A Surviving Somasteroid from the Eastern Pacific Ocean

An archaic asterozoan has been isolated by analysis of gradient fields in fossils and extant groups.

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The archaic echinoderms called Somasteroidea are known from fossils in lower Paleozoic rocks and, until now, were thought to have mostly become extinct early in the Ordovician Period, some 400 million years ago. Their particular interest lies in the structure of the body, which shows affinities with crinoids on the one hand and yet also foreshadows ophiuroids and asteroids on the other.

It is therefore a matter of quite exceptional importance that a living somasteroid is now known to have survived in tropical eastern Pacific waters bordering on southern Mexico. The circumstances which led to its discovery are as follows.

As long known to paleontologists, somasteroids differ from all other echinoderms in having a flattened, star-shaped body in which the skeleton of the arms resembles that of crinoids, being built of elongate rods (called virgalia) arranged in oblique rows on either side of an axial series of ambulacral ossicles. The rows of virgalia, disposed like the pinnules of a biserial crinoid, form the adjacent walls of intervening food grooves, which apparently convey water currents to the ambulacral furrow and thence to the small, central mouth. The ambulacral ossicles are not erected to form an inverted V, as in asteroids, but are in a recumbent attitude; thus, the furrow is not invaginated into the arm but, instead, is merely a shallow groove underlying the ambulacral ossicles. As we can now infer from the living example, somasteroids are also characterized by having tube feet without suckers, and a blind gut similar to that of ophiuroids and luidiid asteroids. The earlier Paleozoic forms had petaloid arms, separated by a narrow, deep interradial fissure; the surviving species is of this primitive type. The more specialized Ordovician members had partially differentiated virgalia, and the body resembled that of a phanerozonid asteroid; the living species shares the first character but not the latter.

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Characters of Existing Asteroids

In the course of a long monographic study now approaching completion I have made a series of dissections of the internal skeletal system of existing genera of Asteroidea, in search of characters which might permit more direct comparison of extant groups with the Paleozoic Asterozoa and thus lead to a more rational classification of the families. It has been generally agreed that the more primitive families of extant asteroids are those phanerozonid forms which lack suctorial tube feet—namely, the Porcellanasteridae, Astropectinidae, and Luidiidae. There has been no agreement, however, as to which of these groups might be the more ancient, though the Astropectinidae have usually been so regarded. In the course of my work I was greatly struck by the elongate, rodlike appearance of the so-called superambulacral plates in certain astropectinid genera, notably in *Persephonaster*. These rather forcibly reminded me of the virgalia of the Ordovician somasteroid *Archegonaster* (Fig. 1). I subsequently found that some Luidiidae also possess similarly enlarged rodlike ossicles. On the basis of the tentative assumption that these do indeed represent virgalia, I was able to narrow the field of my inquiry by eliminating the Porcellanasteridae, since superambulacral ossicles are unknown in this group. A survey of the other families disclosed that rod-shaped superambulacral ossicles occur in only a few genera and that superambulacral ossicles of any type are restricted to the Astropectinidae and Luidiidae. Further work was then concentrated upon these two groups.

Studies on the mode of development of the skeleton in ophiuroids (*1*) had already shown that the skeletal plates in this subclass differentiate under the influence of both longitudinal and transverse axial growth gradients. Thus, the plates come to be arranged in both longitudinal and transverse series, simulating a kind of segmentation in the arm.

A corresponding investigation of the plate arrangement in the ventral body-wall of asteroids now revealed that, whereas the Astropectinidae differentiate under the action of only longitudinal axial gradients (for the marginal and actinal intermediate plates do not form transverse rows with the axial elements), the Luidiidae, on the other hand, differentiate under the same double system of axial gradients that is found in ophiuroids. All other asteroids conform to the astropectinid pattern. This was very interesting, for it meant that the Luidiidae could now be set apart from all other asteroids, and the character which distinguished them proved to be one which they shared with the ophiuroids. I was now convinced that best clues for solution of the problem must lie somewhere within or near the Luidiidae.

Therefore I inferred that possession of both transverse and longitudinal axial growth gradients is a primitive feature which the Luidiidae, like the Ophiuroidea, had inherited from some somasteroid ancestors, because inspection of the way in which virgalia are arranged in somasteroid fossils immediately indicates that both systems of gradients must have been present in these ancient asterozoans.

With the validity of the various assumptions made up to this point taken for granted, it then became no more than a theoretical exercise to deduce what changes a somasteroid would have to undergo in order to give rise to an asteroid of luidiid type. These transformations can be specified rather precisely, but need not be discussed in detail here.

Platasterias

Although Hyman (*2*) stated that only the type genus *Luidia* comprised the Luidiidae, a second genus had been included by Sladen (*3*). This is the rare west American *Platasterias*. It contains only the single known species, *P. latiradiata*, the type of the genus, described by Gray in 1871 (*4*) (Fig. 2.). Fisher (*5*) apparently was never able to examine a specimen, but although he seemed inclined to place it in the Astropectinidae, he left it under the Luidiidae in his monograph, where it received only brief and cursory mention (*6*).

Utilizing published data (for I then had no specimen), I soon realized that if *Platasterias* is really a member of the Luidiidae, it must have evolved in a precisely opposite direction from that which I had deduced for *Luidia*; this, though possible, seemed unlikely, since structures once lost in evolution are only rarely, if ever, regained. Could this mean that *Platasterias* is really the older form and *Luidia* the derivative? It began to seem likely.

The hypothesis became more attractive when account was taken of the petaloid form of the arms and the deep interradial cleft between each adjacent pair of arms, features closely simulating the lower Paleozoic Chinianasteridae (Fig 3). During the course of my studies over the past 20 years I had brought every extant genus of asterozoan under review—at least on the basis of the literature, where I could not secure material—and consequently I was already aware that no other recorded living asteroid possesses a body of this shape. Further, the extreme narrowness of the ambulacral furrows and the flattening of the whole animal (from which the generic name arises) are additional characters reminiscent of the somasteroids. These features might be secondary developments, however, and not necessarily indicative of an ancient lineage.

To resolve this uncertainty it was essential to ascertain the attitude of the ambulacral ossicles and to establish whether virgalia of somasteroid type were present, separated by fasciolar food grooves and forming the walls of such grooves. Inspection of Gray's beautiful lithograph (*4*) indicated that the ventral skeleton was arranged in a way decidedly like that of somasteroids, for the ossicles appeared to form oblique series of elongate elements, disposed in a pinnate fashion. Unfortunately it was not apparent from the lithograph whether channels of the kind I was looking for were placed between the rows of ossicles. Some additional photographs recently published by Caso (*7*) served only to confirm the general accuracy of Gray's lithograph. Nowhere was information available upon the nature of the ambulacral ossicles or their attitude and relation to other ossicles; nor was it possible to ascertain the disposition of the superambulacral plates, or whether such plates are present at all. It was therefore impossible to reach any trustworthy conclusion without dissecting a specimen.

Believing that the investigation had now reached a critical stage, I resolved to set out my inferences as to the possible chinianasterid affinity of *Platasterias*, and I sent them in November last to a colleague in London, Ailsa M. Clark, curator of the department of echinoderms at the British Museum, expressing the hope that some material might be located (for inquiries in Mexico had proved unavailing). My request met with an immediate generous response, and within one week a portion of one arm of a specimen was placed at my disposal. To my immense satisfaction, though no less astonishment, it was evident from the cut ends of the arm that the ambulacral plates were in the recumbent position, as predicted (Fig. 2). It was apparent from the external features that the ventral skeleton is built up of virgalia (though their homology with the ventral plates of asteroids is equally obvious). It was

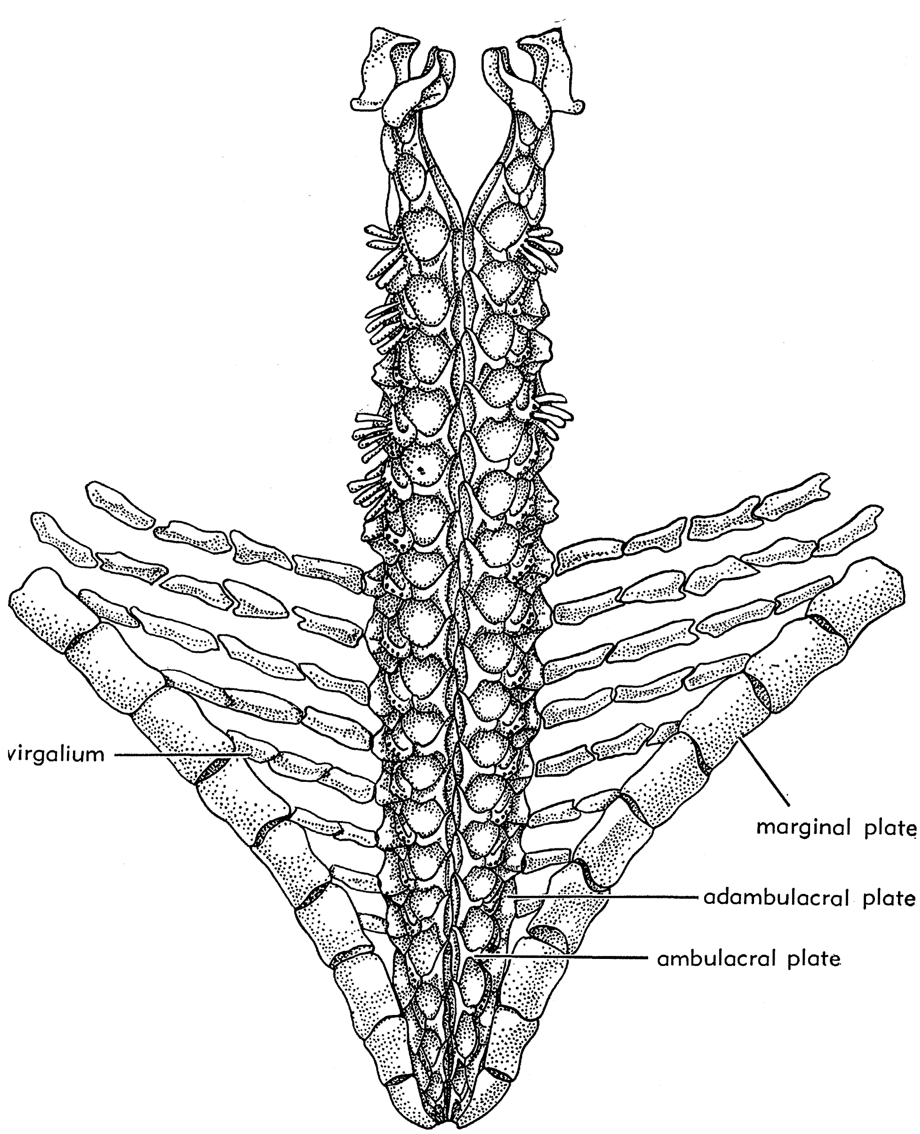

Fig. 1. Lower Ordovician somasteroid, *Archegonaster pentagonus* Spencer, from Czechoslovakia; ventral side, showing food-groove plates (ambulacra, adambulacra) and virgalia directed laterally from them. (About × 3.8) [After Spencer (*9*)]

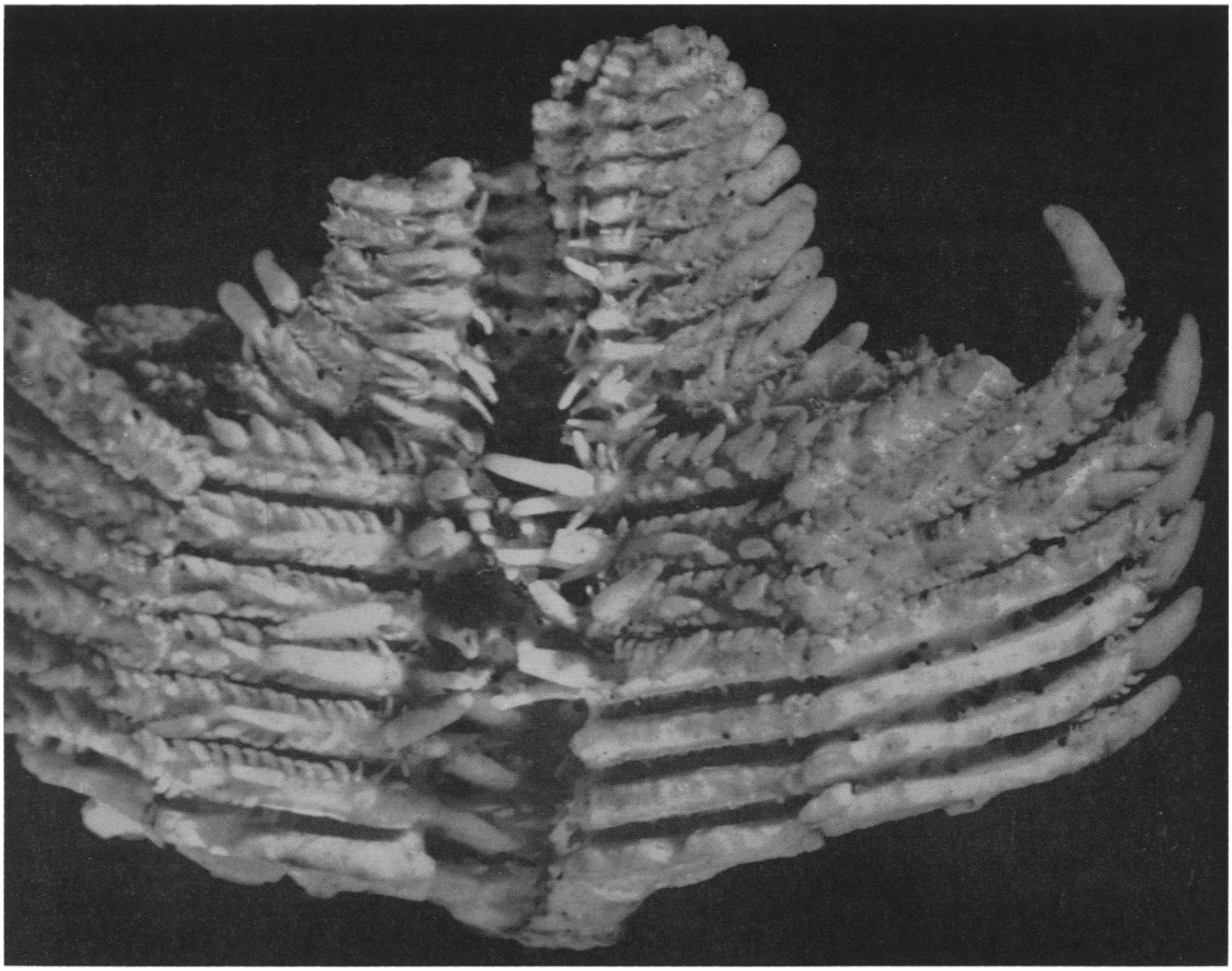

Fig. 2. *Platasterias latiradiata* Gray, from a locality off the west coast of Mexico, showing the partially dissected arm-base (from the level of virgalium series 6 to virgalium series 12, followed by the regenerating portion). At lower right, three virgalium series (each approximately 10 millimeters long) have been denuded of spinules and guarding webs, to expose the fasciolar channels. [M. D. King, Victoria University of Wellington]

also evident that a system of channels like that of somasteroids occurs, though the exact nature of the canals could not be determined without some dissection. To avoid damaging the material I was obliged to moisten it very gradually with detergent and remove each spinule individually. The detergent reconstituted the integument, by now dried after nearly a century in the museum, and it was possible to learn something about the soft parts. As each character was exposed, it became increasingly obvious that in every major demonstrable feature the specimen conformed to the known anatomy of the Cambrian and Ordovician Chinianasteridae, though at the same time there were obvious links with the Luidiidae—more than sufficient to confirm my earlier hypothesis that the Luidiidae are an ancient stock. By early December 1961 the evidence was overwhelming, and I thereupon cabled Ailsa Clark the exciting news that *Platasterias* undoubtedly is a somasteroid, incredible though this may seem.

Platasterias is thus recognized as the oldest type of asterozoan echinoderm as yet discovered in any extant fauna, and only a little more specialized than the Cambro-Ordovician Chinianasteridae. At the same time, the partial differentiation of the skeleton and the nature of the soft parts suggest that *Platasterias* is an early type of asteroid. The virgalia are arranged as in the Chinianasteridae (Fig. 3), not as in the Archegonasteridae (Fig. 1), but they are partially differentiated into adambulacral, superambulacral, and marginal elements in each oblique row, as in the Archegonasteridae and Luidiidae. Therefore *Platasterias* must fall in a separate family, defined as having the petaloid arms and interradial cleft of Chinianasteridae and elongate, pinnately arranged virgalia partly differentiated. As in *Villebrunaster* (Chinianasteridae), the ambulacral plates are opposite and the lateral wing arises from the capitulum of the ambulacral ossicle, directed from the adapical lateral extremity parallel to the rows of virgalia. The familial name is Platasteriidae Caso, 1945, originally defined (as Platasteriinae) by its author on the basis chiefly of the irregular occurrence of actinal intermediate plates (that is, accessory virgalia). While I cannot regard the latter feature as of much significance, the name is valid and merely requires a new definition in the sense indicated.

The Luidiidae are now seen to occupy a position between somasteroids and other asteroids and may be placed at the beginning of the Phanerozonida.

Interpretation

The data yielded by the larvae of echinoderms, unlike data in some other groups, notably the Crustacea, are not susceptible to treatment at their face value; it has been shown (*8*) that this leads only to a *reductio ad absurdum.* If larval forms are interpreted as reflecting ancestral structure or relationships, the larval evidence indicates that ophiuroids and echinoids, which alone have pluteus larvae, must be more closely related to one another than they are to any other group. By the same token, asteroids and ophiuroids, which have different larval forms, are less closely related to each other than ophiuroids are to echinoids and asteroids are to holothuroids. Those who accept such views place the ophiuroids far apart from the asteroids, interpolating the echinoids between them. In my view, such interpretations are quite erroneous and lead to false conclusions. It is more reasonable to infer that the larvae of echinoderms have evolved and therefore no longer reflect phylogenetic relationships. An arrangement of the extant classes which places the ophiuroids far apart from the asteroids is totally out of key with the whole evidence of paleontology and comparative anatomy.

It is pointless to set the facts of embryology as the norm for calculating an ancestry. The fossil record shows clearly that ophiuroids and asteroids have a common ancestry and that echinoids had already evolved as a distinct group long before ophiuroids had diverged from the main asterozoan stem. Embryology cannot accommodate these facts. The embryological approach could not have elicited the finding that the Luidiidae are ancestral to other asteroids, and therefore still less could it ever have pointed to *Platasterias* or admitted that ophiuroids and asteroids have common ancestors.

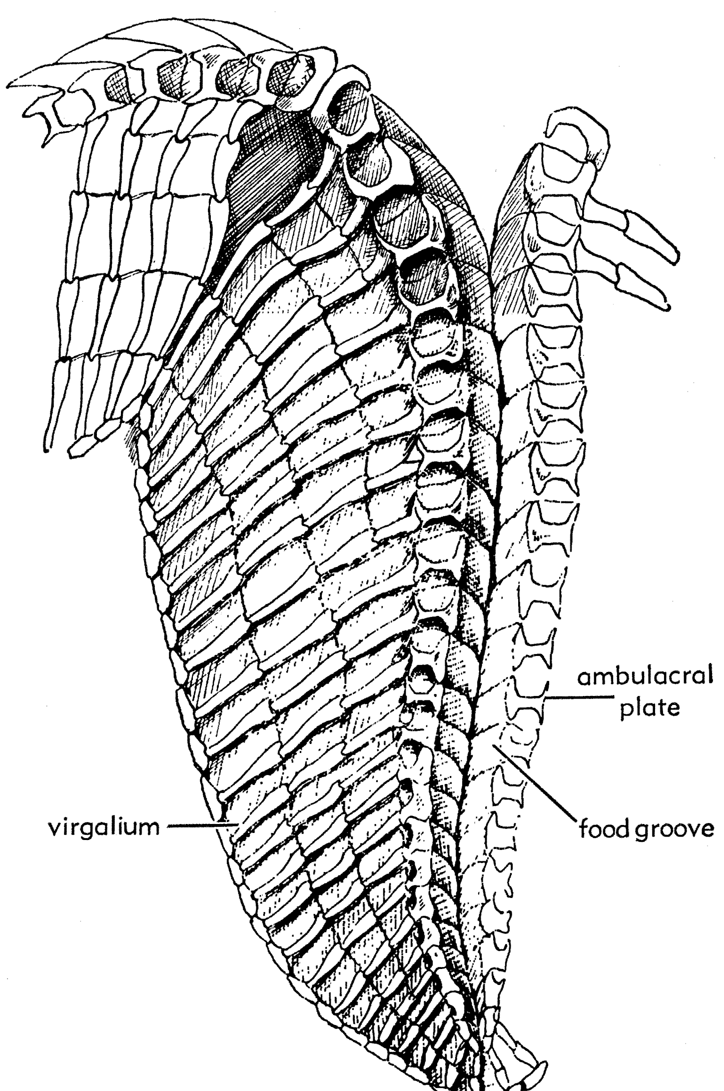

Fig. 3. Part of the oral surface of *Chinianaster levyi* Thoral, from Lower Ordovician rocks of France, showing prominent virgalia formed of elongate rods and deep indentation between two adjacent rays. (About × 6.5) [After Spencer (*9*)]

The methods which have been used to distinguish the most primitive asterozoans may be extended to other echinoderm groups. Plainly we must first search for a living ophiuroid with a virgalium, which I now confidently equate with the so-called sublateral plate of Paleozoic ophiuroids. It can also be seen that the plates in ophiuroids hitherto equated by embryologists (including myself) with the adambulacral series will almost certainly be found to represent the marginal series of somasteroids, not the adambulacrals. A broad field now widens out in which we can make direct comparisons between arms of Asterozoa, crinoids, and the "arms" of echinoids. Those who are familiar with the polyserial plate arrangement in Paleozoic echinoids and the imbrication of interambulacrals upon ambulacrals will surely be as intrigued as I am in comtemplating the obvious analogy in *Platasterias.* May this analogy conceal a genuine homology? Here lies our next major objective, which may well be reached within the next few years. The prospects are bright (*10*).

References and Notes

1. I made these studies in the early 1940's, starting in 1941.
2. L. H. Hyman, *The Invertebrates* (McGraw-Hill, New York, 1955), vol. 4, "Echinodermata."
3. W. P. Sladen, *Challenger Reports: Zoology* (1889), vol. 3, "Asteroidea," p. 893.
4. J. E. Gray, *Proc. Zool. Soc. London* **1871**, 136 (1871).
5. W. K. Fisher, *U.S. Natl. Museum, Bull.* **76**, No. 1 (1911).
6. F. C. Ziesenhenne, of the University of Southern California, informed me by letter that some specimens of *Platasterias* were taken by the *Velero III* from shallow water at Corinto, Nicaragua. All were dried, and some of them were distributed to several museums. Ziesenhenne wrote: "Dr. Fisher asked me to place the next batch in alcohol, but we never did get back to Corinto on the *Velero III.* He was most interested in the internal structure of *Platasterias* and wanted wet material for his studies."
7. M. E. Caso, *Los Equinodermos de Mexico* (Universidad Nacional Autónoma de México, Mexico City, 1961).
8. H. B. Fell, *Biol. Revs. Cambridge Phil. Soc.* **23**, 81 (1948).
9. W. K. Spencer, *Phil. Trans. Roy. Soc. London* **B235**, 87 (1951).
10. H. B. Fell, *Univ. Kansas Paleontol. Contrib., Echinodermata,* Art. 6, in press.