



ANATOMY AND TAXONOMIC POSITION OF *ELMA* H. ADAMS, 1866: A HIGH-SPIRED SOUTHEAST-ASIAN GENUS OF STREPTAXIDAE (GASTROPODA: EUPULMONATA)

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ABSTRACT: This paper describes the reproductive anatomy and the radula morphology of a Taiwanese species of *Elma* H. Adams, 1886, providing the first information on the anatomy of the genus. The species is provisionally identified as the type species of *Elma*, *E. cf. swinhoei* (H. Adams, 1866). Based on this and contrary to previous systematics, we suggest that *Elma* belongs to the subfamily Streptaxinae or Gibbinae, based on the presence of a well-developed penial sheath and the vas deferens which forms a loop under the penial sheath. *Elma* is the first high-spined, Southeast-Asian genus to be thus classified. We discuss possible relationships with other Streptaxoidea including the *Elma*-like genus *Pseudelma* Kobelt, 1904 and the high-spined “*Ennea*” *aliena* Bavay et Dautzenberg, 1912.

KEY WORDS: anatomy, taxonomy, systematics, high-spined, carnivorous, land snail

INTRODUCTION

The Streptaxidae Gray, 1860 are carnivorous land snails which are widely distributed in the tropics (ZILCH 1960). ZILCH (1960) subdivided the family into Streptaxinae and Enneinae. SCHILEYKO (2000: 771) criticised Zilch’s system, because the characters of the taxa overlapped between the two subfamilies, and classified the streptaxid genera into six subfamilies, partly based on the genital characters, especially the male part. The six subfamilies were Streptaxinae, Gibbinae Steenberg, 1936, Enneinae Bourguignat, 1883, Ptychotrematinae Pilsbry, 1919, Marconiinae Schileyko, 2000 and Odontartemoninae Schileyko, 2000. Later, based on molecular and anatomical evidence, SUTCHARIT et al. (2010) introduced the family Diapheridae Panha et Naggs, 2010 to accommodate *Diaphera* Albers, 1850 and *Sinoennea* Kobelt, 1904. With this, Diapheridae and Streptaxidae formed the

superfamily Streptaxoidea Gray, 1860. All genera not classified in the Diapheridae, including those with unknown anatomy, remained in the family Streptaxidae. ROWSON et al. (2010) published the results of an extensive molecular study primarily focusing on taxa from East Africa and the islands of the Indian Ocean and showed that the previously recognised subfamilies in the Streptaxidae were polyphyletic.

The genus *Elma*, introduced by ADAMS (1886), was included in the Enneinae by both ZILCH (1960) and SCHILEYKO (2000), although its anatomy was unknown. Approximately ten species of *Elma* are known; they inhabit Taiwan, Northern Vietnam and mainland China (VARGA 2012). Their shells are high-spined, relatively large (7–24.5 mm), nearly smooth or regularly ribbed, with a pear-shaped, elongated, toothless aperture which has its upper mar-

gin curved backwards. During a recent field trip to Taiwan, one of the authors (A. HUNYADI) collected a live specimen of *Elma* cf. *swinhoei* (H. Adams, 1866). Though only provisionally identified, the specimen is

evidently very similar to *E. swinhoei*, the type species of the genus. The aim of this paper is to describe the anatomy, and to discuss the taxonomic position of the genus based on this information.

MATERIAL AND METHODS

Dissection of a single specimen was performed in ethanol under a Leica stereomicroscope, with a camera attached to provide photographs of the genital structures from which drawings were then produced. To describe the reproductive system, we used the terms “proximal” and “distal” in relation to the interior of the body. The buccal mass was removed and soaked in 2 molar KOH solution for 5 hours before extracting the radula which was preserved in 70% ethanol. The radula was directly examined without

coating in a low vacuum SEM (Miniscope TM-1000, Hitachi High-Technologies, Tokyo).

The material is kept in the following collections: ANSP – Academy of Natural Sciences (Philadelphia, USA); HA – Collection ANDRÁS HUNYADI (Budapest, Hungary); NHMUK – National History Museum (London, UK); NMW – National Museum of Wales (Cardiff, UK); OK – Collection KANJI OKUBO (Tokyo, Japan)

RESULTS

SYSTEMATIC PART

Family: Streptaxidae Gray, 1860

Genus: *Elma* H. Adams, 1866

Type species: *Ennea (Elma) swinhoei* H. Adams, 1866

***Elma* cf. *swinhoei* (H. Adams, 1866)**

Material examined: Taiwan, Xinbei Shi (新北市), Pingxi Xiang (平溪鄉), 1.2 km N of Shifen Pubu (十分瀑布), side branch of road #106, 210 m, 25°03.276'N, 121°47.029'E, leg. HUNYADI A., 04.10.2014, NMW.Z.2015.004.00001 (dissected individual: shell fragments, anatomically examined body and radula on a double-faced adhesive tape in ethanol), HA/1 (1 additional, empty shell from same locality).

Shell (Fig. 1): High-spined, height 10.45 mm, diameter 4.6 mm.

Remarks: The examined specimen (Fig. 1) was collected approximately 37 km east of the type locality of *E. swinhoei*. The shell of the specimen is shorter (H = 10.45 mm) and more oval than the lectotype of *E. swinhoei* (H = 15.7 mm, see: HWANG 2014). On the other hand, in its shape and size the examined specimen is similar to the holotype of *E. swinhoei hotawana*, although the latter was collected ca. 250 km to the south (PILSBRY & HIRASE 1905). We thus provisionally identify the dissected specimen as *E. cf. swinhoei*.

ANATOMY

Genitalia (Figs 2–7): Atrium short; internally with numerous blunt papillae which became larger to-

wards the vagina. Penis long, slender and cylindrical, nearly equally thick throughout; there is a very slight caecum-like thickening near the distal end, without any differentiation on the inner wall. Inner wall of penis with scattered papillae, with brown penial hooks in each papilla, except for some papillae in the apical (proximal) part. Hooks largest in the middle portion of penis and somewhat smaller towards the atrium and vas deferens. Hooks with sharp tips curved towards the atrium. Penial sheath present, covering approximately half of penis; end of penial sheath doubled back on itself with a very slender retractor muscle attaching to the atrium. No epiphallic differentiation observed. Vas deferens enters proximal end of penis slightly laterally (at an angle of ca. 45°) after forming a loop under the penial sheath, with one side of the loop attached to the inner surface of sheath; loop ending approximately at the middle of penial sheath. Diameter of vas deferens is somewhat greater between the spermoviduct and the penial sheath than between the penis and the penial sheath. Penial retractor muscle long, inserting at the penis-vas deferens junction and attached to the diaphragm. Vagina very short, stout. Bursa copulatrix duct long, slender, with somewhat thickened reservoir, reaching the albumen gland. Free oviduct relatively long, thicker than penis; inner wall of the vagina and the free oviduct with elevated, conspicuous folds which converge towards the atrium; oviduct enlarged and folded. Talon small, thickened and curved.

Pallial complex and salivary gland: Pallial complex typically streptaxid, similar to that of *Discartemon* (see: SIRIBOON et al. 2014) and *Huttonella* (see: SIMONE 2013), about 1.5 whorls long, sigmure-

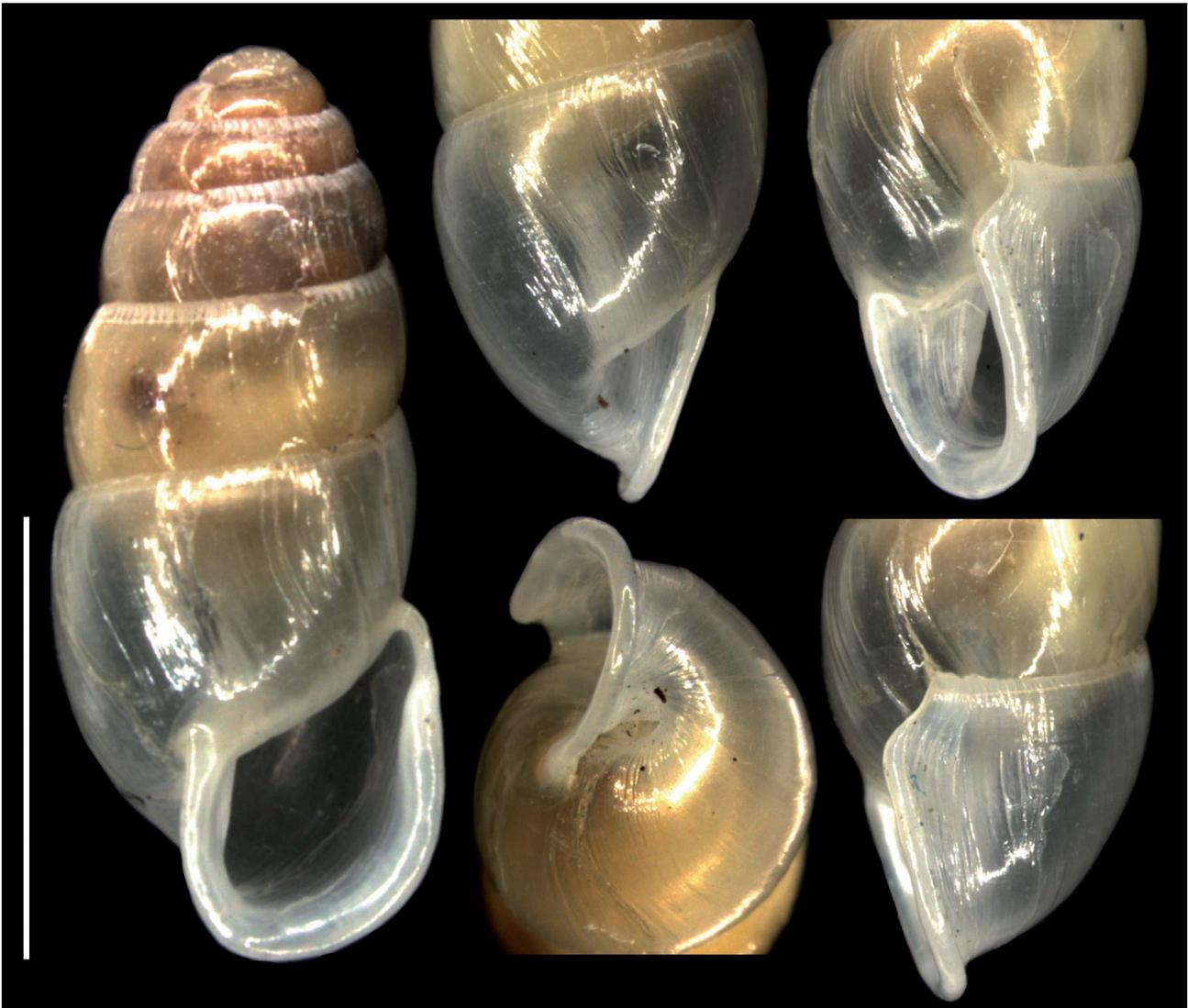


Fig. 1. Shell of the anatomically examined specimen of *Elma* cf. *swinhoei* (H. Adams, 1866). Scale bar 5 mm

thous, with kidney sub-rectangular. Salivary gland single, soft, with two ducts leaving separately (rather than together as in *Huttonella*; SIMONE 2013), each duct of even thickness throughout its length.

Radula (Figs 8–9): Teeth arranged in anteriorly V-shaped rows, each row containing at least 20 teeth. Central tooth sharp, triangular with pointed

cusps, approximately half the size of the first laterals. Lateral and marginal teeth undifferentiated, unicuspid and lanceolate, some even mucronate; anterior laterals with much less pointed cusps; laterals gradually decreasing in length and size, outer laterals much smaller and shorter than the inner laterals.

DISCUSSION

SYSTEMATICS OF THE GENUS *ELMA*

The taxonomy of Taiwanese *Elma* needs revision. Altogether three species or subspecies have been reported from the island (Fig. 10), namely *Elma swinhoei* (type locality: “Tamsui”), *E. swinhoei hotawana* (Pilsbry et Hirase, 1905) (type locality: “Hotawa”), and *Elma oblongata* Yen, 1939 (type locality: “Lungso-tan, Kwangtung”, China, see: YEN 1939) (PILSBRY

& HIRASE 1905, LEE & CHEN 2003, HEMMEN & NIEDERHÖFER 2007). Examination of the types of the taxa described from Taiwan, and a number of specimens recently collected by A. HUNYADI and by K. OKUBO, suggests there is a range of variation with larger and more acute forms present in the south and east (Fig. 10, Appendix 1). No anatomical information was previously available on any of these taxa. Indeed, only one live adult was found, so live indi-

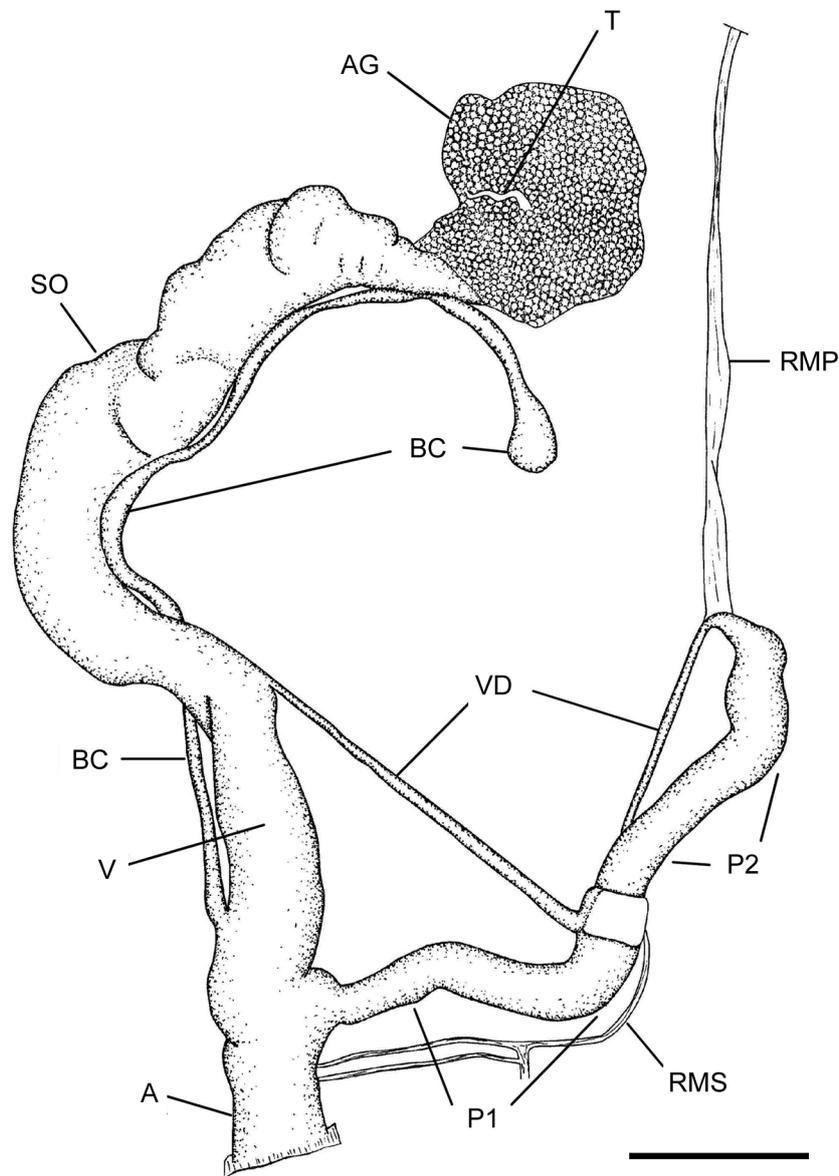


Fig. 2. Genital anatomy of *Elma* cf. *swinhoei* (H. Adams, 1866): A – atrium, AG – albumen gland, BC – bursa copulatrix, P1 – part of penis covered by penial sheath, P2 – part of penis not covered by sheath, RMP – retractor muscle of penis, RMS – retractor muscle of penial sheath, SO – spermoviduct, T – talon, V – vagina, VD – vas deferens. Scale bar 1 mm

viduals may be scarce as seems to be the case with some other streptaxid genera (e.g. SIRIBOON et al. 2014). The anatomically examined specimen (Fig. 1) was provisionally identified as *E. cf. swinhoei* because it was collected approximately 37 km east of the type locality of *E. swinhoei*. However it was similar to the holotype of *E. swinhoei hotawana*, collected ca. 250 km to the south (Fig. 10). We note that a revision is required and that shape variation in Taiwanese *Elma* could in some cases be continuous.

ATTRIBUTION OF *ELMA* TO STREPTAXID SUBFAMILY

The description of the anatomy of *Elma* makes it possible to discuss its relationship to other

Streptaxoidea, with a particular emphasis on its subfamily position. *Elma* was placed in the Enneinae by both ZILCH (1960) and SCHILEYKO (2000), initially based on the high-spired shell, although SCHILEYKO (2000) also used the genital anatomy (from other genera) in his classification. Due to the absence of anatomical data in ZILCH (1960), and the evident oversimplification of his classification, we do not further discuss the Enneinae and Streptaxinae sensu ZILCH (1960), but only in the senses of later authors.

Firstly, *Elma* has penial hooks, confirming its placement in the Streptaxidae rather than the Diapheridae (SUTCHARIT et al. 2010) where most high-spired Asian Streptaxoidea (i.e. *Diaphera* and *Sinoennea*) belong. Incidentally, we hypothesise that

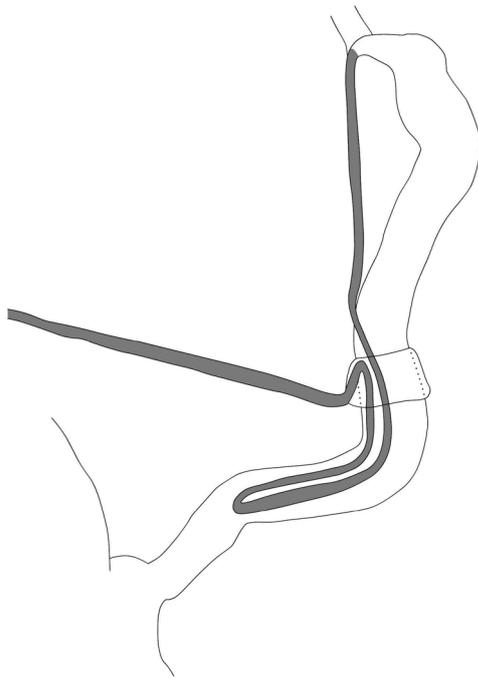


Fig. 3. Penis and vas deferens (grey) of *Elma* cf. *swinhoei* (H. Adams, 1866). Diagrammatic

Indoennea Kobelt, 1904, which is conchologically similar to *Sinoennea*, may also prove to belong to the Diapheridae once its anatomy is known, as may some other small-shelled genera.

Secondly, *Elma* has a well-developed penial sheath, and a vas deferens which forms a loop between the penis and the penial sheath (Fig. 3). The striking presence or absence of these features was considered important by SCHILEYKO (2000) for his subfamily classification. Indeed, the sheath is present throughout some of the major clades revealed in the molecular analysis of ROWSON et al. (2010) and absent throughout others. The additional presence of a loop formed by the vas deferens, however, cannot alone be used to distinguish subfamilies. For example, in the genus *Carinartemis* Siriboon et Panha, 2014, one species has a loop-forming vas deferens, but the other does not (SIRIBOON et al. 2014). It is also possible that the presence of a loop (although not the presence of a sheath) might vary with the maturity of the animal.

The presence of penial sheath makes *Elma* highly dissimilar to the African *Ennea* H. Adams et A. Adams, 1855 (as illustrated by DEGNER (1934) and SCHILEYKO (2000)). In Enneinae sensu Schileyko the only taxa with a penial sheath are the African *Raffraya* Bourguignat, 1883 and the Madagascan *Makrokonche* Emberton, 1994, both ranked by SCHILEYKO (2000) as subgenera of the African *Streptostele* Dohrn, 1866. Like *Elma*, these genera have high-spined, tapering, edentate shells. *Ennea* has a pupiform, dentate shell, and since PILSBRY (1919) it has often been considered a subgenus of the African *Ptychotrema* L. Pfeiffer,

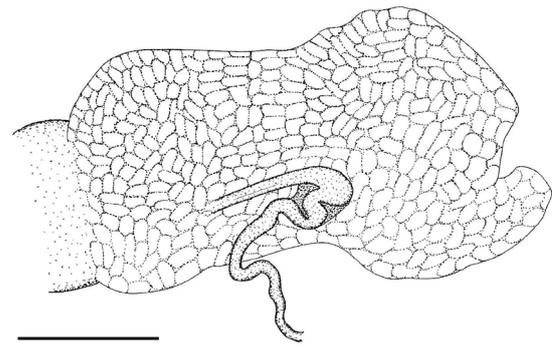
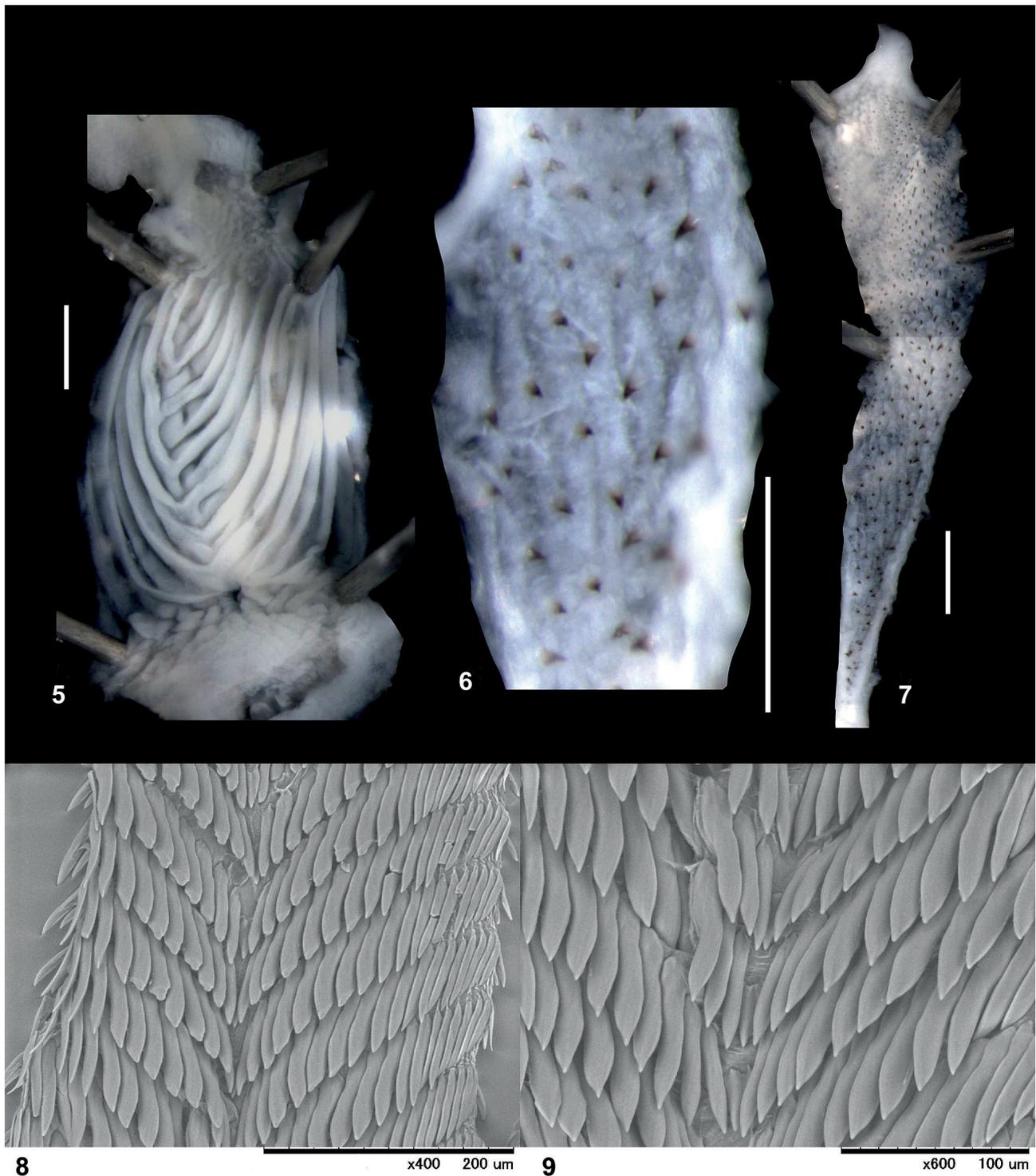


Fig. 4. Talon region of *Elma* cf. *swinhoei* (H. Adams, 1866). Scale bar 500 μ m

1853 (to which it may well be related; ROWSON et al. 2010). However, SCHILEYKO'S (2000) Enneinae are evidently polyphyletic, e.g. including both streptaxid and diapherid taxa (ROWSON et al. 2010, SUTCHARIT et al. 2010). To be useful it should arguably be restricted to close relatives of *Ennea*. The molecular evidence suggests that there are other species and subgenera of *Ptychotrema*, none of which have a penial sheath. *Raffraya* does not appear to be related, while *Makrokonche* has yet to be sequenced (ROWSON et al. 2010). As a result, we do not think that *Elma* should be classified in either the Enneinae or the Ptychotrematinae. Incidentally, a close relationship between *Ennea* and *Ptychotrema* would call into question the usefulness of the subfamily name Ptychotrematinae, used by SCHILEYKO (2000) to place the two genera in different subfamilies.

Likewise, the same features show that *Elma* is dissimilar to the genus *Huttonella* L. Pfeiffer, 1856. Despite being introduced nearly circumtropically, *Huttonella* is probably originally Asian (e.g. SIMONE 2013). The molecular data of ROWSON et al. (2010) show *Huttonella* to be closely related to the African genus *Gulella* L. Pfeiffer, 1856 and to the Mauritian *Maureennea* Schileyko, 2000. All three genera lack penial sheath and are classified by SCHILEYKO (2000) in the Ptychotrematinae. None of the other anatomically known genera in the Ptychotrematinae sensu Schileyko has a sheath. In addition, the small talon (Fig. 4) and the uniform penial hooks (Figs 6–7) of *Elma* contrast with the large talon and the differentiated hooks seen in some of these genera. Overall, we conclude that *Elma* is probably not a member of Ptychotrematinae sensu Schileyko, 2000.

In fact the presence of penial sheath and loop of the vas deferens is sufficient to classify *Elma* into another of the subfamilies used by SCHILEYKO (2000): Streptaxinae or Gibbinae. In SCHILEYKO'S (2000) system, the main difference between the Streptaxinae and the Gibbinae is that the vas deferens does not pass under the penial sheath in the former, but does in the latter. According to ROWSON et al. (2010) species of the genera *Indoartemon* Forcart, 1946,



Figs 5–9. *Elma* cf. *swinhoei* (H. Adams, 1866): 5 – inner wall of vagina, 6–7 – inner wall of penis, 8–9 – radula. Scale bars for Figs 5–7 500 μ m

Streptartemon Kobelt, 1905, and *Streptaxis* Gray, 1837, all in the Streptaxinae in SCHILEYKO'S (2000) system, are clustered together with species of *Edentulina* L. Pfeiffer, 1855 and *Gonaxis* Taylor, 1877 (both Gibbinae) in the same clade. This clade is referred to as the “streptaxines” (Streptaxinae). The anatomy of the type species of *Streptaxis* was illustrated by

BARBOZA DE REZENDE et al. (1962), who described a penial sheath and loop of the vas deferens, although from their figures the exact course of the latter is unclear. *Streptaxis* forms a clade with *Streptartemon* and *Indoartemon* whose genital structure resembles that of *Elma* in the above-mentioned traits (SCHILEYKO 2000, SIRIBOON et al. 2014). Thus, *Elma* could belong

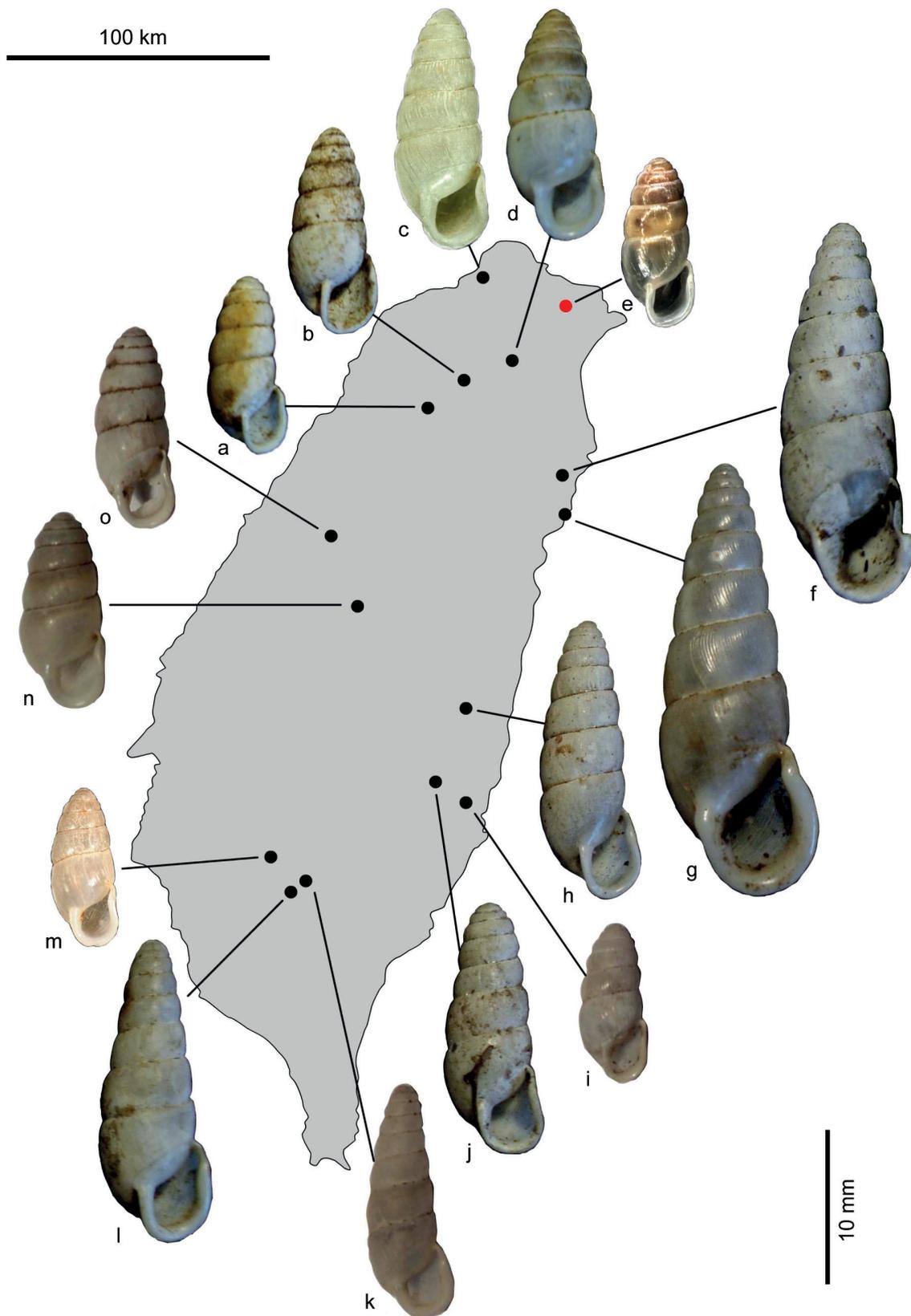


Fig. 10. Type specimens and recently collected specimens of Taiwanese *Elma*: a – 2014/74, b – 2014/71, c – lectotype of *Ennea (Elma) swinhoei*, NHMUK 1866.5.9.14/1, d – 2014/64, e – 2014/70 (anatomically examined specimen, indicated with red dot), f – 2014/79, g – 2014/80, h – 2014/82, i – 19940818A, j – 2014/85, k – 19940820, l – 2014/96, m – lectotype of *Elma swinhoei hotawana* Pilsbry & Hirase 1905, ANSP 89940, n – 19950409, o – 19980809. For explanation of codes see: [Appendix 1](#)



Fig. 11. Topotype of “*Ennea*” *aliena* Bavay et Dautzenberg, 1912, NMW.1955.158.25364

to the Streptaxinae, a subfamily that ranges through Asia, Africa and South America.

Other genera in the Streptaxinae or the Gibbinae sensu SCHILEYKO (2000), again with a similar genital anatomy, were shown by ROWSON et al. (2010) to form a separate clade of taxa restricted to the Seychelles and the Mascarene islands. Among the taxa in this clade, *Stereosteles* Pilsbry, 1919 and *Gonospira* Swainson, 1840 resemble *Elma* in being high-spired, although only *Stereosteles* tapers strongly (as do most *Elma* species). Like *Elma*, both *Gonospira* and *Stereosteles* have a sheath and a loop of the vas deferens, which SCHILEYKO (2000) showed to be present also in the now-extinct Mauritian genus *Gibbus* Montfort, 1810. *Gibbus* could not be included in ROWSON et al. (2010) analysis, but is likely to belong in the same clade as *Gonospira*. If correct, the name Gibbinae could be applied to this clade, and in turn *Elma* could be considered to belong in the Gibbinae. The slight reduction in diameter of the vas deferens would also support the placement in the Gibbinae according to SCHILEYKO (2000). This would be biogeographically notable, since the Asian *Elma* could be descended from the same lineage that gave rise to this Indian Ocean radiation. However, the fact that SCHILEYKO (2000) placed *Stereosteles* in the Streptaxinae and *Gonospira* in the Gibbinae emphasises the problem of accurate classification of these genera at the subfamily level. This is partly a consequence of the great variation in shell morphology in such clades, and the occurrence of multiple clades in some biogeographical regions. The genus *Pseudelma* Kobelt, 1904 was introduced for shells en-

demically to Mayotte Island (Comoros Islands; between Madagascar and Africa), the name reflecting a strong conchological similarity to *Elma*. *Pseudelma* was classified in the Enneinae by ZILCH (1960) along with *Elma*, whereas SCHILEYKO (2000) placed *Pseudelma* in the Gibbinae. Neither author had anatomical information on *Pseudelma*. ABDOU et al. (2008) revised *Pseudelma* and described the anatomy of several species. Based on the absence of penial sheath, the presence of a short penial caecum, the large talon and the uniform, undifferentiated, small hooks in the penis, they transferred *Pseudelma* into the Enneinae sensu SCHILEYKO (2000). *Elma*, however, has a well-developed penial sheath, lacks a penial caecum, and has a small talon. Consequently, *Elma* and *Pseudelma* belong in different subfamilies according to SCHILEYKO'S (2000) anatomical criteria, and probably even the opposite subfamily to that in which they were classified. Their strikingly similar shells can better be explained either by parallel evolution, or as ancestral character states pre-dating the origin of their respective subfamilies.

In summary, we conclude that *Elma* probably belongs neither to the Enneinae nor to the Ptychotrematinae, but should instead be included in either the Streptaxinae or the Gibbinae. *Elma* is the first high-spired Southeast-Asian streptaxid to be classified in one of these two groups. It is also unrelated to either the Asian Diapheridae or to the Comoros *Pseudelma*, although a link to the other Indian Ocean genera in the Gibbinae is not ruled out.

Finally, one other high-spired Southeast-Asian streptaxid deserves a mention. *Ennea aliena* Bavay et Dautzenberg, 1912 (Fig. 11) from Tonkin, Vietnam is striking in its (relatively) large shell size, shape and dentition. It was tentatively classified in *Indoennea* by SCHILEYKO (2011: 26, with a question mark). “*Ennea*” *aliena* certainly does not belong to *Ennea*, and differs from *Indoennea* species in the straight aperture and the absence of a columellar lamella. As we suggest above, *Indoennea* may actually belong in the Diapheridae based on such features. Therefore on a conchological basis, “*Ennea*” *aliena* seems to be more closely related to *Elma* than to *Indoennea*, and may even deserve its own genus. Since *Elma* is shown to belong to the Streptaxinae or the Gibbinae, we hypothesise that “*Ennea*” *aliena* might belong to the same subfamily. This could be tested by obtaining data on its anatomy.

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Appendix 1

The collection data for the additional specimens in Fig. 10 are as follows:

2014/64, Xinbei Shi (新北市), Wulai Xiang (烏來鄉), railway station at Wulai, 500 m, Wulai Pubu (=waterfall, 烏來瀑布), right side of the road, $24^{\circ}52.031'N$, $121^{\circ}32.969'E$, leg. HUNYADI A., 03.10.2014;

2014/70, Taiwan, Xinbei Shi (新北市), Pingxi Xiang (平溪鄉), 1.2 km N of Shifen Pubu (十分瀑布), side branch of road #106, 210 m, $25^{\circ}03.276'N$, $121^{\circ}47.029'E$, leg. HUNYADI A., 04.10.2014, HA/1 (empty shell) + anatomically examined specimen;

2014/71, Taoyuan Xian (桃園縣), Fuxing Xiang (復興鄉), Xiaowulai (小烏來), 600 m along the Xiaowulai Skywalk (小烏來天空步道), 330 m, $24^{\circ}47.381'N$, $121^{\circ}22.141'E$, leg. HUNYADI A., 05.10.2014;

2014/74, Hsinchu Xian (新竹縣), Jianshi Xiang (尖石鄉), Tiandana (天打那), 200–300 m from the bridge, Naluo Wenquan, 400 m, $24^{\circ}41.283'N$, $121^{\circ}13.087'E$, leg. HUNYADI A., 06.10.2014;

2014/79, Yilan Xian (宜蘭縣), Nanao Xiang (南澳鄉), Hengshan (橫山), eastern side of Zhangshushan (樟樹山), 90 m, $24^{\circ}26.042'N$, $121^{\circ}45.101'E$, leg. HUNYADI A., 08.10.2014;

2014/80, Hualien Xian (花蓮縣), Heping Cun (和平村), S of the train station, right side of road #9,

10 m, $24^{\circ}17.715'N$, $121^{\circ}45.169'E$, leg. HUNYADI A., 08.10.2014;

2014/82, Hualien Xian (花蓮縣), Fuyuan Guojia Senlin Youlequ (富源國家森林遊樂區), 260 m, $23^{\circ}35.321'N$, $121^{\circ}21.268'E$, leg. HUNYADI A., 09.10.2014;

2014/85, Hualien Xian (花蓮縣), Yushan Guojia Gongyuan (玉山國家公園), Yuli Zhen (玉里鎮), 800 m along Walami Gudao (瓦拉米古道), Shanfeng (山風), 510 m, $23^{\circ}19.642'N$, $121^{\circ}13.830'E$, leg. HUNYADI A., 11.10.2014;

2014/96, Kaohsiung Shi (高雄市), Maolin Xiang (茂林鄉), Liugui Qu (六龜區), Hulu Gu (葫蘆谷), road above the entrance, 290 m, $22^{\circ}55.514'N$, $120^{\circ}39.207'E$, leg. HUNYADI A., 15.10.2014;

19940818A, Taiwan (花蓮縣) HuaLian County (台灣省) AnTong Hot-spring (安通溫泉), leg. OKUBO K., 18.08.1994, OK/1;

19940820, Taiwan (台灣省), Kaohsiung County (高雄縣), foothills of Mt. MingHai (鳴海山), leg. OKUBO K., 20.08.1994, OK/2;

19950409, Taiwan (台灣省), NanTou County (南投縣), BuLi Town (埔里鎮), GuanYin Bridge No.1 (觀音橋1號) leg. OKUBO K., 09.04.1995, OK/1;

19980809, Taiwan (台灣省), TaiZhong County (台中縣) XinShe Village (新社鄉), LongAn (龍安), leg. OKUBO K., 09.08.1995, OK/1.