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Description of A New Species of *Thordisa* (Nudibranchia: Discodorididae) from Panama

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A new species of *Thordisa* is described from the Caribbean coast of Panama. The phylogeny of the genus *Thordisa* from the tropical Indo-Pacific and eastern Pacific is revised. Morphological and anatomical data from *Thordisa* species were used to construct a phylogeny with increased resolution. The phylogenetic analysis demonstrates the monophyly of *Thordisa* and its relationship to outgroups A*steronotus, Halgerda*, and *Hoplodoris*.

The dorid nudibranch genus *Thordisa* Bergh, 1877, consists of 31 species currently recognized as valid. The genus has been monographed recently (Chan and Gosliner, in press). Several species of *Thordisa* have been recently described by different authors (Chan and Gosliner, *in press*; Ortea and Valdés 1995; Cervera and García-Gómez 1989; Behrens and Hendersen 1981; Lance 1966). One new species of *Thordisa* is described from the Caribbean coast of Panama. A revised analysis of the phylogeny of the genus *Thordisa* is presented here, using three outgroup taxa: *Asteronotus cespitosus* van Hasselt, 1824, *Halgerda dalanghita* Fahey and Gosliner, 1999, and *Hoplodoris estrelyado* Gosliner and Behrens, 1998.

Additional data were taken from the original publications on *Thordisa* (Marcus 1955; Pease 1860). The following species were examined directly: *T. bimaculata* Lance, 1966; *T. filix* Pruvot-Fol, 1951; *T. rubescens* Behrens and Henderson, 1981; *T. sanguinea* Baba, 1955; *T. azmanii* Cervera y García-Gómez, 1989; *T. oliva* Chan and Gosliner, 2006; *T. luteola* Chan and Gosliner, 2006; *T. albomacula* Chan and Gosliner, 2006; *T. nieseni* Chan and Gosliner, 2006; and *T. tahala* Chan and Gosliner, 2006. Thus, previous literature and direct observation and dissection of 14 species of *Thordisa* and members of the outgroup have provided the information on the characters for the present study.

Thordisa harrisi Chan and Gosliner, sp. nov.

Figures 1–4.

Material examined.— Holotype: CASIZ 171542 one preserved specimen, Bocas del Toro, Panama, 2 m depth, 19 June 2005, Larry Harris, length 35 mm (dissected).

Distribution.— This species is only known from the Caribbean coast of Panama (present study).

Etymology.— This species was named for Larry Harris, Professor of Zoology, University of New Hampshire, who has been a mentor and a colleague of the second author for many years. Larry collected the holotype of this new species.

External morphology.— The body of the living animal is oval with a low profile (Fig. 1A).

The notum bears long, villous papillae and rounded tubercles. The longest papillae are concentrated in the middle of the dorsum (Fig. 1B). Some of the longest papillae are bifurcated at the base. The rhinophores are perfoliate with 20-25 lamellae each. The rhinophoral sheath is highly papillate, with 15 papillae along the inner margin. The gill is completely retractile and surrounded by a low even sheath. The six gill leaves are tripinnate and do not extend beyond the edge of the notum. The anterior margin of the foot is bilabiate (Fig. 1C). The oral tentacles are digitiform and do not extend beyond the margin of the foot. The notum of the living specimens has a bright orange ground color with translucent papillae and tubercles. There are small rust-colored spots dispersed over the notum and two brown oval spots in the center that extend from the anterior of the gill pouch toward the rhinophores. The rhinophores and gill are opaque brown. The color of the foot of the live specimens is solid orange. On the ventral side of the mantle is a small red ring of dots surrounding the foot.

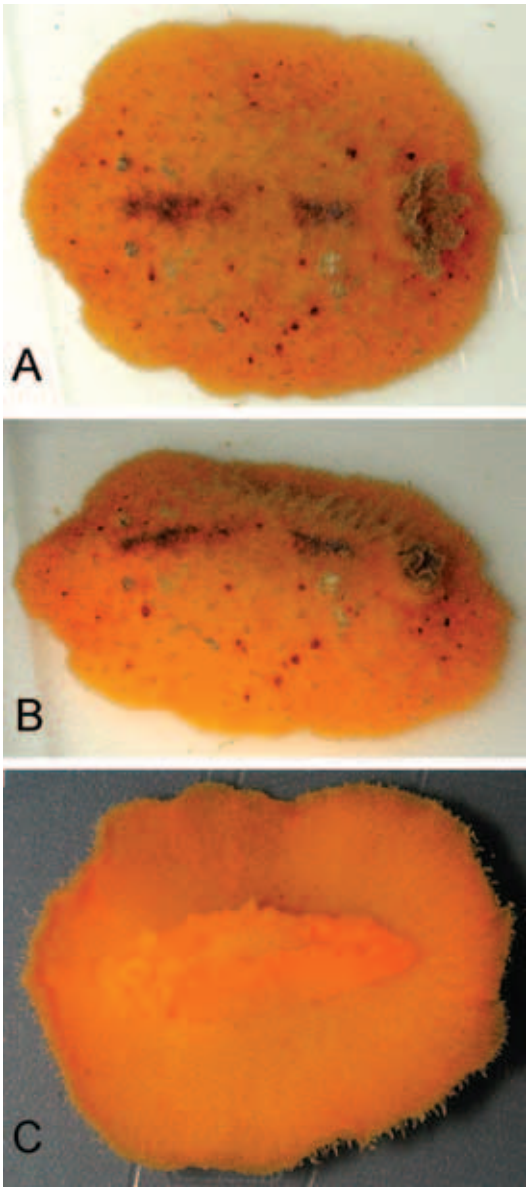

FIGURE 1. Photograph of living animal *Thordisa harrisi* sp. nov. (CASIZ 171542) A. dorsal view. B. Dorsal/side view. C. ventral view. Photos by Sigmer Quiroga.

ANATOMY.— The labial cuticle is smooth and devoid of rodlets. The radula formula is 34x 2-3.1.33-35.0.33-35.1.2-3 at the 15th row from the anterior of the radula. The innermost lateral teeth are smaller, hamate and have a large, wide base (Fig. 2A). The middle lateral teeth are hamate with slender bases and long finger-like tips (Fig 2B). They slightly increase in size toward the margin. The third tooth from the margin is bifurcated at the tip (Fig. 2C). The two to three outer teeth are thinner, having fine pectination at the tips (Fig. 2D). The central nervous system consists of partially fused cerebral and pleural ganglia. The pedal ganglia are situated ventrally and extend outside the junction of the cerebropleural ganglia. They are connected by a circum-esophageal nerve ring (Fig. 3B). The stomach is partly free and medial, and rests on the digestive gland. The digestive gland is approximately twice the length of the stomach. The intestine is straight and dorsally situated.

The ampulla is straight and then curves once before ending in the female gland mass (Fig. 3A) via a short oviduct. The ampullary hermaphroditic duct is three times the length of the duct connecting the prostate. The base of the ampulla meets the uterine duct where the prostate gland begins. The prostate is approximately the same length as the ampulla. The more proximal white portion of

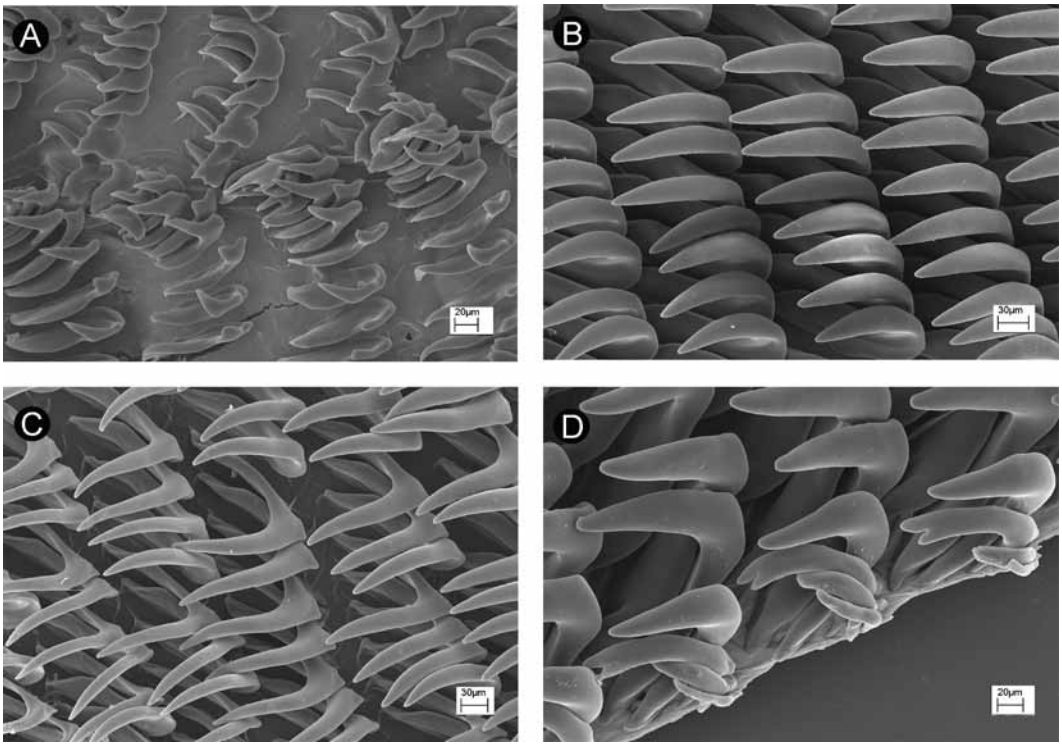

FIGURE 2. *Thordisa harrisi* sp. nov. (CASIZ 171542) Scanning Electron Micrographs A. inner lateral teeth B. middle lateral teeth C. outer lateral teeth. D. close up of outer lateral teeth.

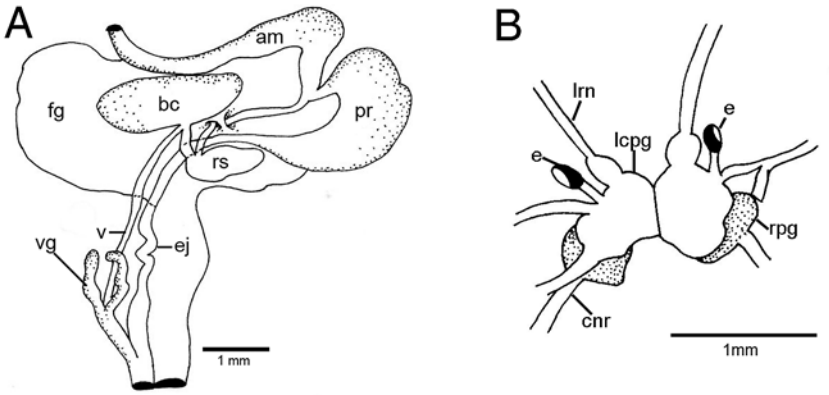

FIGURE 3. *Thordisa harrisi* sp. nov. (CASIZ 171542). A. Reproductive System. Scale bar = 1.0 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; ej, ejaculatory duct; fg, female gland; pr, prostate; rs, receptaculum seminis; v, vagina; vg, vestibular gland. B. Central nervous system. Scale bar = 1.0 mm. Abbreviations: cnr, circum-oesophageal nerve ring; e, eye; lcpg, left cerebral-pleural ganglia; rpg, right pedal ganglia; lrn, left rhinophoral nerve.

the prostate is longer and thinner than the distal yellow portion. The muscular portion of the vas deferens is long and slightly curved. The penial sheath is unarmed. A bi-lobed, unarmed vestibular gland connects to a separate vestibule adjacent to the genital atrium. The lobes of the gland are long, slender and finger-like. The unarmed vaginal duct is straight and thinner than the vas deferens. It leads to the bursa copulatrix, which is approximately twice as large as the receptaculum seminis. The duct of the receptaculum seminis is short and straight.

Discussion.— This is the second *Thordisa* species known from Panama. The first species described from the Pacific coast is *T. nieseni* (Chan and Gosliner 2006), while the present species is found on the Caribbean side of the isthmus. *Thordisa harrisi*, can be distinguished from *T. nieseni* by its bright yellow mantle color, long slender vestibular glands, and bifurcated outer tooth. *Thordisa nieseni* is a bright red mantle color and has pectinate outer teeth.

Thordisa harrisi is similar to a recently described discodorid species "*aliciae*" (Dayrat 2005). Discodorididae "*aliciae*" is found on the Pacific coast in Panama and has a similar external morphology, yet lacks both pectination of the marginal teeth and a vestibular gland. We re-examined the type material of "*aliciae*" housed in the collection at the California Academy of Sciences and confirmed the absence of a vestibular gland. Discodorididae "*aliciae*" also has a series of black spots on the undersurface of the mantle that are absent in *Thordisa harrisi*.

Phylogenetic analysis of *Thordisa*.— The character states recorded for each species of *Thordisa*, were placed into a data matrix from MacClade version 4.0 (Maddison and Maddison 2000) (Table 2). All characters used have equal weight and are unordered (Table 1). Six characters were deleted from the analysis due to being phylogenetically uninformative. The characters deleted are the morphology of the rhinophore sheath (2), the rachidian tooth (4), the relative size of the bursa copulatrix compared to the receptaculum seminis (16), the color of the mantle (19), the mantle pattern (20) and the rhinophore color (23). Characters 19 and 20 were omitted because their states had many intermediate conditions. The data were analyzed by Phylogenetic Analysis Using Parsimony (PAUP*) version 4.0 (Swofford 2003). A heuristic search was performed with the optimality criterion of maximum parsimony. The stepwise addition option of random trees was used, with 100 repetitions, starting from random start trees. Bremer support values (Bremer 1988) were calculated to estimate branch support using PAUP*. Character tracing was performed to understand the characters that united resulting clades.

To establish the polarity of the morphological characters used in this study, three outgroup taxa (*Asteronotus cespitosus*, *Hoplodoris estrelyado*, and *Halgerda dalanghita*) were used based a review of anatomical characters as described in Valdés and Gosliner, 2001; Gosliner and Behrens, 1988 and Fahey and Gosliner, 1999. We used these outgroups based on the phylogenetic study by Valdés (2002). In Valdés' study, these taxa were more closely related to *Thordisa* than other taxa.

The following characters were considered in this analysis:

[The characters preceded by an asterisk were deleted from the final analysis because they were phylogenetically uninformative) (0) = presumed pleisiomorphic (1) = apomorphic, ? = missing data or not applicable.]

1. Labial pits.— The derived character state is only found in *T. oliva* and *T. diuda* (1). In all other species the pits are absent (0).

2. *Rhinophoral sheath.— There is observed intraspecific variation within the rhinophore sheaths of *Thordisa*. Some species are observed to have scalloped edges (1) and others are straight. The outgroups *Asteronotus cespitosus*, *Hoplodoris estrelyado*, and *Halgerda dalanghita* are all known to have straight sheaths (0).

3. Gill.— All of the outgroup taxa, *Asteronotus cespitosus*, *Hoplodoris estrelyado*, and *Halgerda dalanghita* have tripinnate gills (0). Four of the examined species, *T. nieseni*, *T. azmanii*,

TABLE 1. Characters and states considered for the phylogeny of *Thordisa*.

	Character	*0=Plesiomorphic*	*1=Apomorphic*	*2=Apomorphic*	*3=Apomorphic*
1	Labial pits	0=absent	1=present		
2	Rhinophoral sheath	0=straight	1=scalloped		
3	Gill	0=tripinnate	1=bipinnate		
4	Rachidian tooth	0=absent	1=present		
5	Inner lateral teeth compared to middle lateral teeth	0=same	1=smaller		
6	Shape of inner lateral teeth	0=hamate	1=denticulate	2=bifurcate	
7	Shape of middle lateral teeth	0=smooth	1=denticulate		
8	Shape of outer lateral teeth	0=simple	1=pectinate		
9	Vestibular gland	0=absent	1=present		
10	Number of vestibular glands	0=one	1=two		
11	Vestibular gland shape	0=pouch	1=coil	2=lobate	
12	Vestibular gland spines	0=absent	1=present		
13	Number of vestibular gland spines	0=absent	1=one	2=two	
14	Vaginal spines	0=absent	1=present		
15	Penial spines	0=absent	1=present		
16	Bursa copulatrix vs. receptaculum seminis	0=rs is smaller	1=equal in size	2=bc is larger	
17	Papillae	0=short	1=villous		
18	Compound papillae	0=absent	1=present		
19	Mantle color	0=brn/blk/olive	1=tan/translucent	2=yellow	3=orange/red
20	Mantle pattern	0=distinct	1=no distinct pattern		
21	Turbercle coloration vs. mantle color	0=contrast	1=same color		
22	Gill color	0=light color	1=dark color		
23	Rhinophore color	0=dark color	1=light color		

T. villosa and *T. filix* have bipinnate gills (1). *T. sabulosa* Burn, 1957 is the only other *Thordisa* that has been described with bipinnate gills.

4. *Rachidian tooth.—** The rachidian tooth is absent in all specimens (0).

5. Inner lateral teeth compared to outer lateral teeth.— The inner lateral teeth of most species were considerably smaller than middle lateral teeth (1). Four *Thordisa* (*T. albomacula, T. azmanii, T. villosa,* and *T. tahala*) have inner teeth that are equal to the size of the middle laterals (0) as do the outgroup taxa.

6. Shape of inner lateral teeth.— The shape of the inner lateral teeth can be simply hamate, denticulate or bifurcate. Only *Thordisa oliva* was observed to have consistently bifurcated inner teeth (2). *Thordisa nieseni* can have bifurcated tips or simply hamate inner teeth (2). *Thordisa albomacula*, *T. setosa*, and *T. tahala* have denticulate inner teeth (1) whereas the remaining nine species have simply hamate inner teeth (0).

7. Shape of middle lateral teeth.— The middle lateral teeth are either denticulate or simply hamate. *Asteronotus cespitosus, Hoplodoris estrelyado and Halgerda dalanghita* have smooth middle teeth (0). *Thordisa oliva, T. nieseni*, *T. villosa* and *T. luteola* have smooth hamate middle teeth. *Thordisa tahala*, *T. albomacula*, and *T. setosa* have denticulate middle lateral teeth (1).

8. Shape of outer lateral teeth.— The outer lateral teeth of all *Thordisa* are pectinate (1). *Asteronotus cespitosus, Hoplodoris estrelyado and Halgerda dalanghita* have simple teeth (0).

9. Vestibular gland.— The vestibular gland is present (1) in all *Thordisa* except *T. hilaris* (Kay and Young 1969). A gland is also present in *Asteronotus cespitosus* and *Hoplodoris estrelyado* (1). A vestibular gland is absent in *Halgerda dalanghita* (0).

10. Number of vestibular glands.— *Thordisa* has either one (0) or two vestibular glands (1). Two vestibular glands occur in six of the recently described species. This character is not applicable to *Halgerda dalanghita* (?).

11. Vestibular gland shape.— Vestibular glands were categorized into three distinct shapes: pouch, coiled and lobate. *T. filix* is the only *Thordisa* observed to have a long and coiled vestibular gland (1). Three species (*T. albomacula*, *T. tahala* and *T. setosa*) have lobate vestibular glands (2). The remaining taxa have vestibular glands that are pouch shaped (0). This character is not applicable to *Halgerda dalanghita* (?).

12. Vestibular gland spines.— The presence of vestibular glands spines occurs in seven *Thordisa* species and *Asteronotus cespitosus* and *Hoplodoris estrelyado* (1). This character is not applicable to *Halgerda dalanghita* and is unknown for *Thordisa diuda* and *T. setosa* (?). Absence of spines is coded (0).

13. Number of vestibular gland spines.— The number of vestibular gland spines increases with the number of vestibular glands. *Thordisa azmanii*, *T. bimaculata*, *T. villosa*, *T. oliva*, and *T. tahala* all have one vestibular gland spine (0). *T. nieseni*, *T. rubescens*, and *T. luteola* all have two vestibular gland spines (1). *Halgerda dalanghita*, *Thordisa albomacula*, *T. diuda, T. filix, T. sanguinea, T. harrisi* and *T. setosa* do not possess vestibular gland spines. In several species, it is either not applicable or unknown (?).

14. Vaginal spines.— Vaginal spines are present in *Thordisa luteola,* and *T. rubescens* and (1). This character is unknown for *Thordisa bimaculata*, *T. diuda*, *T. filix*, and *T. setosa* (?). Absence of spines is coded (0).

15. Penial spines.— Penial spines usually occur as a single large spine or a series of small spines surrounding the penis. Penial spines occur in five of the *Thordisa* species (1). This character is unknown for *T. rubescens* and *T. setosa* (?). Absence of spines is coded (0).

16. *Bursa copulatrix vs. receptaculum seminis.— The receptaculum seminis (rs) is smaller than the bursa copulatrix (bc) in all the taxa (0) examined except for *Thordisa sanguinea*.

17. Papillae.— Villous papillae occur in thirteen of the *Thordisa* species (1). *Thordisa bimaculata* and all the outgroup taxa have shorter papillae throughout their mantle (0).

18. Compound papillae.— Compound papillae are only found in *Thordisa luteola* and *Thordisa harrisi* (1). Absence of papillae is coded (0).

19. ***Mantle color**.— Mantle color was categorized into four color groups, a brown/black/olive group (0), a tan/translucent color (1), yellow colored (2) and an orange/red color (3).

20. *Mantle pattern.— There are distinctive mantle patterns (0) found in species studied with the exception of *Thordisa azmanii*, *T. filix, T. luteola, T. nieseni,* and *T. oliva,* which all possess a solid colored mantle (1).

21. Tubercle or ridge color vs. mantle color.— Tubercle or ridge color is a contrasting color to mantle color (0) in all species with the exception of *Thordisa filix, T. nieseni* and *T. sanguinea* (1). *Halgerda dalanghita* does not possess tubercles on its mantle (?).

22. Gill color.— The gill of all species was light in color (0) with the exception of *Thordisa luteola*, *T. rubescens*, *T. harrisi*, and *Hoplodoris estrelyado* (1).

23. *Rhinophore color.— The rhinophore color is dark for *Thordisa villosa, T. rubescens, T. sanguinea, T. setosa, T. harrisi*, *Halgerda dalanghita*, *Asteronotus cespitosus* and *Hoplodoris estrelyado* (0). No variation among species was observed and this character was excluded.

TABLE 2. Data Matrix. Character states in species of *Thordisa* and the outgroup taxa *Asteronotus, Halgerda*, and *Hoplodoris*.
? = missing or not applicable, 0 = presumed pleisiomorphic,
1 = apomorphic, 2 = apomorphic 3 = apomorphic

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
T. albomacula	0	0	0	0	0	1	1	1	1	0	2	0	?	0	1	0	1	0	0	0	0	0	1
T. azmani	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	1	1	0	0	1
T. bimaculata	0	1	0	0	1	0	0	1	1	0	0	1	0	?	1	0	0	0	2	0	0	0	1
T. diuda	1	1	0	0	1	0	0	1	1	0	0	?	?	?	1	0	1	0	0	0	0	0	1
T. filix	0	0	1	0	1	0	0	1	1	0	1	0	?	?	1	0	1	0	1	1	1	0	1
T. luteola	0	1	0	0	1	0	0	1	1	1	0	1	1	1	0	0	1	1	2	1	0	1	0
T. villosa	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	2	0	0	0	1
T. nieseni	0	0	1	0	1	2	0	1	1	1	0	1	1	0	0	0	1	0	3	1	1	0	1
T. oliva	1	0	0	0	1	2	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1
T. rubescens	0	0	0	0	1	0	0	1	1	1	0	1	1	1	?	?	1	0	3	0	0	1	0
T. sanguinea	0	0	0	0	1	0	0	1	1	1	0	0	?	0	0	1	1	0	3	0	1	0	0
T. setosa	0	0	0	0	1	1	1	1	1	1	2	?	?	?	?	?	1	0	0	0	0	0	0
T. tahala	0	0	0	0	0	1	1	1	1	0	2	0	0	0	1	0	1	0	0	0	0	0	1
T. harrisi	0	1	0	0	1	0	0	1	1	0	0	0	?	0	0	0	1	1	2	0	0	1	0
Halgerda dalanghita	0	0	0	0	0	0	0	0	0	?	?	?	?	0	0	0	0	0	2	0	?	0	0
Asteronotus cespitosus	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0
Hoplodoris estreylado	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0

RESULTS

One parsimonious tree was produced (Fig. 4). The tree required 37 steps and had a consistency index of 0.541 and retention index of 0.653. Bremer support was (1) for all branches except for clades A and E, which have a Bremer support of (2), as does the clade containing *Halgerda dalanghita* and *Asteronotus cespitosus*.

Clade A corresponds to the ingroup, *Thordisa*. Clade A is united by the presence of inner lateral teeth that are smaller than the middle lateral teeth (5), pectinate outer laterals (8), one vestibular gland (10), and the presence of penial spines (15). This clade includes 14 taxa classified in the genus *Thordisa*. Clade B is united by the presence of villous papillae (17). Clade C is united by the absence of vestibular gland spines (12). Clade D is united by the presence of labial pits (1). Clade E is united by the presence of denticulate inner lateral teeth (6), denticulate middle lateral teeth (7), and a lobate vestibular gland (11). Clade F is united by a reversal from the possession of two vestibular glands to a single one (13). Clade G is united by a reversal of the presence of inner lateral teeth equal in size to middle lateral teeth (5). Clade H is united by the absence of penial spines (15). Clade I is united by the presence of two vestibular glands (10). Clade J is united by the presence of vestibular gland spines (12), which are two in number (13). Clade K is united by the presence of bipinnate gills (3). Clade L is united by the presence of vaginal spines (14) and a dark gill color (22). Clade M is united by the reversal of the presence of inner lateral teeth equal in size to the middle lateral teeth (5).

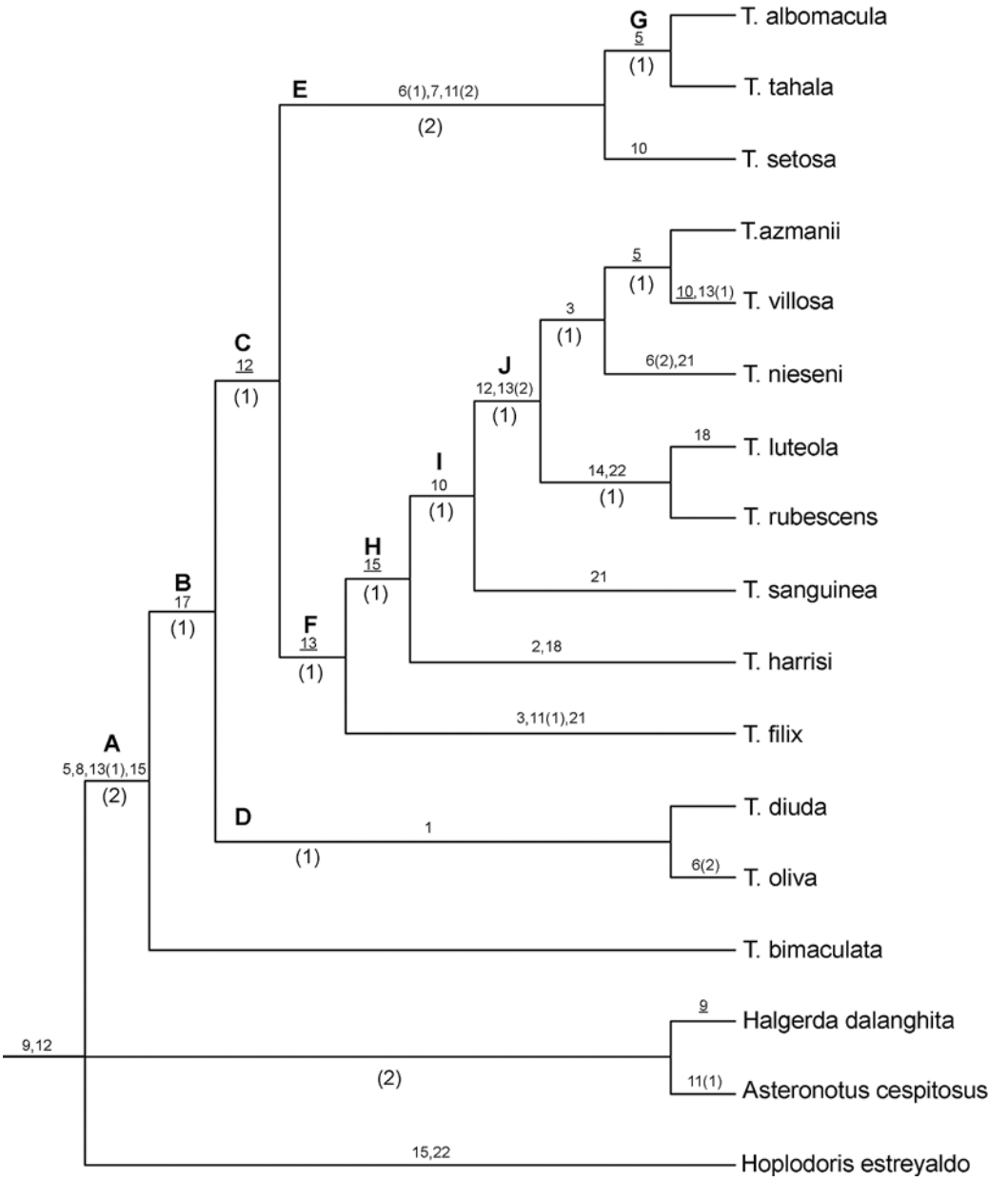

FIGURE 4. Preliminary phylogeny of *Thordisa*. Strict consensus tree of one most parsimonious trees. *Asteronotus*, *Halgerda*, and *Hoplodoris* were chosen as outgroup taxa to polarize the characters. *T*=*Thordisa*. Numbers above lines are character numbers: underlined numbers indicate reversals and numbers in parentheses are character states (Table 1). Letters A to J indicate the 10 clades that constitute the hierarchical pattern resulting from the analysis. Numbers below are Bremer support values.

Discussion

Our analysis demonstrates the monophyly of *Thordisa* and its relationship to the outgroups *Asteronotus, Halgerda and Hoplodoris*. Pectinate outer lateral teeth are a strong synapomorphy of the genus. Characters of the reproductive system such as vestibular gland morphology and genital armature can prove to be important for distinguishing species of *Thordisa*. The unique pits on the mouth of *Thordisa diuda* and *Thordisa oliva* are significant for uniting the two sister species. However, re-examination of other type species should be done to confirm absence or presence of this feature. It is clear that there are several homoplastic characters in our analysis such as teeth size and the number of vestibular glands. Much of the topology of our current tree is similar to the first preliminary phylogeny of *Thordisa* (Chan and Gosliner, in press). The current tree has increased resolution. In particular, the previous trichotomy containing *Thordisa villosa*, *T. nieseni* and *T. azmanii* is now fully resolved to show *T. azmanii* and *T. villosa* as more closely related to each other than to *T. nieseni*. The newly described species *Thordisa harrisi* is the most basal member of Clade H. Many species of *Thordisa* are incompletely described and will need re-evaluation as more material becomes available. Further character analysis and testing of the data are needed to strengthen the phylogenetic hypothesis of the genus *Thordisa*.

Acknowledgements

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