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ARTICLE

New records of teratology in *Chiton cumingsii* and *Chiton granosus* (Mollusca: Polyplacophora) from the Peruvian coast

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Abstract. This paper presents the first teratological records for Peruvian waters of *Chiton cumingsii* Frembly, 1827 and *Chiton granosus* Frembly, 1827, both species very common in the Southeast Pacific. We found five abnormal individuals in *C. cumingsii,* and two in *C. granosus,* including the first recorded splitting abnormalities for these species. An individual of *C. cumingsii* with a new insertion plate in the tail valve was also observed. We observed that splitting abnormalities in Polyplacophora can be classified as perfect or imperfect, depending on whether the splitted valves are clearly recognized as individual fragments or not. Coalescence between the splitted valves seems to be a common phenomenon, and this coalescence can be homogeneous or heterogeneous. As both species show a combination of hypomerism, coalescence and splitting, we suggest that they are probably interrelated and represent an attempt of the developmental mechanisms of chitons to overcome a valve malformation.

Keywords. Hypomerism; Splitting; Coalescence; Chiton.

INTRODUCTION

Teratology is the science that studies permanent structural or functional abnormalities that arise during the embryonic development (Clegg, 1971) in relation to internal factors (genetics), external factors (environment) or a combination of both (Calado & Dos Anjos Pires, 2018). Although members of Polyplacophora (Mollusca) normally have eight dorsal valves, abnormal specimens with an unusual number of valves have been extensively reported in many regions around the world (Taki, 1932; Dell'Angelo & Schwabe, 2010; Torres *et al.,* 2018; Guillén & Urteaga, 2019). Dell'Angelo & Schwabe (2010) provided an overview of teratological cases in chitons, establishing four typical categories: (1) hypomerism, the complete absence of one or more valves; (2) hypermerism, the presence of additional valves; (3) coalescence, the union of adjacent valves; and (4) splitting, the division of one valve into two valves. However, Avila-Poveda *et al.* (2019) have proposed a more complex classification of teratology cases in chitons by considering the degree of coalescence between the valves, and the number of slits and slit-rays of each valve.

Although there are some records of teratology for the western coast of South America (Peña, 1977; Peña & Castro, 1982; Gálvez, 1991; Schwabe, 2001; Torres *et al.,* 2018), the only record of teratology in chitons of the Peruvian coast is the hypomerism reported for one specimen of *Tonicia fremblyana* Kass, 1956 from Pucusana, central Peru (Torres *et al.,* 2018). Even though *Chiton cumingsii* Frembly, 1827 and *Chiton granosus* Frembly, 1827 are among the most abundant species of Polyplacophora along the Peruvian Marine Province (Ibáñez *et al.,* 2019), all recorded teratological cases for both species come from Chile, including hypomerism and coalescence in *C. granosus* (Peña, 1977; Peña & Castro, 1982; Torres *et al.,* 2018) as well as hypomerism and abnormal valves in *C. cumingsii* (Schwabe, 2001). Therefore, the objective of this study is to present new records of teratology in *C. cumingsii* and *C. granosus* from the Peruvian coast and to compare the usefulness of Dell'Angelo & Schwabe (2010) and Avila-Poveda *et al.* (2019) classifications to better describe teratological cases in Polyplacophora.

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MATERIAL AND METHODS

As part of a taxonomical study of the most common species of Peruvian Polyplacophora, we got to review a total of 723 specimens of *C. cumingsii* and 328 of *C. granosus* deposited in the Laboratorio de Biología y Sistemática de Invertebrados Marinos (LaBSIM) of the Universidad Nacional Mayor de San Marcos covering most of the geographic range of both species in the Peruvian coast (Alamo & Valdivieso, 1997). The specimens were identified according to Pilsbry (1893), Bullock (1988) and Kaas *et al.* (2006). Some visible teratological abnormalities were found. The abnormal individuals were examined with a stereo microscope Leica S APO/LED2500 and photographed using a digital camera Nikon Coolpix P90. The following measures were taken for each aberrant individual: body length (L), body width (W), dorsal elevation (E), shell length, *i.e.,* without the girdle (SL), shell width (SW), and number of ctenidia in the right and left side of the body. The ratio of body width/length (W/L) and shell width/length (SW/SL) of abnormal specimens were compared with those of normal specimens from the same locality and similar size. All measures were taken in millimeters with a vernier caliper Mitutoyo CD-6″ CSX-B. The valves were removed from the animals to examine the number of slits and slit-rays in the insertion area and each valve was photographed in dorsal and ventral view. Following Avila-Poveda *et al.* (2019), some normal individuals with 8 valves were randomly selected from both species to search for potential non-visible anomalies. Head valve, valve IV and tail valve were removed from these specimens. In addition to the typical cases of teratology (Dell'Angelo & Schwabe, 2010), we also searched for other abnormalities in the valves or girdle.

RESULTS

Among the total of examined individuals, 723 specimens of *C. cumingsii* and 328 of *C. granosus,* we found five specimens of *C. cumingsii* and two specimens of *C. granosus* with visible abnormalities, most of them showing a complex arrangement of coalescence and splitting. Only one specimen of *C. cumingsii* with non-visible abnormalities was identified (Table 1).

Individuals with visible abnormalities

Hypomerism

Chiton cumingsii, Peru, *Callao:* La Punta (La Arenilla), 5 specimens, 1 abnormal individual, 25.V.2013 (LABSIM 15.03.0194). The abnormal individual presented hypomerism, showing 7 valves (Fig. 1A-B), each valve with a normal appearance in dorsal view. The head and tail valves both have 12 slits. Most intermediate valves have a single slit and slit-ray on each side (Fig. 1C), although the valve III has 1 slit and slit-ray on the right side, but 2 slits and slit-rays on the other side (Fig. 1D). This is not visible dorsally, suggesting a homogeneous coalescence as fusion is complete in 'tegmentum' and 'articulamentum'. The apophysis, ventral tegmental callus, and jugal tract present normal characteristics in all valves. Total body size: 23.01 mm long × 15.06 mm wide (W/L = 0.65), shell size: 22.52 mm long × 12.47 mm wide (SW/SL = 0.55), dorsal elevation: 5.58 mm. The size of the left side (3.58 mm) is not significantly different from the right side (3.59 mm). Ctenidia symmetrical: 39 on both sides.

Chiton cumingsii, Peru, *Callao:* La Punta (12°04′05″S, 77°09′00″W), 17 specimens, 1 abnormal individual, 01.V.2018, E. Salazar col. (LABSIM 15.03.0272). The abnormal individual presented hypomerism, showing 7 valves (Fig. 2A-B), most valves with a normal appearance in dorsal view; valve IV asymmetrical, with the right side larger than the left one. The head valve has 11 slits and the tail valve has 14 slits. Most intermediate valves have a single slit and slit-ray on each side (Fig. 2C), although the

Table 1. Summary of teratological cases reported in this study.

Catalog number	Species	Locality	Body Length (mm)	Nº valves	Valves Symmetry	Left ctenidia	Right ctenidia	Dell'Angelo & Schwabe (2010)	Avila-Poveda *et al.* (2019) and this work
LABSIM 15.03.0194	*Chiton cumingsii* (Fig. 1)	La Punta, Callao	23.01	7	Yes	39	39	Hypomerism	Homogeneous coalescence with imperfect hypomerism
LABSIM 15.03.0272	*C. cumingsii* (Fig. 2)	La Punta, Callao	27	7	Yes	38	38	Hypomerism	Homogeneous triple-coalescence with imperfect hypermerism
LABSIM 15.03.0164	*Chiton granosus* (Fig. 3)	Morro Sama, Tacna	24.22 (curled)	7	No (right asymmetry)	47	46	Hypomerism	Homogeneous coalescence with imperfect hypomerism
LABSIM 15.03.0147	*C. cumingsii* (Fig. 4)	Ancón, Lima	22.03	8 (valve II incomplete)	No (left asymmetry)	38	41	Splitting	Imperfect splitting with heterogeneous coalescence?
LABSIM 15.03.0340	*C. cumingsii* (Fig. 5)	Chorrillos, Barranca	37.63	8	No (right asymmetry)	40	38	Splitting	Imperfect splitting with homogeneous coalescence
LABSIM 15.03.0103	*C. granosus* (Fig. 6)	Punta Piedritas, Lima	34.61	8	Yes	60	60	Splitting	Perfect splitting
LABSIM 15.03.0039	*C. cumingsii* (Fig. 7)	Ancón, Lima	26.90	8	Yes	42	42	Coalescence	Homogeneous coalescence with imperfect hypermerism
LABSIM 15.03.0004	*C. cumingsii* (Fig. 8)	Ancón, Lima	34.47	8	Yes	43	43	Other abnormalities	—

valve IV has 3 slits and 3 slit-rays on the right side, but 2 slits and 2 slit-rays on the other side (Fig. 2D). However, this is not evident dorsally, suggesting a homogeneous triple-coalescence as fusion is complete both in 'tegmentum' and 'articulamentum'. The jugal area in the valve V exhibits an unusual prominent fold in the right side (Fig. 2B). The apophysis and ventral tegmental callus present normal characteristics in all valves. Total body size: 27 mm long × 16.53 mm wide (W/L = 0.61), shell size: 26.28 mm long × 14.20 mm wide (SW/SL = 0.54), dorsal elevation: 6.59 mm. The right side (4.99 mm) is larger than the left side (3.6 mm). Ctenidia symmetrical: 38 on both sides.

Chiton granosus, Peru, *Tacna:* Morro Sama, 13 specimens, 1 abnormal individual, 26.X.2010, F. Cardoso col. (LaBSIM 15.03.0164). The abnormal individual presented hypomerism, showing 7 valves (Fig. 3A-B), most valves with a normal appearance in dorsal view; valve II larger than the other valves; valve IV asymmetrical, with the right side larger than the left one. The head valve has 12 slits and, the tail valve has 13 slits. Most intermediate valves have a single slit and slit-ray on each side (Fig. 3C), although the valve IV has 1 slit and 1 slit-ray on the right side, but 2 slits and 2 slit-rays on the other side (Fig. 3D). However, this is not noticeable dorsally, suggesting a homogeneous coalescence as fusion is complete both in 'tegmentum' and 'articulamentum'. The ventral tegmental callus and jugal tract present normal characteristics in all valves but the apophysis in the valve V exhibits a slight deformation on the right side. Total body size: 24.22 mm long (curled) × 18.2 mm wide (W/L = 0.75), shell size: 21.27 mm long (curled) × 12.14 mm wide (SW/SL = (0.57), dorsal elevation: 5.69 mm. The right side (3.46 mm) is larger than the left side (2.81 mm). Ctenidia asymmetrical: 47 on the left side, 46 on the right side (average = 47).

Splitting

Chiton cumingsii, Peru, *Lima:* Ancón, 6 specimens, 1 abnormal individual, 04.VI.2008 (LABSIM 15.03.0147). The abnormal individual (Fig. 4) presented 8 valves, most valves with a normal appearance in dorsal view. The head valve is larger in the left side, extending posteriorly to the margin of valve III (Fig. 4A-B), having a little scar on the 'articulamentum' (Fig. 4D) although no scar is visible in the 'tegmentum'. Valve II is incomplete, only developed in the right side of the body, with 1 slit and 1 slit-ray, with its jugal area deformed. The head valve has 11 slits and, the tail valve has 17 slits. Most intermediate valves have a single slit and slit-ray on each side (Fig. 4C), although the jugal area in the valve III exhibits an unusual prominent fold in the left side (Fig. 4B). Total body size: 22.03 mm long × 14.45 mm wide (W/L = 0.66), shell size:

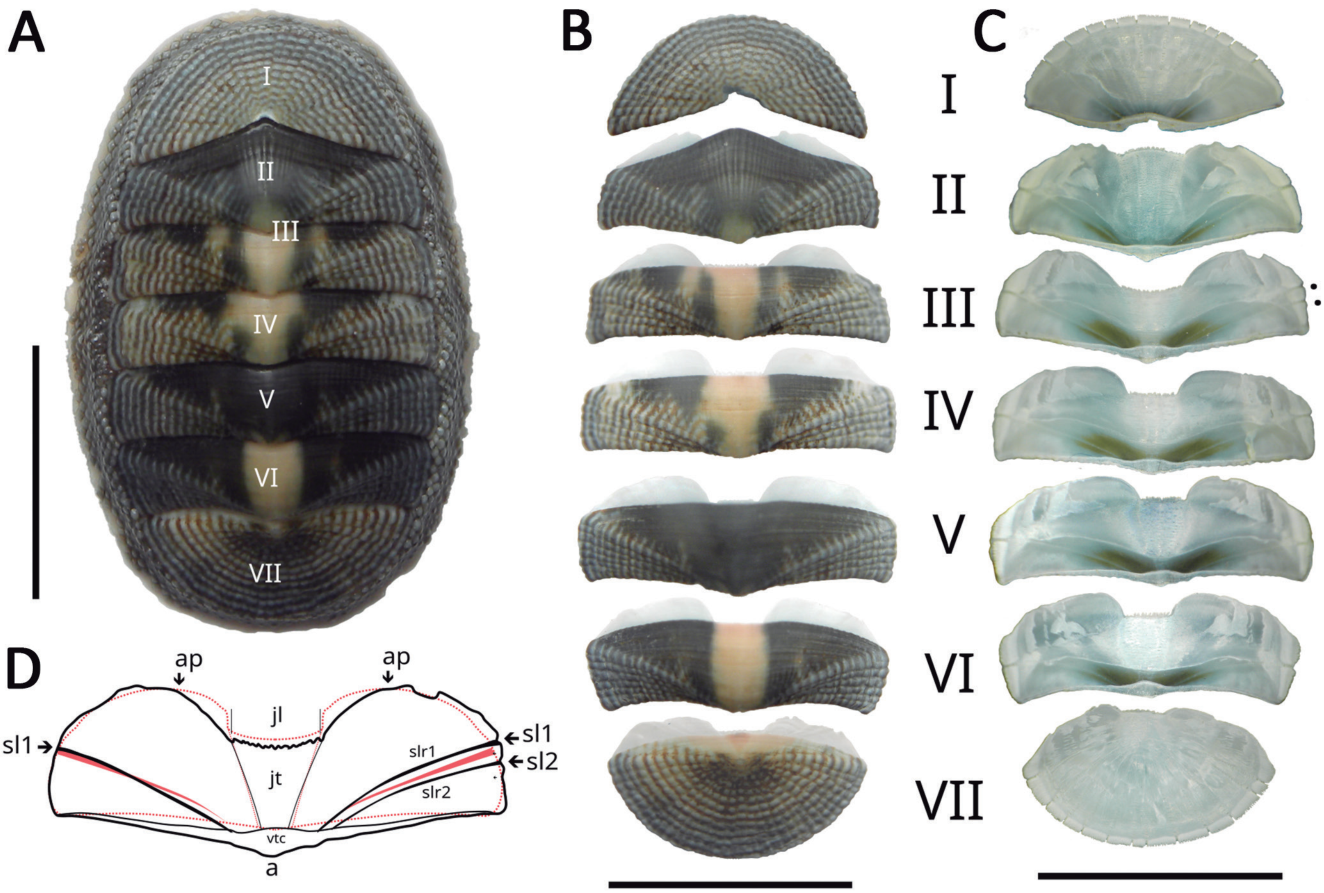

Figure 1. *Chiton cumingsii,* LABSIM 15.03.0194 (L = 23.01 mm). (A) Dorsal view of the body. (B) Dorsal view of separate valves. (C) Ventral view of separate valves. (D) Ventral drawing of abnormal valve III (black) over normal valve III drawing (red). Scale: 1 cm. Abbreviations: a = apex; ap = apophysis; jl = jugal laminae; jt = jugal tract; sl1-2 = slits; slr1-2 = slit rays; vtc = ventral tegmental callus.

20.21 mm long × 11.40 mm wide (SW/SL = 0.57), dorsal elevation: 5.61 mm. Ctenidia asymmetrical: 38 on the left side, 41 on the right side (average = 39.5).

Chiton cumingsii, Peru, *Lima:* Barranca (Playa Chorrillos, 10°45′28″S, 77°46′06″W), 16 specimens, 1 abnormal individual, 25.XI.2018, S. Canteño col. (LaBSIM 15.03.0340). The abnormal individual presented 8 valves (Fig. 5A-B), most valves with a normal appearance in dorsal view; with an additional small plate over the right side of the valves VI and VII (Fig. 5C-D); valves V and VI asymmetrical and reduced on the right margin; additional plate flattened and triangular (Fig. 5C-D). The head valve has 11 slits and, the tail valve has 16 slits. Most intermediate valves have 1 slit and 1 slit-ray on each side (Fig. 5C), although the valves V and VI showed no slit or slit-ray in the right side. The additional plate showed 2 slits and 2 slit-rays (Fig. 5C-D). The right apophysis in the valves V, VI and VII exhibit an abnormal growth. Total body size: 37.63 mm long × 22.75 mm wide (W/L = 0.6), shell size: 33.46 mm long × 17.32 mm wide (SW/SL = 0.52), dorsal elevation: 6.34 mm. Ctenidia asymmetrical: 40 on the left side, 38 on the right side (average = 39).

Chiton granosus, Peru, *Lima:* Punta Piedritas, 3 specimens, 1 abnormal individual, 01.X.2004 (LaBSIM 15.03.0103). The abnormal individual presented 8 valves (Fig. 6A-B), most valves with a normal appearance in dorsal view; valve III longitudinally splitted (Fig. 6C-D), right half larger than the left one, its jugal area and apophysis affected. The head valve has 18 slits and, the tail valve has 19 slits. Intermediate valves have a single slit and slit-ray on each side, including the valve III (Fig. 6C). Total body size: 34.61 mm long × 25.22 mm wide (W/L = 0.73), shell size: 30.84 mm long × 19.24 mm wide (SW/SL = 0.62), dorsal elevation: 10.47 mm. Ctenidia symmetrical: 60 on both sides.

Individuals with non-visible abnormalities

We randomly searched for abnormalities not dorsally visible in 52 individuals of *C. cumingsii* (7.15% of total)

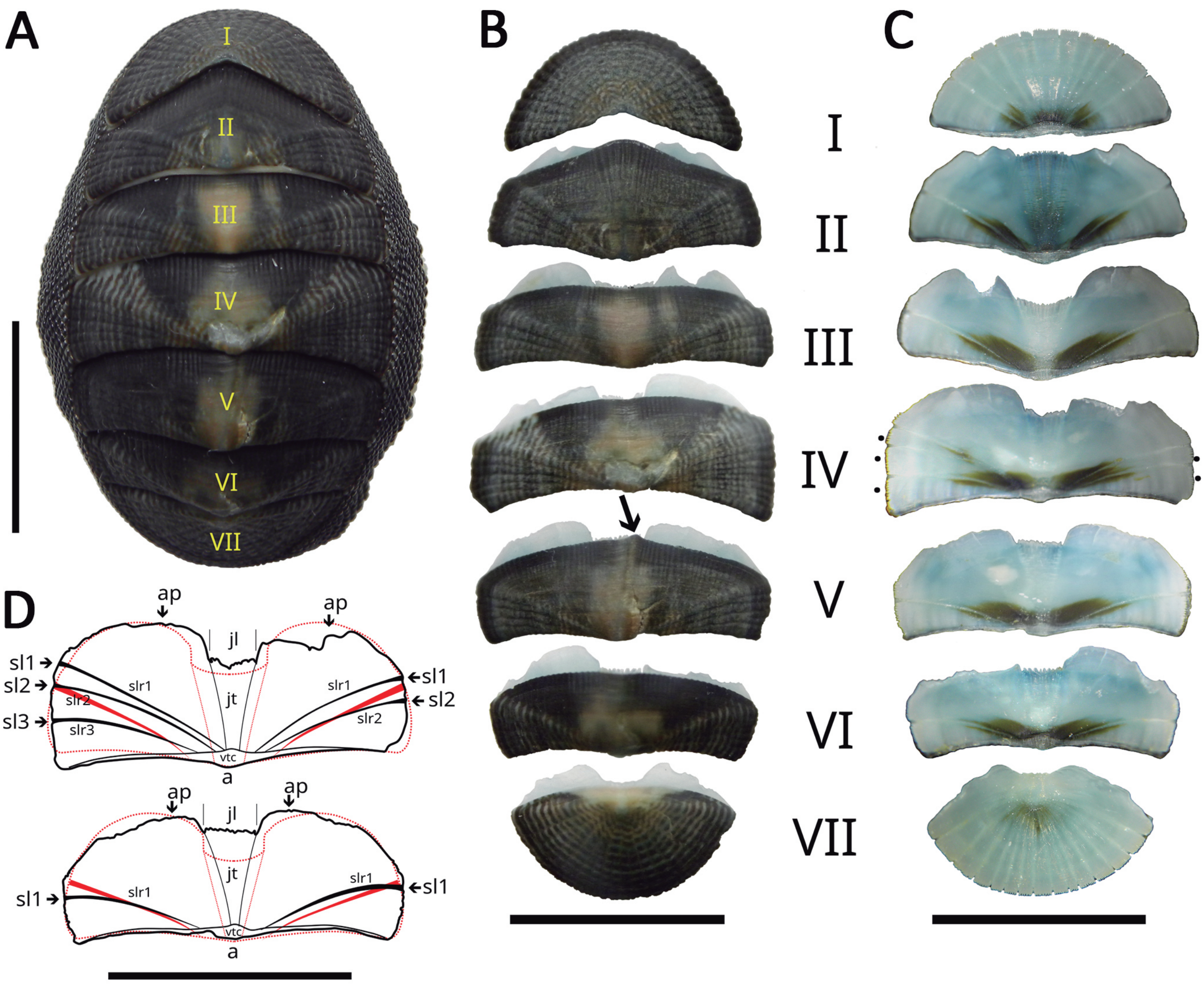

Figure 2. *Chiton cumingsii,* LABSIM 15.03.0272 (L = 27 mm). (A) Dorsal view of the body. (B) Dorsal view of separate valves. (C) Ventral view of separate valves. (D) Ventral drawing of abnormal valve IV (black) over normal valve IV drawing (red) (Above). Ventral drawing of abnormal valve IV (black) over normal valve IV drawing (red) (Down). Scale: 1 cm. Abbreviations: a = apex; ap = apophysis; jl = jugal laminae; jt = jugal tract; sl1-2 = slits; slr1-3 = slit rays; vtc = ventral tegmental callus.

and 33 individuals of *C. granosus* (10.06% of total) whose plates could be better removed without forcing or mistreating them, but we only found a single externally normal-looking specimen with an anomaly in the number of slits and slit-rays in the intermediate valve.

Coalescence

Chiton cumingsii, Peru, **Lima:** Ancón (San Francisco), 11 specimens, 1 abnormal individual, 26.IX.1999 (LaBSIM 15.03.0039). The abnormal individual presented the usual eight valves, all of them with a normal appearance in dorsal view (Fig. 7A-B). The head valve has 11 slits and, the tail valve has 14 slits, and most intermediate valves have a single slit and slit-ray on each side (Fig. 7C), with the exception of valve IV that has 2 slits and 2 slit-rays on the right side (Fig. 7C-D), suggesting a homogeneous coalescence since fusion is complete both in 'tegmentum' and 'articulamentum'. Total body size: 26.9 mm long 17.1 mm wide (W/L = 0.64), shell size: 26.8 mm long 15.68 mm wide (SW/SL = 0.59), dorsal elevation: 8.54 mm. The right side (3.77 mm) is slightly larger than the left side (3.66 mm). Ctenidia symmetrical: 42 on the left side, 42 on the right side (average = 42).

Other abnormalities

Abnormal insertion plate

Chiton cumingsii, Peru, *Lima:* Ancón, 11 specimens, 1 abnormal individual, 20.XII.1987 (LaBSIM 15.03.0004). The abnormal individual (Fig. 8A) presented eight valves, most valves with a normal appearance dorsally, except by the tail valve that shows a new insertion plate developed on the dorsal right side of this valve (Fig. 8B). The ventral side of the tail valve showed a complete fusion of the 'articulamentum' (Fig. 8C). The number of slits and slit-rays was typical for the species; the head valve had 12 slits and 12 slit-rays. The tail valve did not show a normal development of its insertion plate, its teeth and slits are not well defined and the plate border is wavy. Total body size: 34.47 mm long × 20.50 mm wide (W/L = 0.60), shell size: 32.94 mm long × 18.69 mm wide (SW/SL = 0.57),

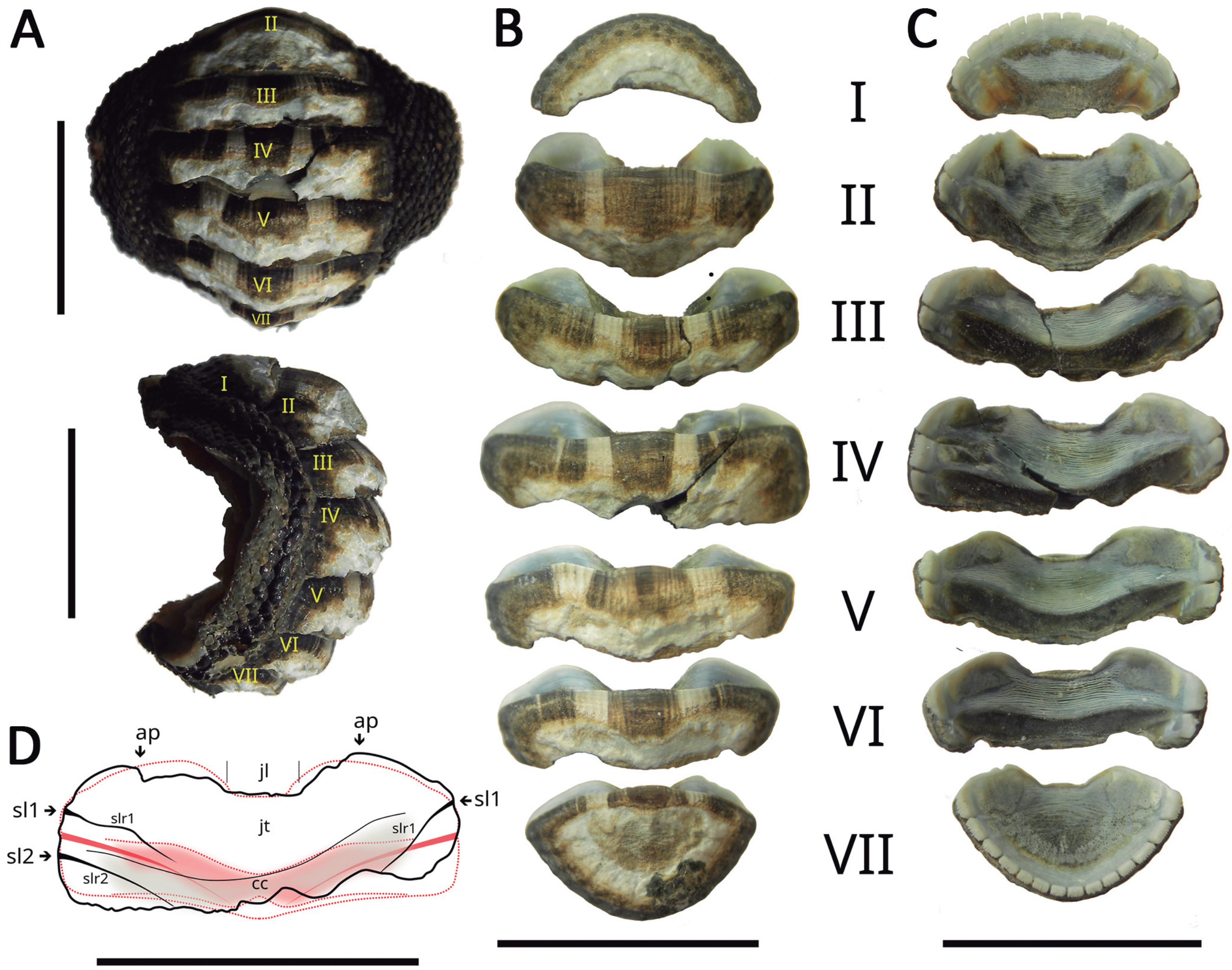

Figure 3. *Chiton granosus,* LABSIM 15.03.0164 (L = 24.22 mm, curled). (A) Dorsal view of the body. (B) Dorsal view of separate valves. (C) Ventral view of separate valves. (D) Ventral drawing of abnormal valve IV (black) over normal valve IV drawing (red). Scale: 1 cm. Abbreviations: ap = apophysis; cc = central callus; jl = jugal laminae; jt = jugal tract; sl1-2 = slits; slr1-2 = slit ray; vtc = ventral tegmental callus.

dorsal elevation: 9.59 mm. Ctenidia symmetrical: 43 on both sides.

The extent of teratological cases

Abnormal individuals with visible anomalies accounted for 0.83% and 0.61% of all the examined specimens of *C. cumingsii* and *C. granosus,* respectively. The proportion of hypomerism was 0.28% and 0.30% for *C. cumingsii* and *C. granosus,* respectively. The proportion of splitting was 0.28% for *C. cumingsii* and 0.30% for *C. granosus.*

We compared both the body width/length and shell width/length ratio of the abnormal individuals of *C. cumingsii* (Fig. 9) and *C. granosus* (Fig. 10), with normal specimens from the same locality, but the ratios of the abnormal individuals are within the range of the normal individuals of *C. cumingsii* (W/L: mean = 0.62 and sd = 0.053; SW/SL: mean = 0.54 and sd = 0.035) and *C. granosus* (W/L: mean = 0.68 and sd = 0.067; SW/SL: mean = 0.60 and sd = 0.028) and not significant differences were found in both species.

DISCUSSION

The abnormalities reported here greatly increase the number of known teratological cases for *C. cumingsii,* previously reported only in Chile by Schwabe (2001) and represent the first report of teratology in this species for Peru. Although Peña (1977), Peña & Castro (1982) and Torres *et al.* (2018) have recorded teratological cases in *C. granosus* for Chile, this is the first report for Peruvian waters, and the first case of splitting for these species.

Hypomerism is the most common abnormality reported in chitons (Dell'Angelo & Schwabe, 2010) and was also the most common teratology observed in this work, representing almost half of the abnormal individuals reported here. Although Dell'Angelo & Schwabe (2010) defined splitting as the division of one plate into two

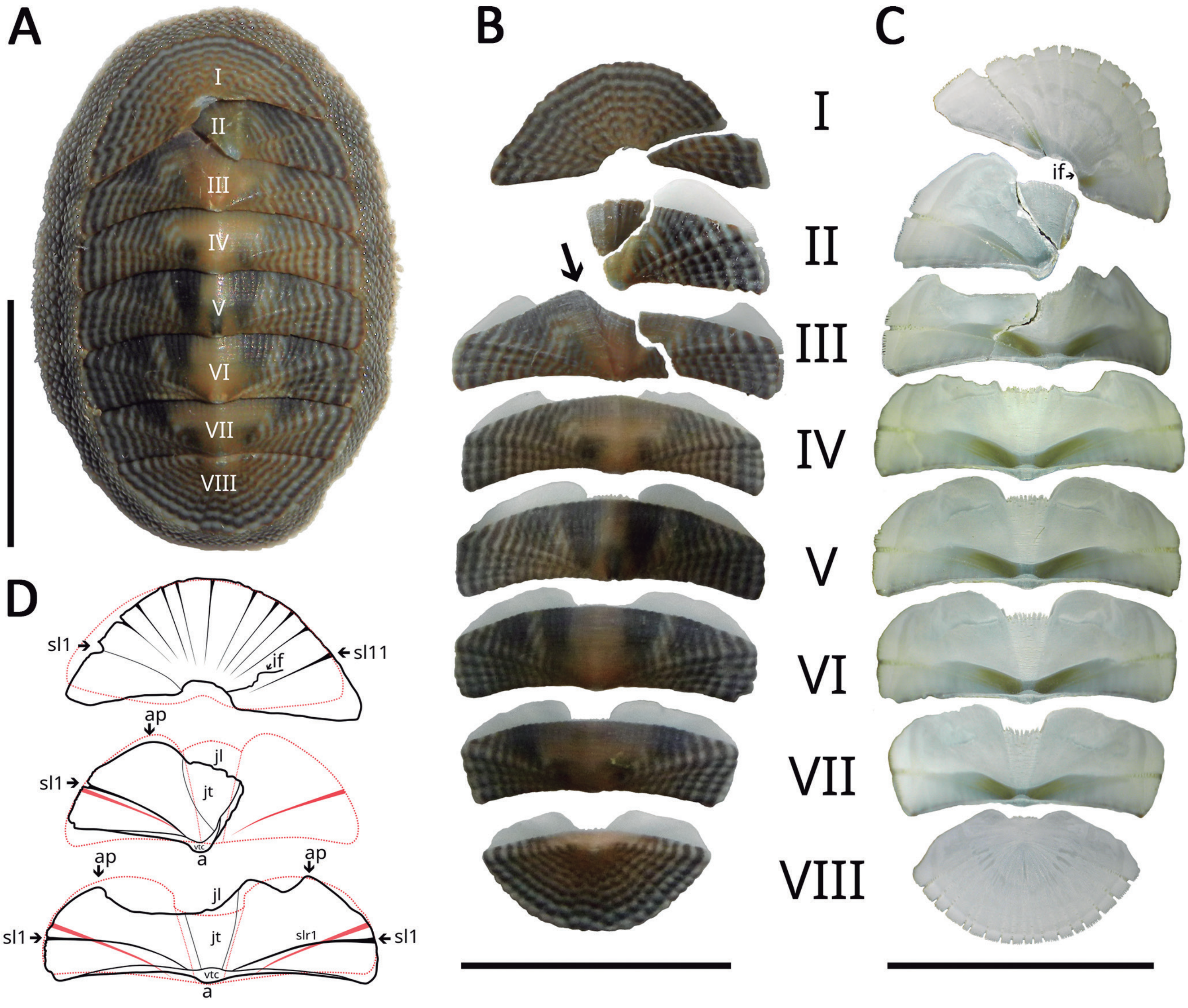

Figure 4. *Chiton cumingsii,* LABSIM 15.03.0147 (L = 22.03 mm). (A) Dorsal view of the body. (B) Dorsal view of separate valves. (C) Ventral view of separate valves. (D) Ventral drawing of abnormal valve IV (black) over normal valve IV drawing (red) (Above). Ventral drawing of abnormal valve IV (black) over normal valve IV drawing (red) (Down). Scale: 1 cm. Abbreviations: a = apex; ap = apophysis; jl = jugal laminae; jt = jugal tract; sl1 = slit; slr1 = slit ray; vtc = ventral tegmental callus.

valves, one of which coalesces with the adjacent one, we consider that the development of a coalescence is not necessary to characterize the teratological case of splitting in chitons, since we found an individual of *C. granosus* (Fig. 6) with longitudinal splitting in the valve III, but no traces of coalescence. Similar abnormalities were reported in the valve III in *Liolophura gaimardi* (Iredale & Hull, 1926, as *L. queenslandica*) and in the valve V in *Acanthopleura granulata* (Kingston *et al.,* 2020).

The splitting observed in *C. cumingsii* in Fig. 5 was very complex, probably arising by a splitting in the right side of both the fifth and sixth valves, followed by coalescence between both fragments as suggested by the presence of two slits in this additional valve. In a similar way, the abnormal condition found in *C. cumingsii* in Fig. 4 probably could also be explained by splitting of the valve II, where the missing left half of this valve was merged with the head valve, as suggested by the scar observed in the 'articulamentum' (Fig. 4C). A similar abnormality has been reported in *Liolophura japonica* (Taki, 1932). However, an alternative explanation could be that the head valve became larger to fill the gap left by the valve II in the left side and the scar is a sign of this abnormal development; a similar case has been reported in *Rhyssoplax jugosa* (Iredale & Hull, 1926). These observations suggest that splitting is more

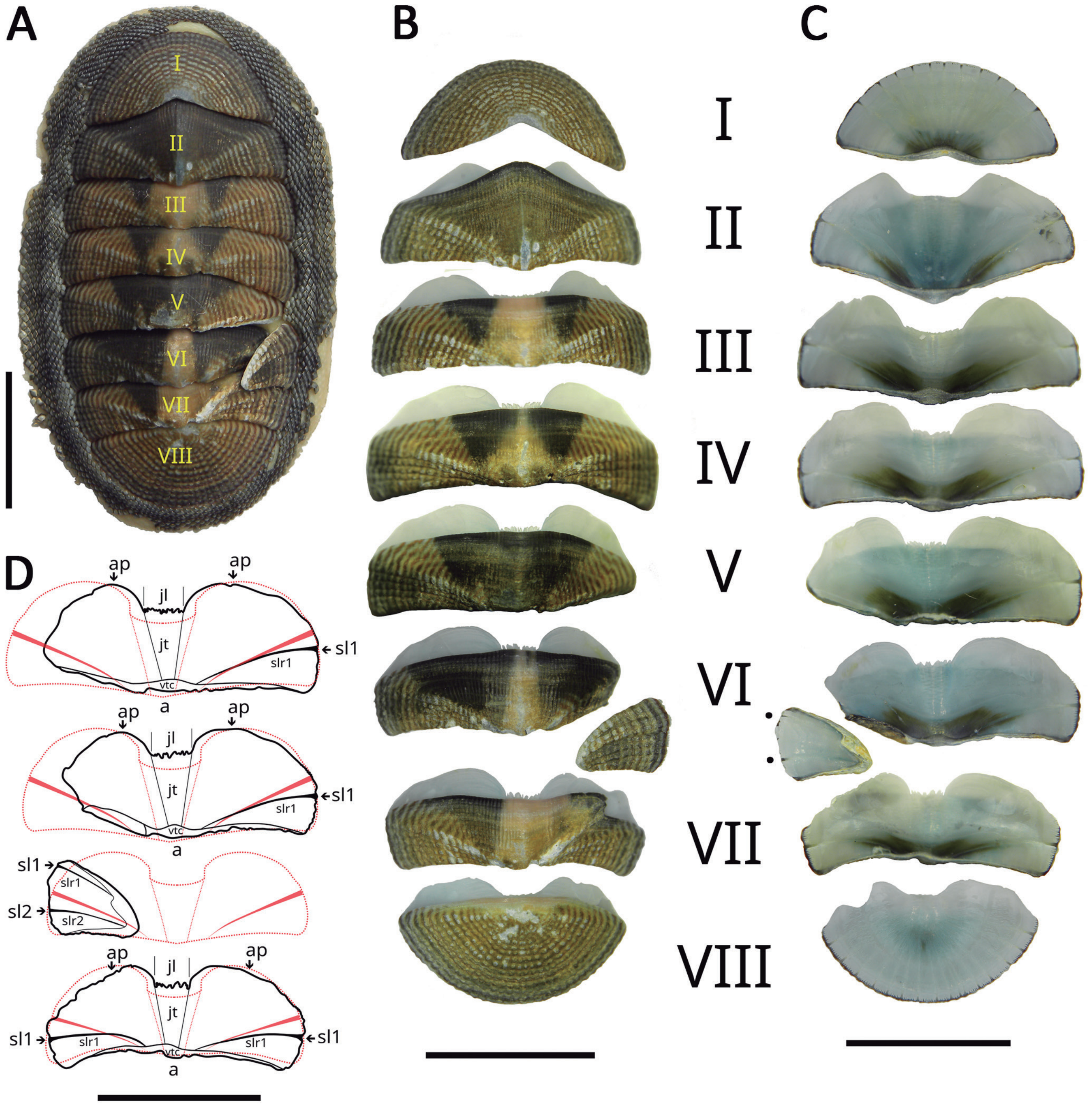

Figure 5. *Chiton cumingsii,* LABSIM 15.03.0340 (L = 37.63 mm). (A) Dorsal view of the body. (B) Dorsal view of separate valves. (C) Ventral view of separate valves. (D) Ventral drawing of abnormal (black) over equivalent normal valves. Scale: 1 cm. Abbreviations: a = apex; ap = apophysis; jl = jugal laminae; jt = jugal tract; sl1-2 = slits; slr1 = slit ray; vtc = ventral tegmental callus.

common than is usually reported in the Polyplacophora literature.

Among the teratological cases found in this work that could be classified according to Avila-Poveda *et al.* (2019), the cases of homogeneous coalescence were the majority, while most cases found in *Chiton articulatus* (Avila-Poveda *et al.,* 2019) showed heterogeneous coalescence, not reported here in *C. granosus*. However, Peña & Castro (1982) reported a 7-valved individual of *C. granosus* that clearly shows heterogeneous coalescence between valves III and IV. No heterogeneous coalescence has been reported in *C. cumingsii* (Schwabe, 2001). Avila-Poveda *et al.* (2019) found that most abnormal coalescences in *C. articulatus* were between valves III and IV, the same was also found in this work both in *C. cumingsii* (Figs. 1, 2) and *C. granosus* (Fig. 3). Other authors have also reported teratological individuals with abnormal coalescence between valves III and IV (Iredale & Hull, 1926: *Rhyssoplax jugosa;* Taki, 1932: *Placiphorella stimpsoni* and *Liolophura japonica;* Peña & Castro, 1982: *Chiton granosus;* Guillén & Urteaga, 2019: *Tonicia atrata*). However, after comparing previous reports of coalescence, Taki (1932) considered that all of the valves in chitons are susceptible to aberrations. Although we agree with Taki (1932), the observations of the present study and Avila-Poveda *et al.* (2019), suggest that the valves III and IV could be more vulnerable in these species to developed coalescence.

The abnormalities observed here in *C. cumingsii* in Figs. 4, 5, as well as in *C. granosus* in Fig. 6, could not be classified according to the work of Avila-Poveda *et al.* (2019), which is focused on hypomerism and hypermerism. However, using a similar approach, the splitting abnormalities observed in this work have been considered perfect or imperfect, depending on whether all the fragments of the splitted valve can be dorsally observed or not. As in the case of hypomerism and hypermerism (Avila-Poveda *et al.,* 2019), the splitting of a valve can also promote the coalescence of the fragments, and depending on its degree of development, this coalescence can be: (i) homogeneous, if no visual traces of the junction can be identified, or (ii) heterogeneous, when the junction shows traces of it. Therefore, the abnormality observed in Fig. 5 is an example of imperfect splitting with homogeneous coalescence since no visual traces of the junction can be identified, although the 2 slits are testimony of the merging between the fragments coming from the valves VI and VII. In contrast, the teratology observed in Fig. 6, is clearly a case of perfect splitting as no coalescence between both fragments has developed. Avila-Poveda *et al.* (2019) suggested that when valves are merged, chitons developed a compensated anatomy, so coalescence represents an intermediate step towards perfect hypomerism or perfect hypermerism. In this work, we suggest that when a splitting occurs, the

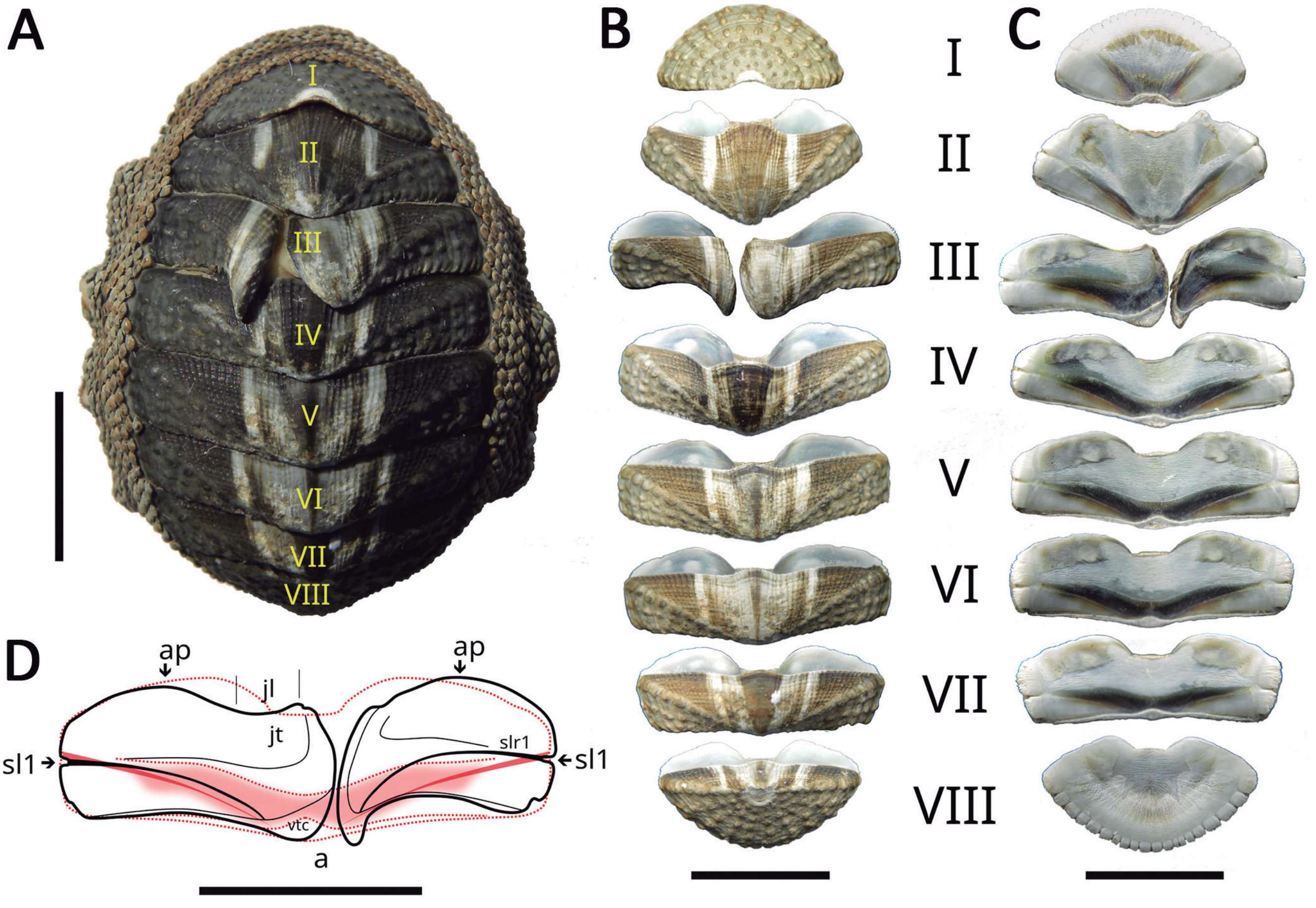

Figure 6. *Chiton granosus,* LABSIM 15.03.0103 (L = 34.61 mm). (A) Dorsal view of the body. (B) Dorsal view of separate valves. (C) Ventral view of separate valves. (D) Ventral drawing of abnormal valve III (black) over normal valve III drawing (red). Scale: 1 cm. Abbreviations: a = apex; ap = apophysis; jl = jugal laminae; jt = jugal tract; sl1 = slit; slr1 = slit ray; vtc = ventral tegmental callus.

compensated anatomy for a chiton would be the development of coalescence between one of the fragments and a normal valve, or between fragments coming from different valves as observed in Fig. 5. Taki (1932) observed that coalescence is more common than regular hypomerism and splitting, and we agree with him, as coalescence seems to be a common mechanism of Polyplacophora development to compensate for malformation during development.

Dell'Angelo & Schwabe (2010) considered that it is very difficult to estimate the percentage of anomalous individuals, with most reports they cited giving a proportion of 1-5 abnormal specimens per 1,000 examined specimens. More recent studies have given a variety of different proportions: 9 in 3,451 (Avila-Poveda *et al.,* 2019: *Chiton articulatus*); 2 in 21 (Dell'Angelo *et al.,* 2012: *Callochiton cupreus*); 8 in 250 and 2 in 120 (Prelle *et al.,* 2013: *Ischnochiton sirenkoi* and *Callistochiton ashbyi,* respectively); 1 in 290, 1 in 750, 1 in 165, and 1 in 1108 (Torres *et al.,* 2018: *Tonicia fremblyana, Chiton magnificus, Plaxiphora mercatoris* and *Chiton granosus,* respectively). In this work, we found 6 abnormal specimens in 723 examined specimens of *C. cumingsii* (0.83%) and 2 abnormal individuals in 328 examined specimens of *C. granosus* (0.61%), the second one very different of the proportion reported by Torres *et al.* (2018) in the same species (0.09%). However, it is not possible to compare proportions of teratological cases between different regions or species, since these studies have been made with different methodologies. Another difficulty in comparing the proportion of abnormal individuals in Polyplacophora is that the number of teratological cases is probably underestimated in most studies, since only tangible abnormalities are usually reported, but Avila-Poveda *et al.* (2019) found that the number of no dorsally visible abnormalities (50) was much greater than the visible abnormalities (9).

Taki (1932) concluded that the development of ctenidia does not have a relationship with hypomerism as stated by Pelseneer (1919) who suggested that an individual with hypomerism tends to have a smaller number of ctenidia than the typical for the species and not necessarily symmetrical. In this work we partially agree with Pelseneer (1919) as we observed that the individuals with a strong asymmetry in the shape of valves (Figs. 3-5) also show an asymmetry in the number of ctenidia

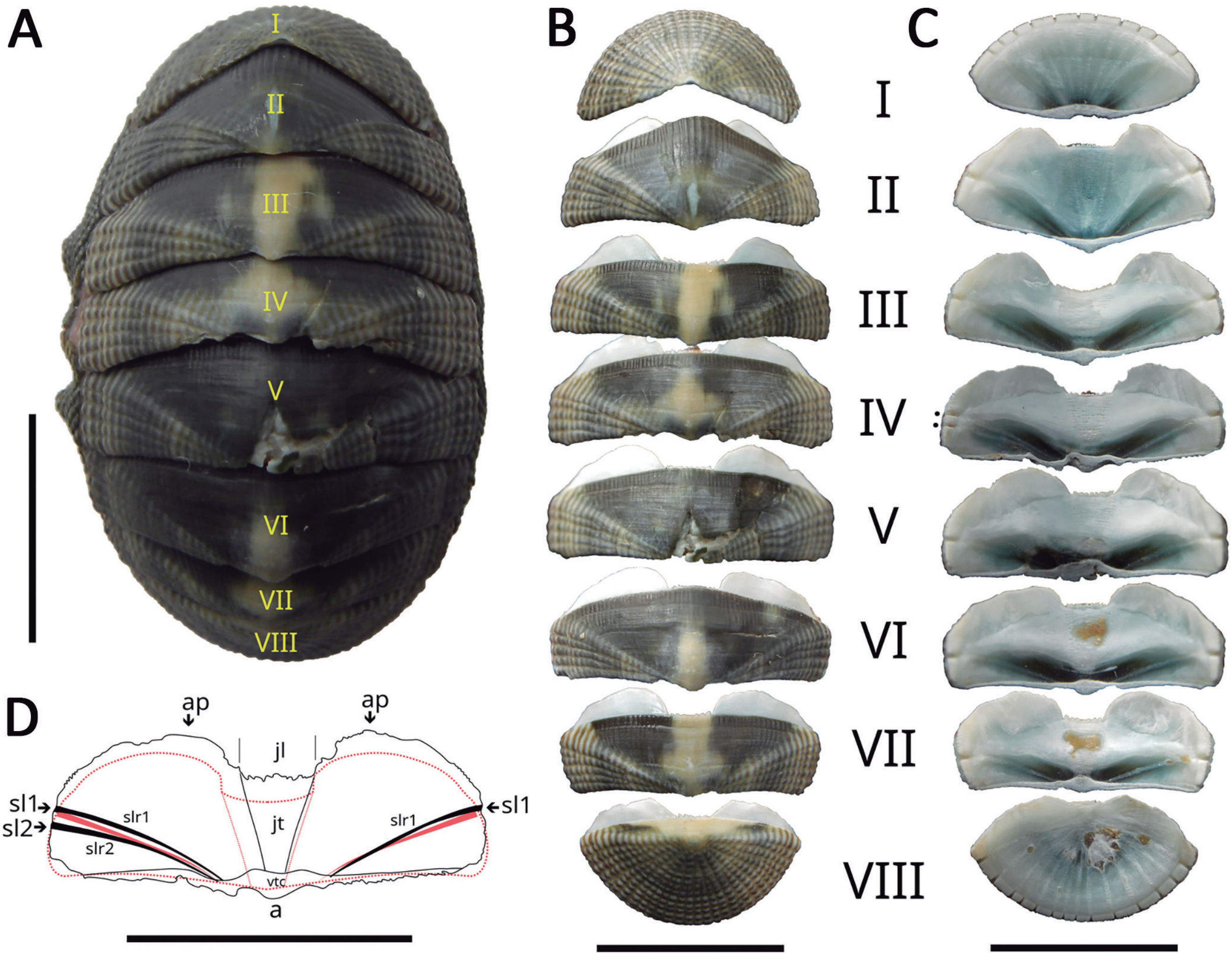

Figure 7. *Chiton cumingsii,* LABSIM 15.03.0039 (L = 26.9 mm). (A) Dorsal view of the body. (B) Dorsal view of separate valves. (C) Ventral view of separate valves. (D) Ventral drawing of abnormal valve IV (black) over equivalent normal valve. Scale: 1 cm. Abbreviations: a = apex; ap = apophysis; jl = jugal laminae; jt = jugal tract; sl1-2 = slits; slr1-2 = slit rays; vtc = ventral tegmental callus.

(Table 1), but this number is not always smaller than the reported for the normal individuals (Kaas *et al.,* 2006: 35 in *C. cumingsii* and 60 in *C. granosus*). Interestingly, the asymmetry in the number of slits and slit-rays does not correlate with the asymmetry in the number of ctenidia. Therefore, we suggest that the symmetry in the number of ctenidia only is affected when the symmetry of the valves is strongly altered as in Figs. 3-5.

The abnormal insertion plate observed in *C. cumingsii* (Fig. 8) has been previously reported in this species by Schwabe (2001), although in the head valve, instead of the tail valve observed in the present work. Dell'Angelo & Schwabe (2010) summarized similar cases of new insertion plates reported for other species of Polyplacophora, observing that in none of these cases the development of this insertion plate is evident in the ventral side. The same is observed here. In opposition to Schwabe (2001), who considered the development of an additional insertion plate an effect of an injury, we consider this probably represents an abnormality in the development of *C. cumingsii* because the "normal" insertion plate does not present normal teeth in the area where the new insertion plate has developed (Fig. 8C-D), and there are no slit-rays on the 'articulamentum' area where the new insertion

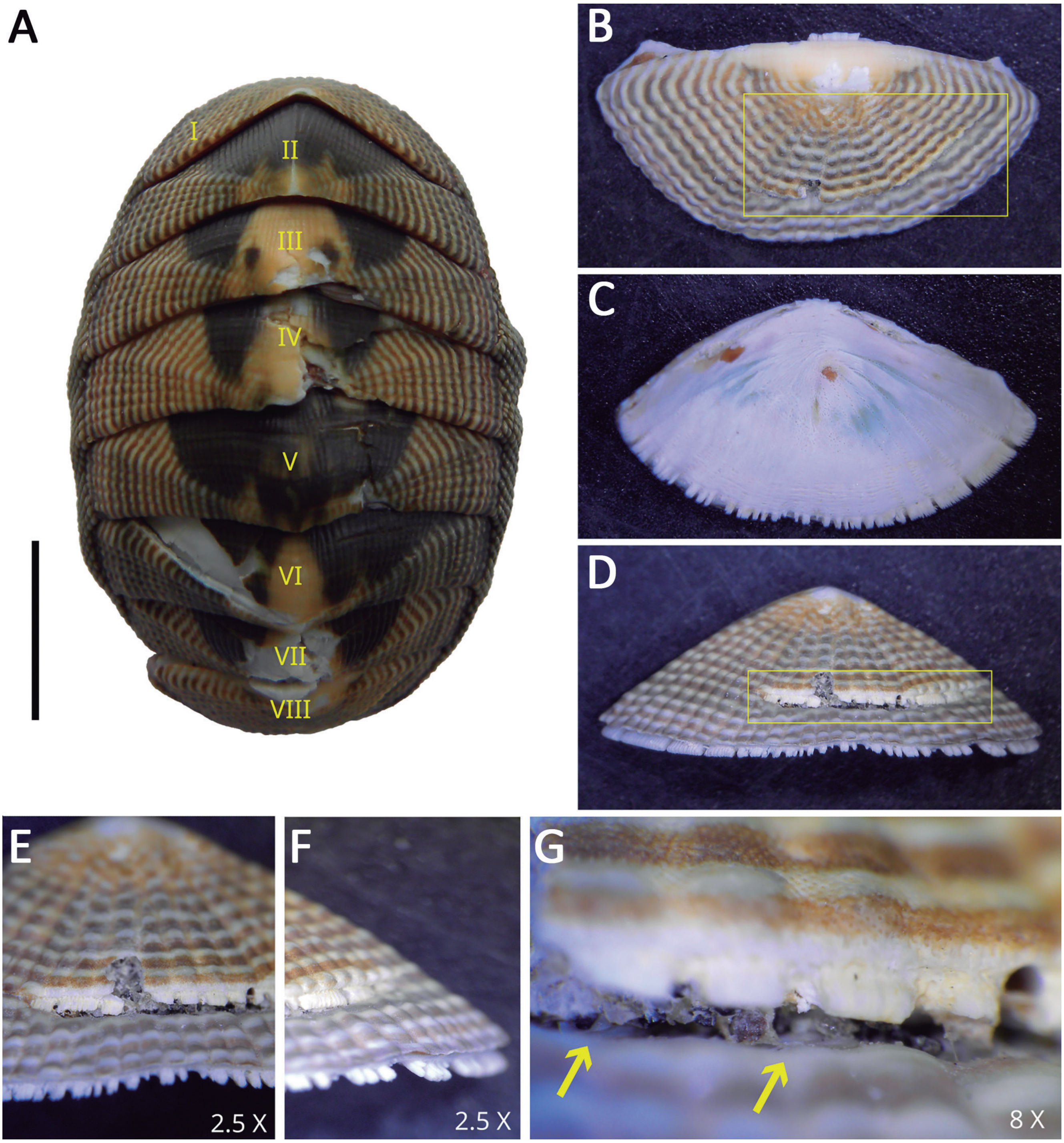

Figure 8. *Chiton cumingsii,* LABSIM 15.03.0004 (L = 33.94 mm). (A) Dorsal view of the body. (B, D) Dorsal view of the tail valve, showing the new insertion plate. (C) Ventral view of the tail valve. E, F, G. Close detail of the new insertion plate. Scale: 1 cm.

plate is observed (Fig. 8C). Developmental studies in Polyplacophora have shown that the head valve and the six intermediate valves are usually formed before the tail valve (Pearse, 1979; Kniprath, 1981), so this led Pelseneer (1919) to suggest that abortion of the last valve to develop could result in hypomerism. Taki (1932) agreed with Pelseneer's hypothesis but considered that splitting and coalescence could affect any valve in Polyplacophora. However, as observed in this work and in Avila-Poveda *et al.* (2019), hypomerism can also be the product of an abnormal development in any valve. Based on the embryological observations of Kowalevsky (1883) and Sirenko (2018) the valves seem to arise as embryological rudiments that later fused, so we suggest that teratological cases in chitons probably arise as a consequence of alterations in the development of these valve rudiments. Although developmental studies are known for many species of chitons, experimental works are very scarce (Pearse, 1979), so we recommend a greater experimental focus in the embryological development of chitons to understand the origin of teratologies. This could help to gain new insights into the developmental mechanisms behind shell form disparity among Polyplacophora (Kingston *et al.,* 2020).

We agree with Guillén & Urteaga (2019) in that development of teratology did not affect the growth and proportions of the abnormal specimens (Figs. 9-10), indicating a reorganization of chiton's development to produce a "normal" individual. Crozier (1919) suggested that the coalescence between valves VII and VIII of *Chiton articulatus* could benefit the animal since the two valves would stick together more easily when the posterior end of the animal is submerged so the mantle is better protected from abrasion from sand grains, but Dell'Angelo & Schwabe (2010) observed that correlation in Polyplacophora between the anomalies and morphological or ecological aspects is scarce. Kingston *et al.* (2020) have suggested that the developmental mechanisms involved in teratological splitting may be relevant for the evolution of morphological disparity in the valves of fossil Polyplacophora. To better understand the ecological and evolutive relevance for chitons of the teratological abnormalities found in this and previous works, we recommend a stronger emphasis on the analysis of

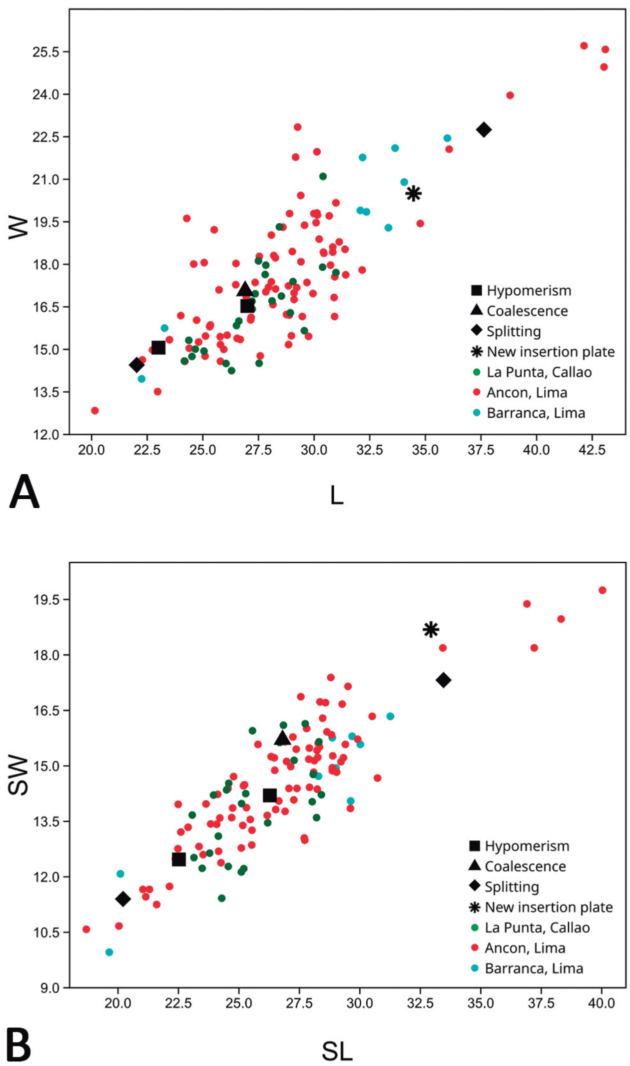

Figure 9. Comparison of normal and abnormal individuals of *Chiton cumingsii* from La Punta, Ancón and Barranca. (A) Total body length and width. (B) Shell length and width. Abnormal individuals represented by black symbols.

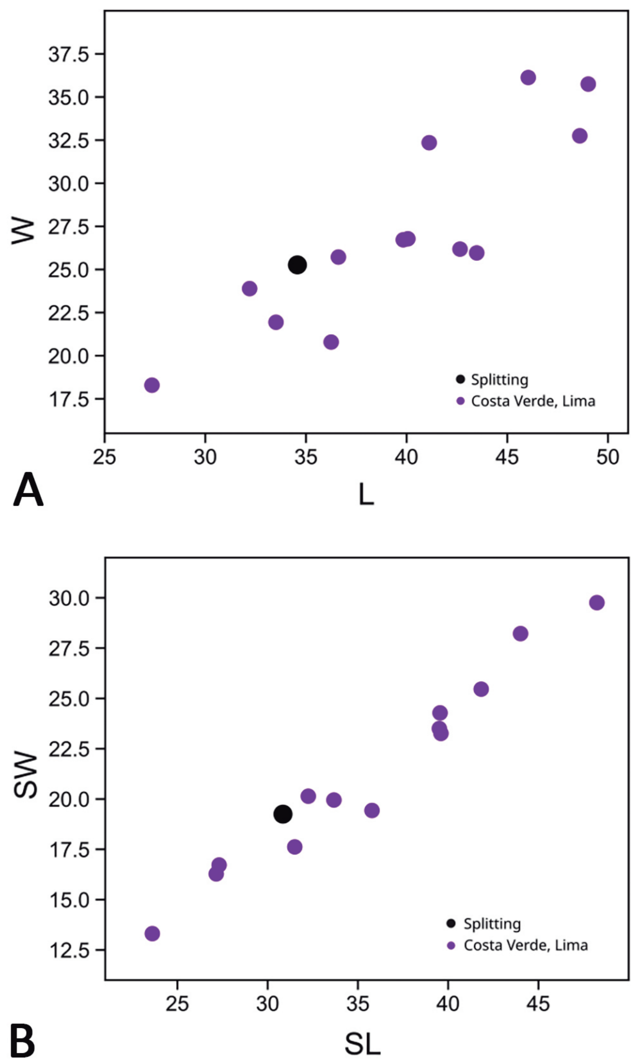

Figure 10. Comparison of normal and abnormal individuals of *Chiton granosus* from Costa Verde. (A) Total body length and width. (B) Shell length and width. Abnormal individual represented by black point.

the interaction between splitting, coalescence and hypo- and hypermerism in chitons, as all of these abnormalities are probably related and could be explained by similar developmental pathways.

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