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High Fecundity, Rapid Development and Selfing Ability in Three Species of Viviparous Land Snails Phaedusinae (Gastropoda: Stylommatophora: Clausiliidae) from East Asia

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Anna Sulikowska-Drozd, Takahiro Hirano, Shu-Ping Wu, and Barna Páll-Gergely (2018) Life history traits are important yet understudied aspects of ecological diversification in land snail faunas. To acquire information for comparative analysis of gastropod life cycles, we conducted experimental breeding of three viviparous clausiliids from Japan and Taiwan. Under laboratory conditions, *Tauphaedusa sheridani* (Pfeiffer, 1866), *T. tau* (O. Boettger, 1877) and *Stereophaedusa* (*Breviphaedusa*) *jacobiana* (Pilsbry, 1902) featured similar times to complete shell growth (12-16 weeks), age of first reproduction (23-24 weeks) and annual fecundity (143-173 neonates per pair of snails). The maximum number of eggs retained in genital tract reaches nine for *T. sheridani*, 11 for *T. tau*, and seven for *S. jacobiana*. The ratio between average shell height of neonate and adult varied between 13.5% for *T. tau*, 13.9% for *T. sheridani*, and 16.7% for *S. jacobiana*. All species were able to self-fertilize. Exposure to long drought affects intrauterine embryo development in all species; additionally, it results in parent and embryo mortality in *S. jacobiana*. Observed differences in the structure of the egg envelope among studied species point to greater than expected differentiation of developmental processes in viviparous Phaedusinae of East Asia.

Key words: Land snail, Reproduction, Viviparity, Parental care, Life history.

BACKGROUND

The land snail family Clausiliidae ("door snails") is the most species-abundant terrestrial gastropod family, containing more than 1,200 known species (Nordsieck 2007). Due to the various habitats, wide range of life history and reproductive strategies, diversity of shell coiling direction, and high number of species and uncountable local forms, Clausiliidae became an evolutionary model group (Uit de Weerd et al. 2006; Kornilios et al. 2015; Koch et al. 2016). Currently, Clausiliidae have seven extant subfamilies (Bouchet et al. 2017). Among the major subfamilies, Clausiliinae and Alopiinae are mainly distributed in Europe, whereas Phaedusinae mostly inhabits Asia. Information on life history traits of multiple clausiliid species is essential for

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comparing characteristics between the family's major lineages. For historical reasons, European clausiliids have been far more extensively studied in that respect than the groups living in other continents (Giokas and Mylonas 2002; Maltz and Sulikowska-Drozd 2008; Szybiak et al. 2015; etc.).

We know based on anatomical studies that the development of eggs in the genital tract is a common strategy among Phaedusinae clausiliids of East Asia (Loosjes 1953; Azuma 1982; Minato 1994; Nordsieck 2001; Motochin et al. 2017; etc.), although almost no observations have been published on living clausiliids kept under laboratory conditions. Viviparous Phaedusinae species retain eggs in their reproductive tract and then deliver neonates. Traditionally, the strategy was named "ovoviviparity", but this term appeared to be ambiguous in many animal groups and should be avoided (see Blackburn 1999). In spite of the wide distribution of viviparous reproduction in Phaedusinae (genera *Phaedusa*, *Euphaedusa*, *Reinia*, etc.), data on their life-history traits remain fragmentary, preventing any comparative analysis.

In this paper, we aim to provide descriptions of the life cycles of three clausiliids - *Tauphaedusa sheridani* (Pfeiffer, 1866), *T. tau* (O. Boettger, 1877) and *Stereophaedusa* (*Breviphaedusa*) *jacobiana* (Pilsbry, 1902) - focusing on their fecundity, size of neonates, time of shell growth and maturation, and selfing ability. The study was conducted under laboratory conditions.

MATERIALS AND METHODS

The nomenclature of clausiliids follows Motochin et al. (2017). The laboratory colony of *Tauphaedusa sheridani* was established in December 2015 with eight adult snails from Dawulun, Keelung City, northern Taiwan (coll. S.P. Wu; 21 Nov 2015; 25°09'31.25"N; 121°42'32.70"E; alt. 210 m). According to the world climatic database (Hijmans et al. 2005), the mean annual temperature of the sampling site is 21.9°C, and precipitation 3,077 mm.

The laboratory colony of *Tauphaedusa tau* was established in September 2015 with 37 individuals from Osaka City, Osaka Prefecture, Japan (coll. T. Hirano; 12 Feb 2014; 34°38'7.5"N; 135°30'11.8"E; alt. 12 m). According to the world climatic database (Hijmans et al. 2005), the mean annual temperature of the sampling site is 15.6°C, and precipitation 1,485 mm.

The laboratory colony of *Stereophaedusa* (*Breviphaedusa*) *jacobiana* was established with eight individuals from Japan, Kagoshima Pref., Tanegashima, Kumage-gun, Nakatane-chō, Sakai Shioya near Tanegashima Hot Springs (coll. Y. Nakahara, J.U. Otani, B. Páll-Gergely; 14 Dec 2015; 30°27'49.44"N, 130°57'36.18"E). According to the world climatic database (Hijmans et al. 2005), the mean annual temperature of the sampling site is 18.4°C, and precipitation 2,724 mm.

Adults were kept in plastic containers (300 cm^3) and provided with cellulose tissues and fragments of limestone. The snails were fed with lettuce, cucumber and zucchini. Humidity in the containers was almost constant and close to 100% as a result of regular spraying. During the whole year, snails were kept at room temperature (18-25°C) and under natural light conditions. Adults were kept in pairs or groups of three. Observations on growth and maturation of juveniles were conducted in groups of individuals kept in the climatic chamber (POL-EKO KK350 TOP) under constant temperature (21°C) and humidity exceeding 70%. Additionally, to test the ability of self-fertilization, subadults of F1 generation were isolated prior to attaining the ultimate shell size and kept singly until the end of the experiment.

The presence and development of eggs in the reproductive tract were examined both for snails kept under standard (high humidity) conditions and those exposed to 60 days of drought (no food, no water spraying). Snails were dissected and all brooded eggs were counted. The developmental stage of each egg was classified as follows: stage I - egg filled with amorphous substance, no visible shell; stage II - egg with embryo; embryonic shell with < 1 whorl; stage III - egg with embryo; embryonic shell with ≥ 1 whorl; stage IV - shelled embryo without complete egg envelope.

Shells of dissected adults, intrauterine eggs and embryos, and randomly selected neonates were photographed using a stereomicroscope Leica M205C, with camera Leica DFC 295 built on top; and then the shell height was measured with microscope *software* Leica Application Suite V4.5. Whorls were counted according to Ehrmann (1933). For growth rate observations, shell height was measured to the nearest 0.05 mm with measuring eye-piece, under stereomicroscope Nikon SMZ800.

After conducting the experiment, snails were culled in ethanol and then dried. The material is kept in the Department of Invertebrate Zoology and Hydrobiology, University of Łódź, Poland.

RESULTS

Tauphaedusa sheridani
(Fig. 1)

The F0 individuals (n = 8) placed in the culture were on average 16.55 mm high (SD = 0.72) and consisted of 9.9 whorls (SD = 0.3). They released offspring repeatedly during the experiment (total 741 neonates). During a year, they produced 115 to 195 neonates per pair of snails (mean 164.5, SD = 34.4, n = 4). During a week, the pairs delivered 3.5-4.8 neonates on average (median 4.7, n = 4). On delivery, the neonates had shells 2.00-2.73 mm high (mean 2.3 mm, SD = 0.15, n = 31) with 2.5 whorls (Fig. 1B). Time needed for shell growth ranged between 88 and 113 days (n = 10). The first reproduction of F1 generation was recorded 160 days after birth.

The fecundity of the F1 generation was recorded for 18 snails kept in pairs. During a year, they produced between 109 and 226 neonates per pair of snails (mean 166, SD = 36.8, n = 9). During a week, an average of 3-6.5 neonates were delivered per pair of snails (median 5, n = 9). Also, virgin *T. sheridani* were capable of reproduction (100% out of 8 individuals). They started releasing neonates seven month after birth and continued until the end of the experiment. During a year, between 65 and 90 neonates were released per virgin snail (mean 77.4, SD = 9.1, n = 8) and during a week, between 1 and 6 (median 2, n = 8).

Tauphaedusa sheridani, kept under high humidity, contained 4 to 9 eggs and embryos in the reproductive tract (mean 6.8, SD = 1.37, n = 15) (Fig. 1D, E). The majority of the retained offspring (49%) were at the first stage of development (without shelled embryo). Embryos advanced in development (stage IV) were found in low numbers in every adult (range 1-4, mean 2.2, SD = 0.8, n = 15). The embryos' stage IV shell height varied from 1.48 to 2.47 mm (mean 2.02 mm, SD = 0.25, n = 33) and number of whorls from 1.5 to 3 (mean 2.25, SD = 0.5, n = 33).

No adult *T. sheridani* died during the 60-day exposure to drought. In snails dissected immediately after the experiment, the mean number of eggs and embryos was 5.4 (SD = 1.4, range 3-9, n = 27). The majority of embryos (80%) were advanced in development (stage IV). The shell height of embryos varied from 1.4 to 2.4 mm (mean 2.10 mm, SD = 0.20, n = 113) and number of whorls from 2.0 to 3.0 (mean 2.5, SD = 0.22, n = 113).

Tauphaedusa tau
(Fig. 2)

The F0 individuals placed in the culture released offspring repeatedly during the experiment (total 2,630 neonates). During a year, they produced between 101 and 237 neonates per pair of snails (mean 168.7, SD = 39.8, n = 11). During a week, pairs delivered 2.0-5.2 neonates (median 3.8, n = 14). At the moment of release, the neonates had shells 1.5-2.25 mm high (mean 1.90 mm, SD = 0.18, n = 30) with 2.0-2.5 whorls (Fig. 2B). For the first group of juveniles, the period of shell growth lasted 78-99 days (n = 7). The first reproduction was recorded 132 days from birth. The second group of juveniles attained the ultimate shell size after 88 - 117 days (n = 11). The first reproduction was recorded 162 days from birth. Measured adult F0 individuals were on average 14.12 mm high (SD = 0.57, n = 18) and consisted of 9.7 whorls (SD = 0.3, n = 18).

In the laboratory, virgin *T. tau* were capable of reproduction (100% out of 9 individuals). They started producing neonates eight month after birth and continued until the end of the experiment. During a year, between 2 and 60 neonates were released per virgin snail (mean 30.44, SD = 15.03, n = 9). During a week, between 1 and 6 offspring were delivered (median 2, n = 9).

Tauphaedusa tau (F1 generation), kept under high humidity, contained 3 to 11 eggs and embryos in the reproductive tract (mean 7.06, SD = 2.66, n = 17) (Fig. 2D, E). The majority of the retained offspring (44%) were at the first stage of development (without shelled embryo). Embryos advanced in development (stage IV) were found in most snails (mean number 1.9, SD = 1.5, n = 17). The embryos' shell height varied from 1.2 to 2.2 (mean 1.74 mm, SD = 0.24, n = 33) and number of whorls from 1.5 to 2.75 (mean 2.2, SD = 0.38, n = 33). No adult *T. tau* died during the exposure to 60 days of drought. In snails dissected immediately after the experiment, the mean number of eggs and embryos was 3.30 (SD = 2.07, range 0-9, n = 27). The majority of embryos (65%) were advanced in development (stage IV). The shell height of embryos varied from 1.0 to 2.1 mm (mean 1.70 mm, SD = 0.20, n = 50) and number of whorls from 1.25 to 2.75 (mean 2.2, SD = 0.36, n = 50).

Stereophaedusa (*Breviphaedusa*) *jacobiana*
(Fig. 3)

Eight F0 individuals placed in the culture

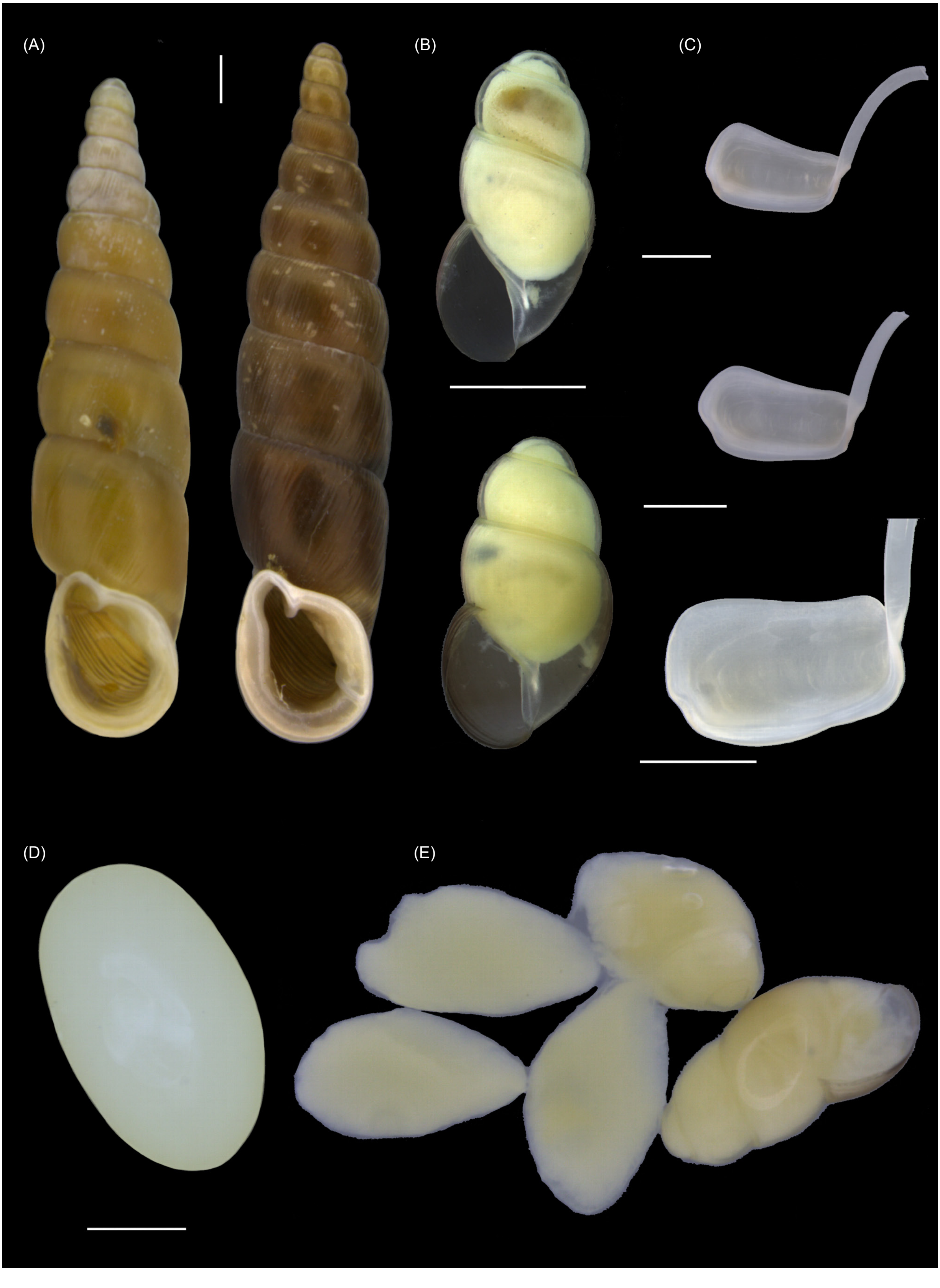

Fig. 1. *Tauphaedusa sheridani*. (A) adults (F1 generation); (B) neonates; (C) clausilia; (D-E) - eggs and embryos from dissected adults. Scale bar = 1 mm.

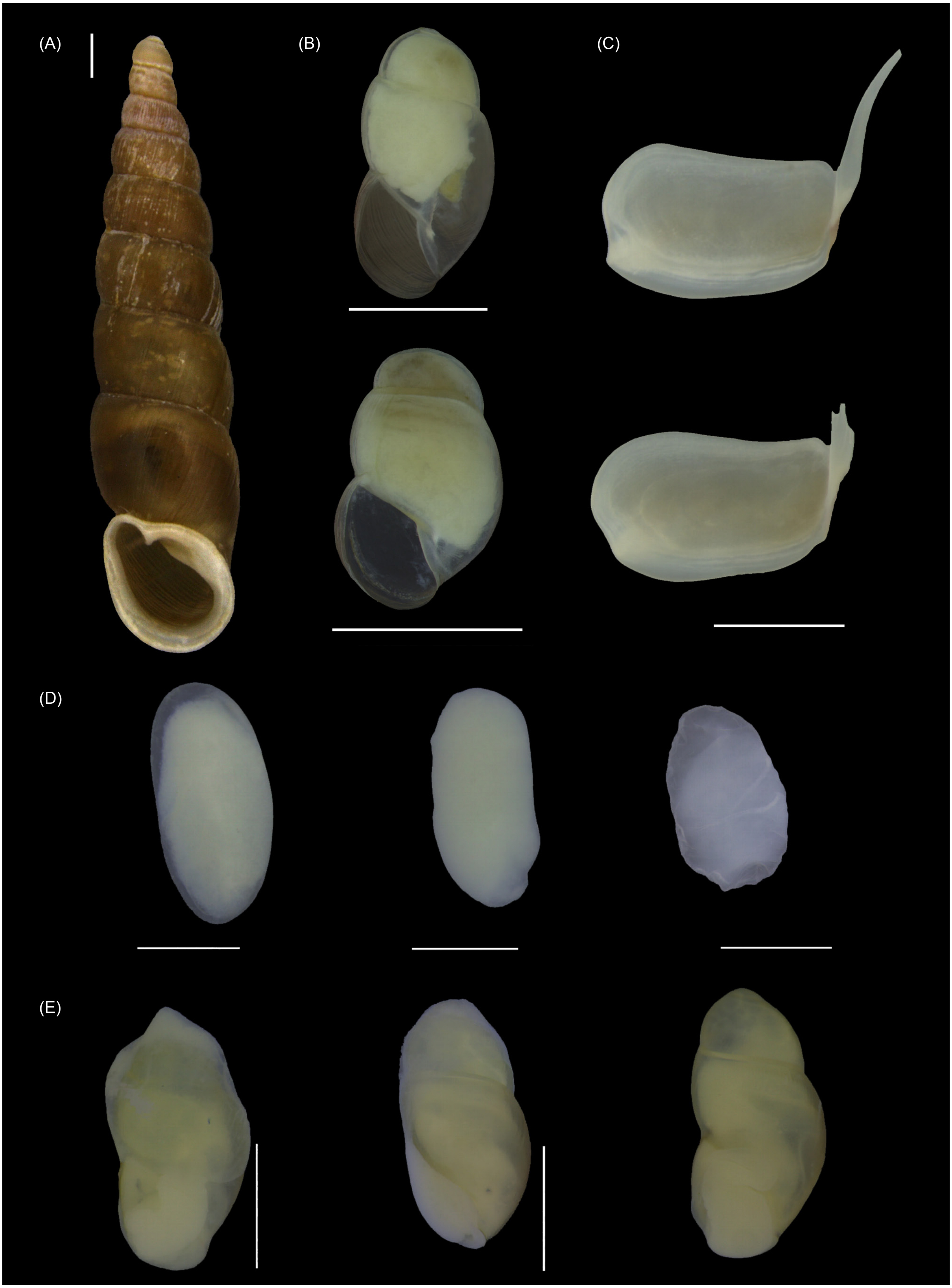

Fig. 2. *Tauphaedusa tau*. (A) adult (F1 generation); (B) neonates; (C) clausilia; (D-E) eggs and embryos from dissected adults. Scale bar = 1 mm.

were 12.53 mm high (SD = 0.36) and consisted of 7.97 whorls (SD = 0.51) on average. Kept in pairs they released offspring repeatedly during the experiment (total 779 neonates). During a year, they produced from 97 to 159 neonates per pair of snails (median 143.5, *n* = 4), while during a week, 3.5-5.5 neonates were delivered per pair of snails (median 4.0, *n* = 4). At the moment of release, the neonates had shells 1.86-2.57 mm high (mean 2.09 mm, SD = 0.15, *n* = 28) with 2.0-2.5 whorls (Fig. 3B). Time needed for shell growth ranged between 88 and 115 days (*n* = 10). The first reproduction was recorded 168 days after birth. The reproduction of virgin *S. jacobiana* was recorded in only one of 10 isolated snails. It delivered 41 juveniles over 6 months.

Stereophaedusa jacobiana (F1 generation), kept under high humidity, contained 5 to 7 eggs and embryos in the reproductive tract (mean 6.2, SD = 0.84, *n* = 5). Retained progeny had egg envelopes with visible crystals of calcium carbonate (Fig. 3D, E). The majority of the offspring (52%) were at the first stage of development (egg without shelled embryo). The stage I egg length varied from 1.67 to 2.53 mm (mean 2.08, SD = 0.28, *n* = 16). The stage IV embryos still had parts of egg envelope with calcium carbonate crystals. Their shell height varied from 1.57 to 1.96 mm (mean 1.84 mm, SD = 0.12, *n* = 13) and number of whorls from 1.25 to 2.5. The exposure to 60 days of drought resulted in loss among adults of *S. jacobiana* (3 dead out of 13), and among retained progeny (in 3 out of 10 surviving adults). In the remaining snails, the mean number of eggs and embryos was 2.3 (SD = 2.98, range 0-7, *n* = 7). The majority of embryos (87%) were advanced in development and their shell height varied from 1.57 to 2.27 mm (1.84 mm, SD = 0.16, *n* = 14).

DISCUSSION

Although the available literature data on the life history traits of Phaedusinae are sparse, the presence of embryos in the reproductive tract has been mentioned in a high number of species (Loosjes 1953; Loosjes and Loosjes-van Bemmel 1973; Azuma 1982; Ohtsuki and Takahashi 1982; Motochin et al. 2017, etc.). The comparative analysis of the number and size of offspring, growth rate, selfing ability, and annual fecundity presented here contribute to a better understanding of reproductive trait diversity in viviparous taxa. The effects of long drought on

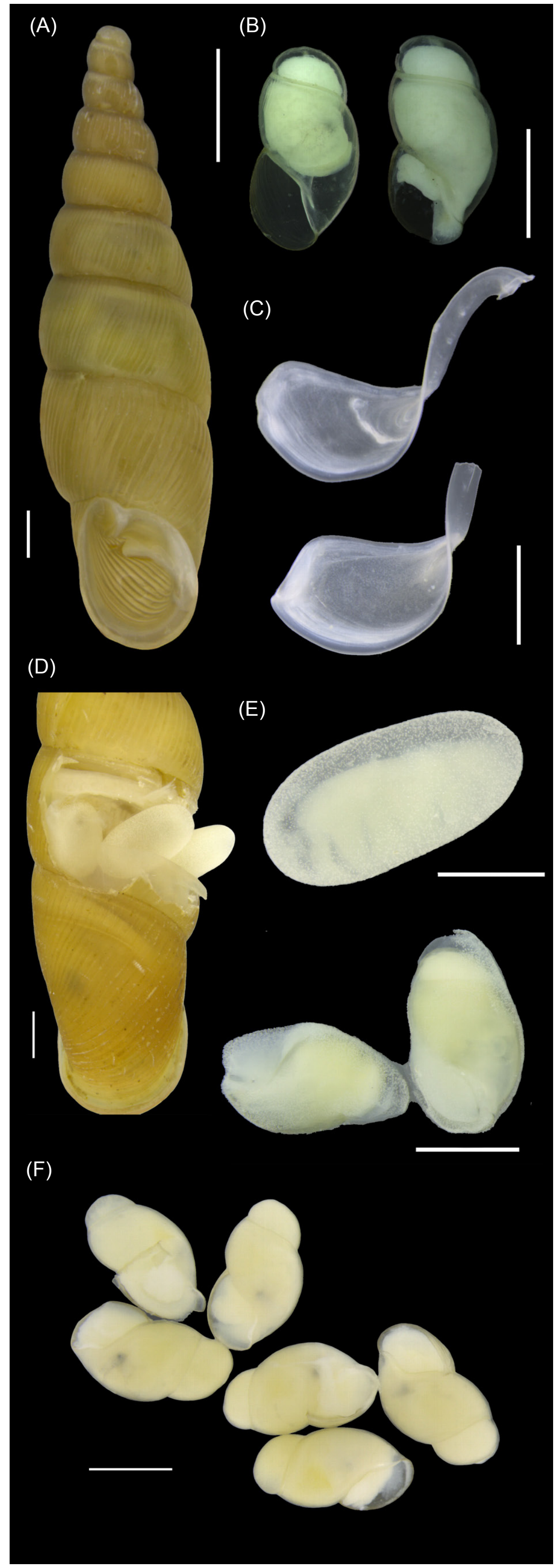

Fig. 3. *Stereophaedusa jacobiana*. (A) adult (F1 generation); (B) neonates; (C) clausilium; (D) dissected adult with eggs; (E-F) egg and embryos from dissected adults. Scale bar = 1 mm.

the studied snail's reproductive traits, as well as intra- and interspecies variations in shell size and fecundity, are summarized in figures 4-5, and tables S1-S6.

Among life history traits, the size of a single offspring in relation to adult size is one of the most important measures of parental investment (Royle et al. 2012). In our study, the ratio between

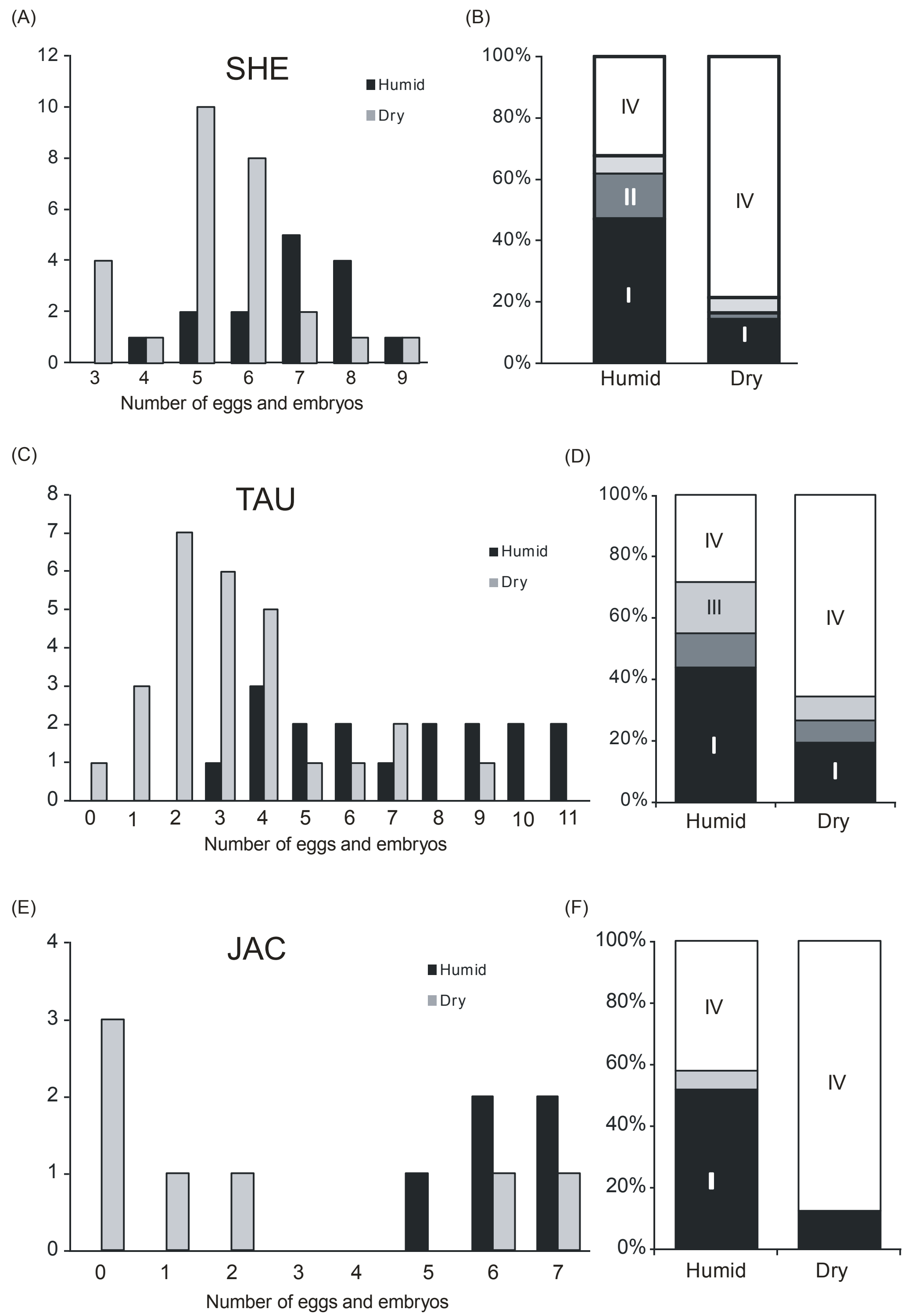

Fig. 4. Reproductive activity of *T. sheridani* (SHE), *T. tau* (TAU), and *S. jacobiana* (JAC) under humid and dry conditions: (A, C, E) number of intrauterine eggs per dissected individual; (B, D, F) percentage of intrauterine embryos at various developmental stages.

average shell height of neonate and adult varied between 13.5% for *T. tau*, 13.9% for *Tauphaedusa sheridani* and 16.7% for *S. jacobiana*. It points to higher parental investment per single offspring in *S. jacobiana* compared to *Tauphaedusa* species. On the other hand, all three species produced neonates with the similar whorl number (2.5-3), while *Phaedusa paviei* (Morlet, 1892) - a much bigger door-snail from Vietnam - delivered offspring with 3.8 whorls (Sulikowska-Drozd et al. 2018). The retained embryos in the studied taxa were previously illustrated in a few taxonomic papers: two-shelled embryos in *T. tau* (Loosjes and Loosjes-van Bemmel 1973); 5 egg-shaped offspring in *S. jacobiana*; and two eggs and a shelled embryo in *Tauphaedusa digonoptyx* (O. Boettger, 1977), a species closely related to *T. tau* (see Azuma 1982). Minato (1994) provided a detailed drawing of *Stereophaedusa valida* (L. Pfeiffer, 1850), a species closely related to *S. jacobiana*, with two embryos in its reproductive tract. We showed that the maximum number of offspring kept in the reproductive tract is much higher than reported before and ranges from seven in *S. jacobiana* to 11 in *T. tau*. Similarly, Sulikowska-Drozd et al. (2018) found up to 11 embryos (mean 4.29, SD 2.4) in the oviduct of *P. paviei*. For the non-Phaedusinae clausiliid *Alinda biplicata* (Montagu, 1803), the number of retained embryos reaches even 20 (mean 9.4, SD 2.8) (Sulikowska-Drozd et al. 2013); however, European species of a small size, such as *Ruthenica filograna* (Rossmässler, 1836) or *Balea perversa* (Linnaeus, 1758), kept up to four embryos (Wirth et al. 1997; Szybiak 2010). It appeared that the number of offspring in Asian Phaedusinae is more uniform than in other Clausiliidae lineages, where is linked primarily to adult shell size (Maltz and Sulikowska-Drozd 2008).

Shell size in land snail species is a variable character (Goodfriend 1986). The shell height and number of whorls of adult individuals kept in our culture (F0 and F1 generations) correspond with published data for *T. sheridani*: 15-16 mm and 9-10 whorls (Hsieh et al. 2013; Hwang 2014); for *T. tau*: 15 mm and 10 whorls (Azuma 1982); and for *S.*

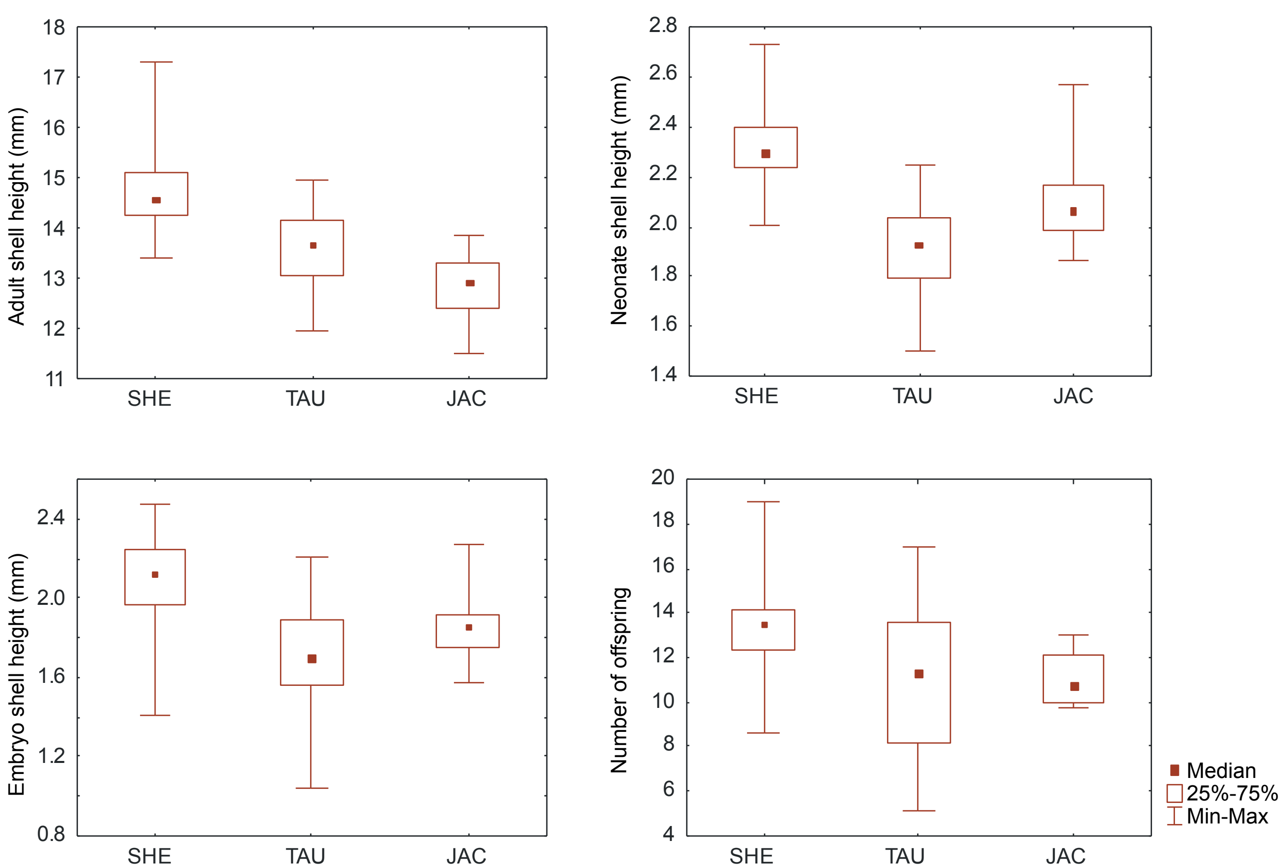

Fig. 5. Comparison of the selected life-history traits in *T. sheridani* (SHE), *T. tau* (TAU), and *S. jacobiana* (JAC). Number of offspring concerns monthly fecundity of a pair of snails.

jacobiana: 12.0-12.4 mm (Minato 1994).

The fecundity of snail pairs in the laboratory culture varied both inter- and intraspecifically, but was high compared to other clausiliids. Here, the mean number of neonates released annually were approximately 150 per pair; however, it reached 99 offspring per pair in *P. paviei* and only 17-33 neonates per pair in the non-Phaedusinae *Alinda biplicata* (see Maltz and Sulikowska-Drozd 2014; Sulikowska-Drozd et al. 2018).

The studied species are also able to produce progeny by self-fertilization. This ability is found in both *Tauphaedusa* species. Pulmonate gastropods are hermaphrodites, so they produce both kinds of germ cells, however selfing was proved only for a limited number of species and is often accompanied by long waiting time and reduction in fecundity (Escobar et al. 2011). Self-fertilization has already been recorded for a few door snails under laboratory conditions (Maltz and Sulikowska-Drozd 2014), and in the wild (Wirth et al. 1997). In contrast to observations of *Alinda biplicata* (see Maltz and Sulikowska-Drozd 2014), the reproduction of virgin *T. tau* and *T. sheridani* occurred without significant losses in fitness. High offspring production and selfing ability suggest high spreading potential of *Tauphaedusa* species.

For all species, time required to growth the shell and attain reproductive maturity was similar and relatively short (11-16 and 24 weeks, respectively). There is wide variation in development time among non-Phaedusinae European clausiliids and several species, even kept at optimal density in the laboratory, required twice as much time for shell growth and maturation (Maltz and Sulikowska-Drozd 2008); for example, 26-32 weeks in *Laciniaria plicata* (Draparnaud, 1801) and *Pseudalinda stabilis* (L. Pfeiffer, 1847). *Balea perversa* and *R. filograna* were observed to develop rapidly in laboratory colonies: over 13 and eight weeks, respectively (Baur and Baur 1992; Szybiak 2010).

The species studied here inhabit areas with high annual rainfall. Under humid laboratory conditions, the neonates were delivered in low numbers but frequently (almost every week), and the development of embryos was sequential (various stages of egg development in a single oviduct). Exposure to drought resulted in mortality of adults and retained embryos in *P. jacobiana*, while in other species it hindered the production of new offspring. Drought hardiness seems to be higher in *Tauphaedusa* than in *S. jacobiana*. The same decreasing fecundity and high number of developmental abnormalities were recorded by Sulikowska-Drozd and Maltz (2014) for another viviparous clausiliid, *Alinda biplicata*, kept under dry conditions.

The major qualitative difference between *S. jacobiana* and two species of *Tauphaedusa* concerns the structure of the egg envelope while the offspring is still retained in the reproductive tract. In *S. jacobiana*, distinctive calcium crystals are distributed in the gelatinous egg envelope as observed in typically oviparous clausiliids species, as well as during the dissections of viviparous non-Phaedusinae like *Vestia turgida* (Rossmässler, 1836) (see Maltz and Sulikowska-Drozd 2008). In contrast, the egg envelopes in *Tauphaedusa* are translucent and without crystals during the entire embryonic development. The reduction of the egg envelope is probably an adaptation to viviparity. Although the developing embryo in viviparous gastropods is believed to only use egg reserves for nourishment (lecytotrophy), the issue of intrauterine maternal feeding (*e.g.* by uterine secretion without any placenta-like structure) should not be refuted without in-depth histochemical studies. The reduction in egg envelop might be advantageous if such a transmission between parent and embryo develops.

CONCLUSIONS

We observed significant differences in developmental processes among viviparous Phaedusinae species, despite the similarities in many of their life history traits (*e.g.* fecundity, brood size, maturation time, ability to self-fertilize). Additional studies on the life history traits of Phaedusinae are necessary to elucidate the mechanisms leading to the high diversification and evolutionary success of the group in East Asia.

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Authors' contributions: ASD designed the study, conducted laboratory experiments, measurements and snail dissections, performed the statistical analyses and prepared the manuscript. TH collected and identified material from Japan. SPW collected and identified material from Taiwan. BPG collected and identified material from Japan. All authors participated in revising the manuscript.

Competing interests: ASD, TH, SPW and BPG declare that they have no conflict of interest.

Availability of data and materials: The supplementary data sheet is available online/ provided by the corresponding author on request.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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Supplementary Materials

Table S1. Shell size of adult snails of F0 (wild) and F1 (laboratory) generations. (download)

Table S2. Neonate size, time of shell growth, and the age at first reproduction. (download)

Table S3. Fecundity recorded for pairs of snails. (download)

Table S4. Reproduction of virgin snails. (download)

Table S5. Eggs and embryos in snails kept under high humidity conditions. (download)

Table S6. Eggs and embryos in snails exposed to 60 days of drought. (download)