowers the rate of sinking will be of distinct advantage in that it prolongs the stay at optimum levels, and reduces the expenditure of energy in the return to such levels, when once gravity gets the upper hand of the locomotor powers of the organism.

Temporary cessations in the locomotor activities of *Triposolenia* expose the organisms to the action of gravity and descent begins while the organism is in a vertical position, with the minimum form resistance to the downward movement.

It is obvious that if the organism should turn so that it should lie on the side the area of displacement would be greatly increased and the descent delayed. *This is accomplished by the terminal asymmetry of the antapical horns in Triposolenia.* As has been indicated in the description of the species in the previous paper, the ends of the antapicals are bent to the left for a short distance in all species which have been examined on this point. The effect of this asymmetry is to turn the organism upon its right face, as soon as it begins to descend while oriented with the anterior end uppermost. The greater resistance offered by the right face of the tips veers the antapices to the left and throws the organism over on its right side, as shown in Fig. B. This may be beautifully demonstrated by dropping in the air a paper model of *Triposolenia* in which the antapicals are slightly bent. The turning of the model, made from a drawing showing an enlargement of 675 diameters, is accomplished easily within a meter of descent, and often in less than that distance, that is, within ten lengths of the organism. The rapidity and despatch with which the model turns is remarkable and is significant of the effectiveness of this structure in changing the orientation of the organism when sinking with a vertical orientation.

The deflecting effect of the bent ends of the antapicals naturally decreases as the organism turns upon its side, since they include a rapidly decreasing proportion of the total surface of resistance. When once turned upon the side the horizontal orientation of the model continues for a short time and the descent proceeds with frequent changes of position in a fluttering, waver-

Fig. B. Diagram of sinking *Triposolenia*.

ing manner which involves frequent returns to the horizontal position. In the case of *Triposolenia* in suspension in the sea-water, to whose specific gravity it closely approaches, the horizontal position and the subsequent shiftings presumably occupy a longer time than in the case of the model in the air. This is easily demonstrated by sinking a model of firm hard paper in a tall jar of water.

Other genera than *Triposolenia* exhibit this type of asymmetry. It is seen in a similar structural deflection in the allied genus *Amphisolenia* in a large number of species, especially in those of linear form. Linear species of Ceratium also have marked deflection of the left antapical horn to the left and dorsally. This is noticeable in *C. fusus* Ehrbg. and *C. strictum* (Okamura). In species of *Ceratium* with anteriorly deflected antapicals the two horns are sometimes deflected ventrally in a sweeping curve. In *Peridinium* and *Heterodinium* the girdle is often oblique antero-dorsally and ventro-posteriorly. These various types of asymmetry all have the tendency to orient the passively sinking organism broadside to the direction of descent and thus to increase the area of resistance. These forms of bilateral or dorso-ventral asymmetry among the Dinoflagellates are thus adaptative to flotation.

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